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Basics, Methods and Case Studies

Elgene Owen Box *Editor*

Vegetation Structure and Function at Multiple Spatial, Temporal and Conceptual Scales

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Dedication

Photo 1 Kazue Fujiwara, April 2014

From the ninth to twelfth century, the Fujiwara clan was the most powerful political force in Japan, naming emperors and generally running the government. I learned this history a few days after first meeting Kazue Fujiwara, while we were standing in front of an explanatory historical sign in Nara, site of the early capital (just before Kyōto). Immediately, I turned to her and blurted out something to the effect of "You're royalty!" Even as late as the nineteenth century, the wife of the Emperor Meiji was a Fujiwara descendant, and to this day Fujiwara remains one of the more common and most respected family names in Japan.

As it turns out, the "Fuji" (藤) in Fujiwara (藤原) has nothing to do with Mt. Fuji (富士, = wealthy samurai). Instead, it is the name of an indigenous Japanese plant, *Wisteria floribunda*. The name Fujiwara ("wisteria field") was actually an honorific, bestowed by the emperor Tenji upon Nakatomi-no Katamari (614–669), whose descendants took Fujiwara as the name of their clan. This "fuji," along with its alternate pronunciation "tō" (like English "toe"; only in combinations), still appears in a surprising number of common Japanese family names, such as Fujimori (藤森), Fujita (藤田), Itō (伊藤), and Satō (佐藤).

Kazue Fujiwara (藤原一繪, Photo 1) was born in less auspicious circumstances, in the wartime Tōkyō of 1944, as it was being bombed, both conventionally and with incendiary bombs designed to destroy vast areas of mainly wooden houses. It's hard to imagine a time when Kazue was not strong, but at that time she was not, and so her mother took her to Tōhoku (northeastern Japan), near Sendai, where the Fujiwara family is still numerous. As Japan recovered after the war, Kazue returned to Kantō (the Tōkyō area) to attend primary school in Tōkyō and Chigasaki, and middle school in Chigasaki (Kanagawa Prefecture, down the coast from Yokohama). She graduated from high school in 1963, in Hiratsuka (also in Kanagawa).

In 1963, Kazue also entered Yokohama National University, where she studied general biology and was fond of road rallies. During this time, though, she also met the young [associate] professor Akira Miyawaki and became interested in his ideas of vegetation study, especially since he had relatively few students at the time. After graduating in 1967, she became a graduate researcher under Miyawaki in the Department of Biology (until 1973) and also a high-school biology teacher (1967–1969) in Fujisawa and Yokohama. In 1969, she received a CNRS stipend and studied terril vegetation (and French) with Prof. Reinhold Linder in Lille (April–June 1969). After France, she moved to Germany and joined the famous group of Reinhold Tüxen in Rinteln (July–September 1969), where she studied raised bogs and learned German. Kazue returned to Japan in the autumn of 1969, already the unusually cosmopolitan Japanese woman that we know now.

When she returned to Japan, Kazue applied her knowledge of wetlands to summarize the vegetation of the world-famous Ozegahara wetlands (Miyawaki and Fujiwara 1968a, 1969, 1970; cf. Tüxen et al. 1972). During the 1970s, much of her time was spent describing vegetation in cities, prefectures, and regions, with maps of actual and potential vegetation (e.g., Miyawaki and Fujiwara 1968b; Miyawaki et al. 1971), and writing on the creation of green environments in urban areas, around factory sites, and on reclaimed land (e.g., Fujiwara 1973a,b). In 1973, Kazue obtained the official title Assistant Professor (助手) at Yokohama National University, where she continued working while also finishing her Doctor of Science degree (from Tōhoku University in Sendai, in February 1978). She made an urban-ecology city tour of the Soviet Union and Europe (1977) and continued to write on the natural vegetation of Japan (e.g., Fujiwara 1979). She was also married during this time, to a taxonomist (who took the family name Fujiwara); built a house in Chigasaki; and had two daughters, Yōko (1975) and Maki (1980).

In the 1980s, Kazue was able to start publishing more independently. One of her most important publications came from this period, a detailed classification and analysis of the evergreen broad-leaved forests of Japan (Fujiwara 1981–1986). Her paper with Miyawaki on the evergreen and secondary forests of the Bōsō Peninsula, east of Tōkyō, helped demonstrate that evergreen broad-leaved forest is actually the potential natural vegetation of a large part of Japan, even where covered now by secondary deciduous forests (Miyawaki and Fujiwara 1983). In 1987, she wrote her paper on "Aims and Methods of Phytosociology," which to this day is still probably the best brief but sufficient explanation in English of how to do phytosociology (Fujiwara 1987a). Japanese and Chinese versions followed (Fujiwara 1997; Fujiwara and You 1999).

Also during the 1980s, Kazue continued her work on the vegetation of Japan (e.g., Fujiwara 1985); its mapping (Miyawaki et al. 1983b; Miyawaki and Fujiwara 1988); and on revegetation projects (e.g., Miyawaki et al. 1983a). The largest project during the 1980s, though, was the exhaustive description and analysis of the "Vegetation of Japan" (10 volumes, Miyawaki 1980–1989), for which Kazue was a major field researcher and author of text, tables, and maps. She was also a main field researcher and co-author for a four-year project on the mangroves of Thailand (Miyawaki et al. 1985; Fujiwara 1987b). In 1985, she began lecturing officially, as a part-time Lecturer at Hōsei University in Tōkyō. Finally in 1986, she obtained the position of Associate Professor (助教授 — *jokyōju*) at Yokohama National University, in the Department of Vegetation Science of the only recently established (1978) Institute of Environmental Science and Technology.

Kazue's first trip to China was in autumn 1985, and this began a long interest in Chinese evergreen broad-leaved forests (cf. Box et al. 1989, 1991a,b; 1998) and Chinese vegetation in general (see below). In 1986, she visited the warm-temperate region of the southeastern USA for the first time, began studying its forests (e.g., Box and Fujiwara 1988), and subsequently became a most knowledgeable and valuable member of the three-year Eastern North American Vegetation Survey (1988–1990), funded by Japan and summarized by Miyawaki et al. (1994). In addition to planning and fieldwork, she also played a major role in plant identification and vegetation analysis, and wrote chapters describing the evergreen broad-leaved forests and mangroves of the southeastern USA, in comparison with East Asia (Fujiwara and Box 1994a,b).

In 1993, on the mandatory retirement of Prof. Miyawaki at age 65, Kazue was able to obtain his position as Professor (教授) of the Department of Vegetation Science. From this time on she quickly accumulated many graduate students, from overseas as well as from Japan. Among other things, this led to more wide-ranging fieldwork with the students. This involved study of forests and their rehabilitation in Japan (e.g., Fujiwara et al. 1993) but also in Malaysia (Alias et al. 1995, Fujiwara et al. 1995, Alias and Fujiwara 1998, Hamzah and Fujiwara 2000); Thailand (Kawla-ierd et al. 1995; Tejajati et al. 1999); Myanmar (Aung et al. 2004); and in other parts of tropical Asia (cf. Fujiwara 1993); as well as in Bhutan, Nepal, and China. One result was an encyclopedia piece on "Ecosystems of Asia" (Box and Fujiwara 2001). Work with students also took Kazue to other continents, for fieldwork and vegetation analyses in Brazil (Euler et al. 2005) and Senegal (Abdulaye and Fujiwara 2007). She also continued comparative work in eastern North America (e.g., Fujiwara and Box 1999) and was a Fulbright Fellow at the University of Georgia in 1999.

An increase in the number of Chinese graduate students around 2000 led to more fieldwork in China, as well as [Chinese] Mongolia and Manchuria. This led to first vegetation descriptions and syntheses on *Fagus* forests of China (Wang and

Fujiwara 2003; Wang et al. 2005, 2006b); the widespread *Quercus mongolica* forests of northern China (You et al. 2001); and on north-Chinese deciduous forests in general (Wang et al. 2006a). A major new project on "Integrated Vegetation Mapping in Asia" brought the opportunity for even wider-ranging field study in East Asia, including the Russian Far East (Primorye, Sakhalin, Kamchatka), central and northern Siberia (Yakutia), and dry areas of Central Asia (Dzungaria and the Tarim Basin). This work resulted in a major synthesis of East Asian vegetation (Fujiwara 2008) as well as syntheses on cool-temperate deciduous forests (Tang et al. 2008, 2009; Zhi-Rong et al. 2010) and on warm-temperate forests (e.g., You et al. 2008) (see Fig. 1).

When forced in 2010 to retire from the national university at age 65 (*teinen* system), Kazue moved to Yokohama City University. There she continues her vegetation study and revegetation work in China (e.g., Li et al. 2013; cf. Fujiwara et al. 2000) and other countries, including Nepal (since 2010), Turkey, and most recently Indonesia. She first visited Kenya in 1990 in connection with world mapping (project of Shunji Murai, Tokyo University) and has studied its forests, for revegetation work, since 2006 (e.g., Hayashi et al. 2006; Furukawa et al. 2011a,b). Using her extensive experience with Asian coastal vegetation (e.g., Hayasaka and Fujiwara 2005, 2007; Fujiwara et al. 2010), Kazue and her students were also quick to study effects on coastline vegetation by the great tsunami events in the Indian Ocean in December 2004 (Hayasaka et al. 2009) and in northeastern Japan in 2011 (Fujiwara et al. 2012).

One of Kazue's particular talents was to identify topics of general interest and to organize appropriate special sessions at major national, regional, and international meetings. At the INTECOL symposium in 1990 in Yokohama, she organized a special session on evergreen broad-leaved forests and coordinated three other symposia, combining their proceedings into a book on "Forest Ecosystems of East and Southeast Asia" (Box et al. 1995). For the INTECOL meeting in 1998 (Firenze), she organized a special session on "Climate Change and Vegetation Shift," focusing on early evidence of vegetation responses to warming. For the International Botanical Congress in 1999 (St. Louis), she organized a session on "Vegetation of Analogous Environments of the Northern versus Southern Hemisphere." In 2002, for the INTECOL meeting in Seoul, she organized a first session on "Ecology in Beech and Oak Forests," following it up 10 years later with "*Quercus* versus *Fagus* in Asian and other Temperate Deciduous Forests," for the annual IAVS meeting, also in Korea (Mokpo). Tatsuō Kira (1949) had recognized that deciduous forests could constitute stable, zonal forests in the warm-temperate zone under certain conditions, and in 2010 Kazue organized a special session on this topic for the annual IAVS symposium, in Lyon. This resulted in a book on "Warm-Temperate Deciduous Forests around the Northern Hemisphere" (Box and Fujiwara 2014a), which included Kazue's syntheses of East Asian warm-temperate deciduous forests (Fujiwara and Harada 2014; Tang et al. 2014) and comparison with counterparts in eastern North America and southern Europe.

In addition to topical sessions, Kazue has also served on the organizing committees for the 1984 IAVS meeting, the 1990 INTECOL symposium, and the 1993

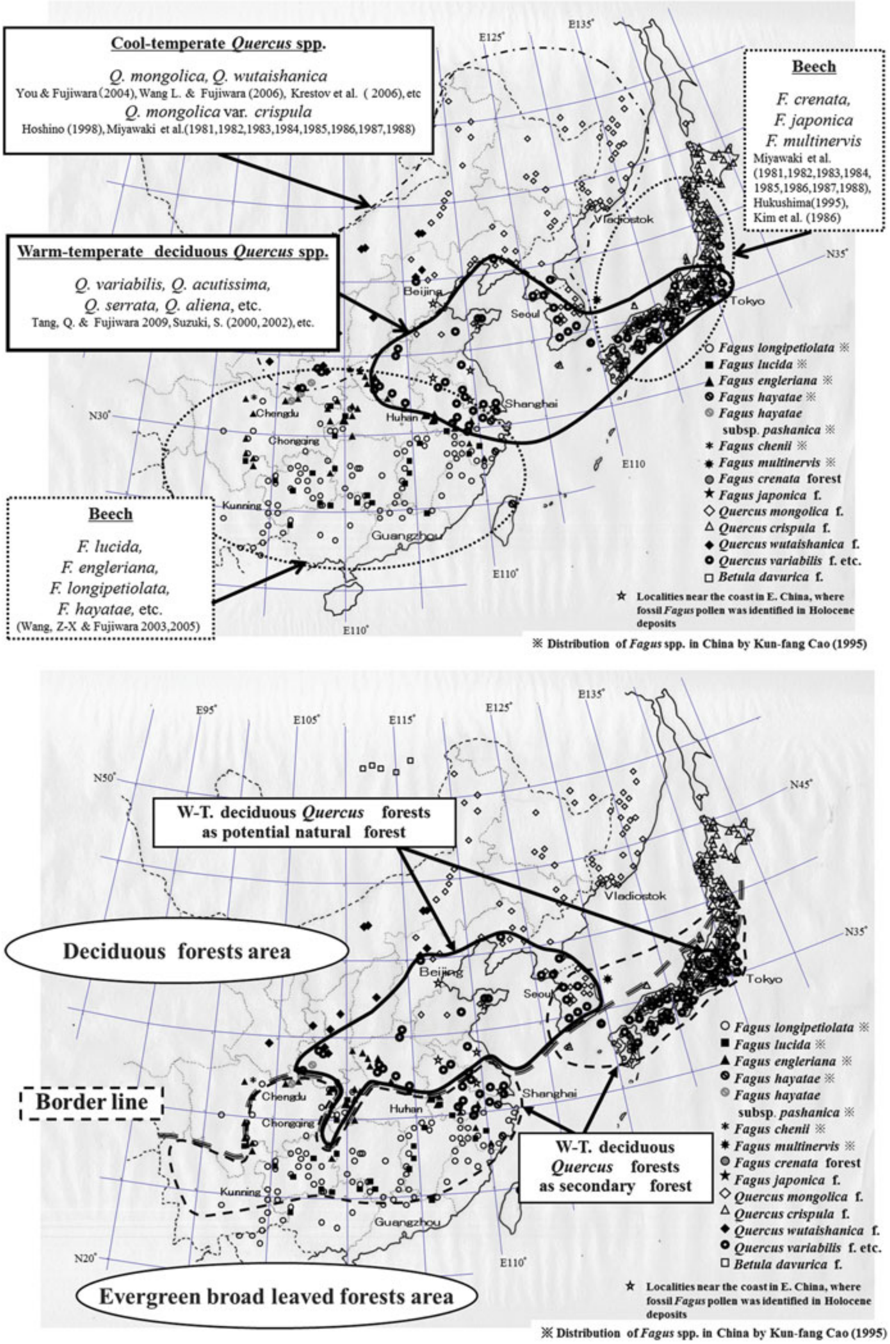

Fig. 1 Areas of cool-temperate and warm-temperate deciduous broad-leaved forests in East Asia (from Fujiwara and Harada 2014)

Botanical Congress, all held in Japan. In 2000, she was the overall organizer of the IAVS symposium in Nagano and its excursions throughout Japan. She was an IAVS Vice-President from 2000 through 2007, still serves on the IAVS Advisory Council (since 1994), and is a familiar figure at IAVS annual meetings (Photo 2), missing only one meeting since 1991. She also served as an INTECOL board member (2001–2008), has long been a major contributor to the Japanese Ecological Society, and has organized special sessions for them and for meetings of the East Asian Society for Ecology.

Photo 2 Kazue Fujiwara, at an IAVS meeting in the 1990s

Kazue Fujiwara is perhaps best known as one of the world's foremost phytosociologists, adhering closely to classical standards and procedures but also able to use phytosociology in all kinds of environments worldwide and to apply it to vegetation analysis and rehabilitation efforts. She is also known for her extensive knowledge of the vegetation of the whole world, having studied vegetation in the field in about 50 countries or comparable regions (e.g., Baja California, see Photo 3), on all continents except Antarctica. In this regard, she has been a valuable author of cross-continental and global-scale comparisons and syntheses (e.g., Box and Fujiwara 2005, 2012, 2013, 2014a, 2014b).

Photo 3 Kazue Fujiwara, during the IAVS excursion in Baja California, Mexico, 2010 (photo by Andy Greller)

Some of Kazue's publications include me as [alphabetic] first author because they were written in English. I can assure you that she provided as much input to those pieces as I did, sometimes more. She has certainly been a valuable co-author, critic, and colleague. I would like to take this opportunity to thank Kazue, publicly and most profoundly, for all I have learned from working with her — in the field, in data analysis, in writing (especially generalization), and in scientific life in general.

We the authors all hope that this book will be a fitting honor to Kazue, and we join her other admirers in wishing her many more active and rewarding years.

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Introduction: Scales and Methods

This book of invited papers is both a commemorative volume (*Festschrift*) honoring Prof. Kazue Fujiwara and a potential textbook for graduate-level courses or seminars in vegetation study. Heinrich Walter, who probably knew world vegetation better than any of his contemporaries, sometimes showed a certain disdain for what he called "*Schreibtisch-Ökologie*" (desk ecology), saying also: "*Weiß man nichts, so schreibt man über Methode*" (When one does not know anything, he writes about methodology). But methodology has an important place in science, since it responds to particular scientific questions and often raises others. Kazue Fujiwara herself was one of the world's foremost phytosociologists, among other things, and wrote one of the best explanations of that methodology (Fujiwara 1987). Appropriately, therefore, this book presents a wide variety of methodological approaches in vegetation science.

The sections and chapters in this book also represent a full range of objectives, scales, regions, and vegetation types. Book sections are organized from global to local scale. Objectives range from more or less global perspectives involving zonation and plant functional types, to regional and local vegetation description and analysis, to revegetation, woodlot management, and other aspects of conservation. Regions and vegetation types range from tropical and temperate forests to continental steppes and Mediterranean-type scrub to fine-scale turf, sedge, and moss communities (or synusiae) embedded in wider landscapes. Southern Hemisphere perspectives are also included.

As Dieter Mueller-Dombois points out in his chapter, study of vegetation dynamics requires study at various temporal as well as spatial scales, often simultaneously. Temporal scales may range from seasonal to annual to longer term, as over the course of succession or other stand development. And even regional and global studies require understanding of processes at landscape, stand-level, and finer spatial scales. Methodology and scale are thus often closely interrelated, and the studies in this book illustrate this interdependence.

Some basic methodologies and other organizing concepts in vegetation science are listed in Table 1. The relevance or validity of some of these items is currently

Table 1 Methodologies of vegetation study

Classification	Clustering	Envelope modeling
Gradient analysis	Ordination	Phytosociology
Plant functional types	Potential natural vegetation	Zonation
Allometry	Description	Generalization
GIS analysis	Inventory	Mapping
Measurement	Modeling	Sampling
Satellite monitoring	Scaling	Validation
Adaptation analysis	Bioclimatic analysis	Dynamics analysis
Ecological analysis	Environmental analysis	Integrity analysis
Regional synthesis	Synusial analysis	Topographic analysis
Transition analysis		
Autecology	Comparative ecology	Cultural ecology
Ethnobotany	Geobotany	Physiological ecology
Sustainability science		
Biodiversity management	Conservation biology	Conservation strategy
Ecosystem services	Invasion biology/ecology	Plantation management
Production ecology	Reforestation	Rehabilitation
Restoration	Revegetation	

Listed here are major methodologies of vegetation study and of ecology and other organismal biology in general. The groupings represent: (1) widely used methodologies and some currently debated "hot topics"; (2) more general tools and other aspects of research; (3) other analytical methods of inquiry, involving established objectives (usually with the word "analysis"); (4) related fields of study; and (5) applied activities in conservation, land management, and ecosystem restoration or rehabilitation, which require their own as well as more basic methodologies. Some are relevant only at a particular spatial or other scale, but all are listed here, as a checklist. Most are described briefly in this Introduction, in boldface type, with literature references where possible

debated, including phytosociology (cf. Carrión and Fernández 2009; Ewald 2003), the concept of potential natural vegetation (cf. Chiarucci et al. 2010), and (climatic) envelope modeling. Also included are more "accepted" methods such as ordination and gradient analysis. As Ewald (2003) has pointed out, classification (as by phytosociology) and ordination are both clustering methodologies that may have much in common, including a common numerical basis in statistics (see also Kent and Coker 1992; Legendre and Legendre 1998). Finally, also listed in Table 1 are more general aspects of vegetation research such as basic description, sampling, measurement, and mapping; some more targeted analytical perspectives, such as bioclimatic, environmental, and ecological analysis; related perspectives and fields of study, such as ethnobotany and cultural ecology; and applied activities such as biodiversity management, revegetation efforts, and other aspects of conservation. Most of these methods are treated somewhere in this book and are identified briefly (in boldface type) in the relevant sections of this Introduction.

This book and Introduction are organized from global to local scale, followed by sections on conceptual methodologies, applications, and perspectives for the future. We hope that this book will be useful to both students and practitioners, for its reviews and examples, and as a potential reference. We also hope it will be a fitting tribute to Kazue Fujiwara, who has always been comfortable thinking and working at local to global scale and over different temporal scales, from present day to the 30 years or more involved in succession and most revegetation projects.

Global Scale

At global and other broad scales, one of the most basic methodologies is the inductive process called **generalization**. This involves inference of broad relationships, including broad geographic patterns, based on recognition of patterns and relationships seen at finer scales. The product of good generalization should be a "complete" general conceptual system. Both chapters in this global section present such systems.

Generalization is perhaps best illustrated at global scale and may also involve **modeling**, which puts general ideas to the test. Models may be conceptual or quantitative. At broad scales, quantitative models are usually driven by climatic data or satellite imagery — but rarely by both, although such integration could be very useful, and I suggested it to NASA very early. The question of rigorous model **validation** was first treated by Caswell (1976) and was considered subsequently by Rastetter (1996) and Rykiel (1996) at global scale, and more locally by Box et al. (1993) and Araújo et al. (2005), among others. Whether conceptual or quantitative, though, broad-scale models and other generalizations are inherently *geographic* in nature, since the world has a great variety of different conditions in different, often disjunct geographic regions. So geographic models and other generalizations should also be *validated geographically* (Box and Meentemeyer 1991), i.e., in a stratified manner that tests under the different environmental conditions that obtain in all relevant regions, such as the world's different biomes.

The first chapter, on "World Bioclimatic Zonation" (Box), treats this need by providing a more complete global bioclimatic **zonation** system, based on the "genetic" principles implied by global atmospheric circulation patterns. Bioclimatic zonation and its relationship to global atmospheric circulation were well recognized more than 100 years ago, and some systems were presented that are still in use, including the quasi-zonal Köppen (1931) climates used for most atlas and wall maps. This chapter is both a review of the development of zonation concepts and an attempt to patch some of the remaining flaws. First comes a somewhat detailed history of the development of genetic (i.e., mechanism-based) classification systems. The most widely used genetic system of world climate types, namely that of Walter (1977), is then expanded to resolve its one major flaw, to cover subtypes and transitions more explicitly, and to provide a still relatively simple global (terrestrial) system that corresponds well with biomes and broad-scale vegetation types (cf. Walter 1954; Box 1995; Box and Fujiwara 2013). Genetic systems have advantages especially under changing climatic conditions, since they are tied more directly to mechanisms and do not rely on empirically based boundaries, as in the Köppen system. It may also be possible to quantify such systems, focusing not only on physiological limits but also on required durations of warm-wet conditions, as suggested already by Lauer and Rafiqpoor (2002).

The other global-scale chapter expands the concept of **plant functional types** (PFTs), which were an outgrowth of the "life forms" of Drude (1896) and other early, mainly German-educated ecologists (e.g. Warming 1895; D'Arcy Thompson 1917; cf. Barkman 1988; Fekete and Lacza 1970, 1971; Szuko-Lacza and Fekete 1969, 1972). Basic ecological plant types were first used in modeling in a world **climatic envelope** model involving 90 types (Box 1981; the term "climatic envelope" was probably first used in this context by Dobson 1978). The present-day term "plant functional type" was anticipated, in the same year, by the "plant functional attributes" of Gillison (1981). The PFT concept is now not only used in vegetation analysis and modeling (cf. Foley 1995; Cramer 1997; Peng 2000) but has been proclaimed the veritable "holy grail" (!) for unifying ideas of plant–environment relationships (Lavorel and Garnier 2002). Concepts of PFTs, however, have always differed (cf. Box 1996; Smith et al. 1997; Wullschleger et al. 2014).

The chapter by Gillison herein, on "Vegetation Functional Types and Traits at Multiple Scales," presents a complete system for describing both plants and vegetation in terms of functional attributes that are also related to plant morphology. This system has been applied in many parts of the world, yielding a large database for use in inferring broad plant–environment relationships (Gillison 2013). This chapter also includes good summaries of several other widely discussed, potentially global systems for relating plant structure and environmental conditions, including the CSR strategies of Grime (1979), the Leaf-Height-Seed (LHS) strategies of Westoby (1998), the Leaf-Economics Spectrum of Wright et al. (2004), and the Gillison (2002, 2013) system of Leaf-Life Form-Root (LLR) strategies. According to Gillison, "a key question concerns whether the relatively new trait-based ecology is better placed than traditional methods to cast light on how functional characteristics interact across varying environmental scales and whether functional types and traits can be exploited to improve our understanding of ecosystem dynamics." This chapter reviews the more traditional scale-related aspects of vegetation classification and then compares these with recent advances involving plant functional types and traits, especially those involving holistic plant strategies.

Regional Scale

This section presents a wide variety of studies, objectives, and methodologies, including basic analytical description, environmental and ecological analysis, regional synthesis, comparative ecology, and mapping. Some studies analyze the vegetation of a region, while others look at the ecology of certain vegetation types over a region. For these chapters we start in East Asia, with evergreen broad-leaved forests, continue with tropical evergreen forests and mountains, and then proceed to largely drier situations in higher latitudes, from inner-Asian steppes and scrub to the vegetation of Mediterranean-type climates in Europe and California.

Environmental analysis involves relating vegetation and plant taxa to the environmental conditions where they occur. One should look at all relevant environmental factors, but two main approaches are represented herein: climatic and topographic.

Bioclimatic analysis relates vegetation and its component taxa, especially the main structural elements, to climatic conditions. This involves not only identification of limiting factors but also estimating the quantitative values of variables that can be used to express these factors. Factors may be "negative" in the sense of hard limits, such as limiting cold temperatures, or "positive" in the sense of plant or vegetation requirements, such as length of a warm-wet growing season.

The first chapter is on "Evergreen Broad-Leaved Forests of East Asia," by Song Yong-Chang[1] and Da Liang-Jun (East China Normal University, Shanghai), and actually represents a **comparative ecology** (cf. Cole et al. 1991) and zonation of this general forest type around the Northern Hemisphere. Prof. Song has written extensively over his long career on evergreen broad-leaved forests, both in Asia and in comparison with other Northern Hemisphere regions, based on his long association with colleagues in Europe (including Tüxen) and in the International Association for Vegetation Science. Song's results are synthesized in a recent, exhaustive two-volume treatment of the *Evergreen Broad-Leaved Forests of China* (Song 2014, in Chinese). The present chapter serves as a summary of these Chinese types of evergreen broad-leaved forest (all called "subtropical" herein) and similar forests in other parts of East Asia, in small areas of eastern North America, and in the Mediterranean region, where the evergreen broad-leaved forests and woods are mainly sclerophyllous but where some laurophyllous taxa also occur. This chapter also serves as an introduction to the Chinese system for naming vegetation types based on two dominant taxa (cf. Wu 1980/1995).

The second chapter, by Song Kun and Da Liang-Jun, involves what might be called **transition analysis** (or ecotone analysis) as applied to the "Evergreen-Deciduous Broad-Leaved Forest Ecotone in Eastern China." Part of this region was identified already by Eyre (1968) as a region of mixed evergreen-deciduous broad-leaved forest, a combination which usually is not stable. (The more shade-tolerant evergreen trees usually win.) This region has long been of interest because there are few places in the world where such a transition could occur over a large area and because even the quasi-natural vegetation of this region was destroyed many centuries ago. The location of the ecotone is estimated by Song and Da by relationships to temperature but also to topographic factors, as done in the "Vegetation of China" (Wu 1980/1995) and by some other authors (e.g., Fang et al. 2002), whose ideas are summarized herein. The ranges of the main evergreen broad-leaved trees are considered to determine the boundary of the ecotone, providing a model for defining ecotones in general. Forests in this transitional

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[1] Note that family names (usually one syllable) come first in Chinese, followed by given names that may be one or more commonly two syllables.

region have also been described phytosociologically and interpreted bioclimatically by Fujiwara and Harada (2014) and by Tang et al. (2008, 2014).

A third chapter from China involves the “Ecology of Relict Tertiary Deciduous Trees in Subtropical China,” by Shang Kan-Kan, Song Kun, and Da Liang-Jun. China is well known for its rich diversity of Tertiary relict conifers, due to the general lack of Pleistocene glaciation but also to the fact that southern China represents the world’s largest upland region in a humid warm-temperate/subtropical climate. Relict deciduous trees are less well known, except perhaps for *Ginkgo biloba* and the deciduous conifer *Metasequoia glyptostroboides*. Southeastern China and the adjacent Himalayan region represented an important Pleistocene refugium for the Tertiary relict flora, but the region is covered now (where natural vegetation exists) by evergreen broad-leaved forests. This chapter uses both bioclimatic analysis and **topographic analysis** to explain the survival and ecology of relict deciduous trees, many with isolated, disjunct distributions in this mountainous area. Resulting forests of these relict deciduous trees are called “topographic climax” forests, often reproducing vegetatively and forming mosaics (on particular landforms) within the zonal vegetation. Most species are clearly pioneer species and function as “gap-repairing” species.

Classification involves creating groupings for entities that are similar and separating them from entities that are different. This is also an inductive procedure, and was done first somewhat intuitively and empirically, based on the most obvious similarities, such as physiognomy and climatic affinities. Phytosociology provided a standardized methodology for classification of plant communities by floristic composition, based on large numbers of full-floristic vegetation samples. This approach was expanded with the advent of computers and statistical algorithms, one of the first of which was actually based on the famous “traveling salesman” algorithm (Lieth and Moore 1971). Statistical ordination provided a completely automated means of classification by clustering, based on algorithms such as that of Bray and Curtis (1957; cf. Whittaker 1974). The word “ordination” came from Goodall (1954) but was suggested originally by the *Ordnung* of plant lists by Ramensky (1930).

We see classification procedures of various kinds throughout this book, beginning with a “Classification of Lower-Montane Evergreen Forests in Southern India and Sri Lanka,” by Andrew Greller and colleagues. Among other things, this study provides basic quantitative **description** of the composition of taxon-rich humid tropical forests from three mountain areas in Sri Lanka and several ranges in the Western Ghats of Kerala (windward southwestern India) and adjacent (leeward) Tamil Nadu. These forests are dominated by members of typical tropical-rainforest families (e.g., Myrtaceae, Sapindaceae, Anacardiaceae), as well as by Dipterocarpaceae, but cultivation of cardamom has led to massive disturbance of such forests, which are unusually rich in endemics. The forests were sampled by belt transects, and dominant tree taxa were identified. The forests were then classified into 12 distinct types by **cluster analysis** using dendrograms based on the Bray–Curtis algorithm. This classification demonstrates a clear compositional distinction between lowland and nearby lower montane forests. Results are compared with classifications of other tropical mountain forests, including proposed elevational trends in leaf morphology and other tree and forest attributes. There is also a brief comparison with forests from the Southern Hemisphere.

Another, but much less diverse situation of humid tropical forests is that of oceanic islands such as Hawaii, where Dieter Mueller-Dombois and James D. Jacobi report on the "Dynamics of the Hawaiian Rainforest at Multiple Scales." This chapter is a truly multi-scale study and begins with a clear model statement of **dynamics analysis** and of the spatial and temporal scales that it requires. This chapter also summarizes a recently published book that resulted from five decades of multi-scale study on native Hawaiian rainforests (Mueller-Dombois et al. 2013). Unlike most rainforests, less-diverse island rainforests do generally have clear dominant taxa. In the Hawaiian Islands, the dominant is a single species, *Metrosideros polymorpha*, well known for its cohort dieback phenomena described by Mueller-Dombois (1980, 1985, 1987). Dynamics in these mono-dominant forest stands includes establishment, development, turnover by auto-succession, bog formation, and fragmentation, which occur over different temporal scales but must also be studied at different spatial scales, from small plots to whole stands. "Forest decline" usually involves some outside factor such as disease and is not the same as cohort senescence, which is a natural process of simpler forest stands and may include various aspects, such as premature senescence. This chapter demonstrates how different perspectives through scale changes were needed for synthesizing the subject matter into a coherent story.

The remaining chapters in this regional section involve vegetation of climates that have some aspect of significant dryness. The first study is an analytical **description** of "Steppes and Shrub Thickets in Onon Dahuria," by Irina Safronova and Ekaterina Golovina of the Komarov Botanical Institute in St. Petersburg. Outside Russia, Dahuria is not well known and appears as a regional name only rarely in atlases and dictionaries. On the other hand, Dahuria has provided many botanical names, such as *Betula dahurica*, *Larix dahurica*, *Rhododendron dahuricum*, and *Rosa davurica*. This somewhat mountainous steppe region is in southern Siberia, just north of Mongolia. It has an extremely continental climate, with deeply frozen soils. The so-called "expositional" forest-steppe vegetation is influenced strongly by elevation and topographic position, especially north versus south-facing slopes. There is no statistical analysis but rather a detailed **inventory** of species and community types, including basic description of stand composition and dimensions, and of dominant and other main species. Species richness is moderate, and these are true steppes, i.e., there is usually some bare space not covered completely by the vegetation (projective cover of 50–80 %). The main community types are described as grass steppes, forb and forb-grass steppes, and shrub steppes, with localized areas of shrub thickets. Forbs play a large role in these steppes, as can be seen in the many photos.

Mapping is another central activity in vegetation study, and vegetation mapping has a long history rich in different approaches and techniques, as illustrated, for example, by Faliński (1991), Pedrotti (2004/2013), Bohn and Neuhäusl (2003), and Küchler and Zonneveld (1988). The next chapter herein, by Carlo Blasi, summarizes "The Vegetation Series of Italy and Applications in Biodiversity Conservation," describing various mapping methods. Blasi describes the aim of this Italian program as a "complete overview of the basic naturalistic knowledge in Italy" bearing in mind that the primary objective was conservation. One result of this project was a map of the Vegetation Series of Italy (Blasi et al. 2004), accompanied by a monograph for each region. Another result was definition and mapping of environmental heterogeneity, by integrating phytosociology (and synphytosociology) with ecological land classification. The project produced an extraordinary wealth of data that can be used for updating knowledge of floristic and vegetation biodiversity, for land planning and biodiversity assessment and monitoring. These data also permit defining and evaluating connectivity and assessing the structural and functional topology of ecological networks, particularly the land network.

The last two chapters in this section focus specifically on the vegetation of regions with a Mediterranean-type climate, in its two occurrences in the northern Hemisphere. Many adaptations have been attributed to this climatic situation, one of which is marcescence, i.e., the holding of brown leaves on their branches through the winter. This has been interpreted as a vestige of evergreenness but occurs also in various situations transitional from deciduous to potentially evergreen forest. It occurs mainly in Fagaceae, especially oaks (*Quercus* spp.), including several oak species in southern Europe, where marcescence appears to be confined mainly to the submediterranean transition and to species such as the widespread *Quercus pubescens* (Abadía et al. 1996; Garcia et al. 2014). The chapter by Beatríz Vilches de la Serna and colleagues, on "Marcescent *Quercus pyrenaica* Forest on the Iberian Peninsula," is a kind of **adaptation analysis** that looks at the autecology of another, endemic marcescent species, which is seen as an indicator of the southern limit of Euro-Siberian broad-leaved forests. This chapter is also a good study in the history of plant names and problems of taxonomic nomenclature, including a herbarium-label error that led to the original name. (*Q. pyrenaica* is almost completely absent from the Pyrenees). Another feature of this chapter is the treatment of plant occurrence in *dehesa*, i.e. the *bocage* (hedgerow) system of open grassland within wooded margins, as occurs in other parts of Western Europe.

The second chapter on Mediterranean vegetation concerns the "Mediterranean Ultramafic Chaparrals of California," by Daniel Sánchez-Mata and María Pilar Rodríguez-Rojo. The term "mafic" refers to silicate minerals that also contain magnesium and iron (but less silicon), as are derived from the less viscous mafic magma and lava that may extrude over larger areas without forming volcanic cones. Ultramafic rocks are found worldwide but especially in some areas, where their chemical composition results in serpentine soils that give rise to distinctive vegetation (see many photos) and numerous local endemics. This study in California involved locating stands of serpentine vegetation and describing the vegetation composition and dynamics, including seral stages. Sampling was by phytosociological relevés, with analysis by several clustering procedures, including de-trended correspondence analysis and canonical correlation analysis (with "beta-flexible linkage" and Sorensen distance). Clustering analysis resulted in recognition of five species groups, four of which were given new syntaxonomic names at the association level. Understanding the plants and vegetation of serpentine soils must also include study of their **physiological ecology**, including how they are able to function despite accumulations of heavy metals. This ability makes some such species useful in revegetation efforts, especially on previously mined landscapes.

Landscape Scale

Vegetation study at local (landscape) scale usually involves detailed vegetation sampling and description, sometimes along environmental gradients, classification of communities, and sometimes more complete inventory of all types and taxa in an area. The data collected are often analyzed by statistical **ordination** (see Kent and Coker 1992; Whittaker 1974) or by **phytosociology** (see Conceptual Methodologies section), both of which involve some kind of clustering procedure. Ordination and gradient analysis are well accepted methods of what has been called "exploratory data analysis" (Tukey 1977; Chatfield 1986; Sibley 1987), as opposed to "confirmatory data analysis," i.e. hypothesis testing based on statistical probabilities (see Kent and Coker 1992). True analysis of vegetation, however, requires insight into environmental limitations and causal mechanisms, not just statistics.

The first chapter in this section represents just such an **ecological analysis**, in which Ulrich Deil treats "Amphibious Vegetation in the Afro-Alpine Belt and the Role of Cryoturbation in Creating Regeneration Niches." This is a regional study but involves analysis of vegetation in very small areas of annual turfs embedded in tussock grasslands, which occur on several of the high volcanoes of East Africa (3500–4500 m). The stands are compared, by means of a constancy table (168 relevés), with similar situations from the Ethiopian Highlands, the Drakensberg of southern Africa, and Marion Island (South Africa). The ecology of the short-living herbs is described in terms of regeneration and establishment in open patches created (in the perennial turf) by cryo- and bioturbation and by needle ice and frost-heaving. On such a dynamic but cold substrate, geocarpy becomes an important adaptation. The plants colonize the shores of oligotrophic lakes with fluctuating water levels and germinate under water (tenagophytes). There are even some similar floristic and ecological characteristics with boreal and subarctic littoral vegetation and with *Crassula* communities in the oro-tropical Andes.

The next chapter is also a kind of regional analysis that studies a particular vegetation type and its dynamics at landscape scale. This study, by Dan Gafta and Sorana Muncaciu, treats the case of "Large Habitat Range but Low Floristic Variation" in *Festuco rubrae-Agrostietum capillaris* grasslands of Romania. It represents a good example of the use of Bray–Curtis **ordination** and a "fuzzy C-median algorithm" to classify 414 grassland stands and infer the main ecological factors underlying the observed floristic variation. Clusters were evaluated in terms of species fidelity and plant functional groups identified, including grazing-tolerant versus truly ruderal species and species of acidic versus basic substrates. The facies found differ from five subassociations identified shortly before by phytosociological classification; they were also “fuzzier.” The fuzzy clustering is less useful for identifying “types” but does yield insight into successional pathways under different environmental conditions and grassland use modes. As in most such cases, the low floristic variation is explained by the fact that the dominant species are mainly generalists. Some perhaps less well-known literature from Eastern Europe is also introduced.

The next three chapters are also from Europe, are shorter, and involve non-woody vegetation occurring only locally. Franco Pedrotti describes “The *Caricetum distichae* Association in Italy,” which occurs at seven sites in the Trentino-Alto Adige region of northeastern Italy, plus two other sites. All sites are in the montane belt except for one in foothills in Lazio. *Carex disticha* is a very rare species and is on the red list of plants of Italy, for both the national and regional level. Fine-scale study of species **autecology** is necessary for conservation of such endangered species, and this chapter approaches this goal through phytosociology.

Another fine-scale study for conservation purposes, by Kevin Cianfaglione and Franco Pedrotti, describes “The Vegetation of the Pie Vettore Debris” in the Sibillini Mountains of central Italy. The “debris” is calcareous detritus, and the study reports on the dynamics of its generally shrubby vegetation cover. This vegetation is considered to be primary, as in other detritus locations, in particular in the Alps. Some common botanical and ecological characteristics can be identified.

The last two chapters in this section treat lower plants. Fine-scale analysis of bryophyte, lichen, and fungus synusiae within vascular plant communities, for example, has proven useful for inferring patterns in community organization and species interactions, for revealing good ecological indicators, and for suggesting science-based conservation measures.

Still in Italy and at fine scale, Michele Aleffi and Franco Pedrotti provide a **topographic analysis** of “Microtopography-Induced Differentiation of Moss Synusiae in Wet Grasslands covering a Karst Plain”. Bryophyte assemblages are somewhat dependent on surrounding vascular communities, but this varies with the substrate, i.e. rock or soil. Epilithic bryophytes may form distinct, independent communities, but epigeic bryophytes intermix more frequently with vascular plants, and their assemblages are generally considered to be dependent structural parts (e.g., synusiae) of a concrete vegetation unit (phytocoenosis). The differentiation of synusiae is based on at least four important features: specific microhabitat, characteristic species composition, spatial extent limited to one stratum, and similarity of means for exploiting the environment by all component species. Bryophyte assemblages have been classified syntaxonomically, but the resulting syntaxa (representing synusiae) do not correspond conceptually to plant associations *sensu* Braun-Blanquet. Although less frequent in recent literature, the **synusial approach** to analysis of cryptogam vegetation is still quite useful. This chapter examines the moss synusiae growing on the soil of a karst plain covered by hygrophilous and meso-hygrophilous grasslands that are conditioned strictly by the micromorphology and water content of the substrate. Particular questions concern floristic differentiation due to different karst habitats, identification of the best species for discriminating between different microtopographies, and identification of the main ecological gradients accounting for the floristic differentiation.

The following chapter by Gillian Rapson (New Zealand) involves the **sampling** process itself and asks "At What Scale and in What Vegetation Types Should We Sample Non-Vascular Plants?" The fact that many field scientists are not able to identify and sample lower plants often makes this a moot question; it is not trivial, though, because lower plants often reveal patterns and relationships that do not appear in higher plants. But sampling lower plants is also problematic: the samples sent to specialists for identification often come back as total surprises, i.e. as taxa not identified at all by the field researchers among their other samples. The most important groups of lower plants are probably the bryophytes and lichens, especially at higher latitudes. The methodology of identification or sampling is, strictly speaking, not what is considered here. The questions of where and in what kinds of vegetation to sample lower plants, however, are very much methodological questions. Given the "patchy" occurrence of many lower plants, especially bryophytes, sampling strategy (design) may affect vegetation interpretation significantly.

Conceptual Methodologies

This section considers questions involving two of the most commonly used basic methodologies of vegetation study, namely phytosociology (cf Fujiwara 1987, Dierschke 1994; Westhoff and van der Maarel 1974) and gradient analysis (cf ter Braak and Prentice 1988, Whittaker 1967). One of the best books on ecology in the 1980s was the short book by Rob Peters (1991) entitled *A Critique for Ecology*, which provided insightful criticisms of the ecology of that time but is perhaps even more relevant today. As opposed to theories and paradigms, methodologies may seem less vulnerable to criticism and overthrow. Two notable exceptions are perhaps [climatic] envelope modeling (not treated further herein but see, for example, Kadmon et al. 2002; Pearson and Dawson 2003; Hijmans and Graham 2006) and phytosociology, which has been criticized continuously over the years, for its "deterministic" view of communities (e.g. Gleason 1939), its sampling procedures (e.g. Godfryd and Hansell 1985; Chytrý 2001; Willner 2001; Chytrý and Otýpková 2003), and most recently for its relevance at all. Some additions to phytosociology have been suggested, for example by Dale (1988), by Pignatti (1994, 1995), and by Pignatti et al. (1995). The relevance of phytosociology today has been considered ably, from both sides, by Ewald (2003).

The **phytosociology** chapter in this section, by Guillaume Decocq, is entitled "Moving from Patterns to Processes: a Challenge for the Phytosociology of the 21st Century?" It begins with a thoughtful historical summary of phytosociology, from its roots up to the present, and provides an insightful critique. Phytosociology is described as "based on the postulate that, at a given place and time, vegetation reflects the combined influence of biotic and abiotic environmental factors," and thus can be considered a discrete repetitive unit, i.e., a "combination of plant species sharing the same ecological requirements" and occurring on "an ecologically homogeneous piece of land." Although phytosociology was successful in Europe and many other countries, its theoretical background, concepts, and tools were challenged during the 20th century by Anglo-American plant ecology. An anecdote of unknown origin says that the European asks "What is it?" and the American asks "How does it work?" Now that European vegetation has been described in great detail, phytosociology is no longer considered "in vogue" in Europe and some other areas. This chapter considers some of these questions and how to bridge the gap between classical phytosociology, which still has much to offer, and more "functional" plant ecology (vegetation ecology). It also presents some perhaps less known French literature and some new methods in phytosociology, such as the "integrated synusial phytosociology" of Gillet and Gallandat (1996). Some challenges to phytosociology are seen as challenges also to the relevance of ecology and modern science in general.

The chapter on **gradient analysis**, by Brooke Wheeler and Robert K. Peet, presents "A Multi-Scale Analysis of Plant Diversity along Soil Nutrient Gradients." This covers different subregions and floristic provinces of the southeastern USA, from coastal plain, through fall-line sandhills and piedmont, to the (lower) Appalachian Mountains. The more coastal portion in particular is a region in which small changes in soil texture and soil moisture can translate into quite different plant communities (albeit sometimes with the same dominant tree species). As the authors point out, soil effects on plant diversity have never really been analyzed comprehensively. Their approach combines **nested sampling** and gradient analysis, thus involving plot, gradient, sub-region, and whole-region scales. Vegetation sampling was coordinated with plot-level soil data from the Carolina Vegetation Survey. Soil data include texture, pH, organic content, and content of various cations and other nutrients. This ability to do nested sampling at different spatial scales with a quite large data-base that includes soil is attractive indeed. It is perhaps no surprise that greater soil variation was found between subregions than within, but the approach does suggest some major factors and how the importance of different soil factors changes in the different subregions. The study also presents a novel use of path models and structural-equation models for describing complex relationships between soil factors and plant diversity.

Applied Vegetation Science

Once new concepts and paradigms are established, it becomes fashionable to try to tear them down. Criticism of the "climax" was almost immediate and led to the "polyclimax theory" (Tansley 1935; see brief history in Meeker and Merkel 1984). Even the ecosystem concept has been criticized seriously (O'Neill 2001). [Traits and PFTs are not yet vulnerable because the "holy grail" has not yet been "found" (cf. Lavorel et al. 2007)]. Criticism of the concept of potential natural vegetation (PNV) led to refinements such as "potential replacement vegetation" (Chytrý 1998). PNV criticism has been renewed recently (Carrión and Fernández 2009; Chiarucci et al. 2010) and answered ably (e.g., Loidi et al. 2010; Loidi and Fernández-González 2012; Somodi et al. 2012). Mucina (2010), in particular, provided a useful tabular inventory of uses of PNV and related concepts, with references.

Paradigms and other major concepts may have shortcomings, but they also usually have practical uses, for example, as guides to management, monitoring, revegetation, and other conservation activities. PNV remains a useful concept for guiding reforestation and other vegetation recovery efforts (e.g., Miyawaki and Fujiwara 1988; Alias et al. 1998; Zerbe 1998; Miyawaki and Box 2006). Application of vegetation science to practical problems may involve many strategies and methodologies, especially in attempts to rehabilitate or restore ecosystems.

Chapters in this section treat three quite different contemporary problems in applied ecology: invasive species, vegetation restoration, and the management of sustainable woodlots and other tree plantations. Specific questions include:

- How potentially invasive species are controlled in their native areas
- Whether vegetation restorations should include successional species in their designs
- How to insure both productivity and sustainability in local-use woodlots

This last effort is especially significant since productive woodlots take the pressure off nearby natural forests.

When is a weed not a weed? This question, concerning a widely naturalized, invasive weed of Europe and North America, is investigated by Michiko Shimoda and Norifumi Yamasaki in their chapter on "*Fallopia japonica* in Japan: Why is it not a Pest for Japanese People?" This study involves not only **invasion biology** (the autecology of potentially invasive species) but also some historical study, **ethnobotany** and **cultural ecology**. *Fallopia japonica* is a widespread native species of Japan and adjacent countries and has been one of the most familiar and useful wild plants for centuries. It is eaten widely (as are most plants in Japan) and has medicinal uses. As a result, one Japanese dictionary of local plant names recorded more words for *F. japonica* than for any other species listed. In this study, the habitats and growth characteristics of *F. japonica* were surveyed and described from the foot to the alpine belt of Mt. Fuji, where it occurs at both man-made and natural sites, but always restricted to open, sunny situations. *F. japonica* is a constituent species of diverse herbaceous, shrub, and open-woodland communities and is considered a character species of *Artemisietea principis*. It may also occur commonly in meadows (dominated by tall grasses), but, in all these situations, it is difficult for *F. japonica* to cover large areas, despite frequent management by cutting and mowing. So it appears that it is not controlled by competitors or herbivory in its native area, as are many invasive alien species, but perhaps by vegetation structure. The question is why this control does not happen elsewhere.

Restoration of damaged or destroyed vegetation and ecosystems involves more than just rehabilitation of functions but actual restoration of the components and functional integrity of the original ecosystem, with the native, original species, as far as possible (Jordan et al. 1988; see also Pimentel et al. 2000 and a definition of restoration ecology in Cairns 1995, p. 6). Restoration ecology thus requires good understanding of the **potential natural vegetation** (PNV), which may be the original vegetation or the subsequent potential after changes to the physical environment (such as soil erosion) (Tüxen 1956). A central question for potentially closed vegetation, where shade tolerance is a controlling factor, is whether to plant mature-stage trees only or a mix of mature-stage and seral-stage trees and shrubs. In the benign, humid warm-temperate climate of southern Japan, which permits evergreen broad-leaved forest almost everywhere, it was shown by Miyawaki (1992) that, with sufficient site preparation, it is possible to plant mature-stage native trees only and still achieve a facsimile of the original vegetation within 10 years or so, which would grow into a more diverse, nearly natural forest over the next 1–2 decades. Would this approach be as successful in other regions, with other climates, and where the potential vegetation might be deciduous rather than evergreen?

Some basic questions in **reforestation** efforts are addressed by Laskurain and colleagues, from northern Spain, in their study on “Iberian Atlantic Forest Restoration: an Experiment based in Vegetation Succession.” This study followed three experimental plots, one for each of the three main natural forest types in northern Spain, namely Mesophytic Oak Forest, Eutrophic Beech Forest, and Oligotrophic Beech Forest. Each plot was planted with three different densities and three combinations of indigenous tree and shrub species, including mature-stage and seral-stage trees and shrubs. As in other successful reforestation efforts, survival rates and overall results were improved by good site preparation and the planting of saplings with already well-developed root systems. Monitoring over 14 years showed that, in spite of a low overall survival rate, the inclusion of seral-stage shrubs not only increased biodiversity but also accelerated succession by suppressing invasion by shrubs such as *Rubus* and *Ulex*, which often inhibit succession in degraded lands. This demonstration of a role for seral shrubs in revegetation is significant, but it may be more important in situations involving deciduous forest.

Another all-too-common modern-day problem involves the creation and **production ecology** of sustainable tree plantations (woodlots) that can supply wood for fuel and construction and take the pressure off of nearby native forests. Design of such “production forests” requires, among many other things, the ability to measure (or at least estimate) yields accurately without destroying the vegetation. Methodologies for both destructive and **non-destructive sampling** of forests for estimation of biomass and productivity began in earnest with the International Biological Program of 1964–1974 (DeAngelis et al. 1981). Those studies, though, targeted natural or nearly natural ecosystems. The next chapter herein, by Nobukazu Nakagoshi and colleagues, involves “Carbon-Stock Measurement of Community Forest in Lampung Province, Sumatra”, i.e. biomass and productivity estimation in various kinds of mostly disturbed land cover. The problem addressed is how to estimate carbon stock in community forest, in a tropical setting involving four land-cover types: selectively cut, shrub-mixed dryland farm, shrub-bush cover, and bare land. As with natural vegetation, the accuracy of estimations is improved greatly by including even one additional year. In this Sumatran example, field carbon stocks were estimated, for 2006 and 2009, using allometric methods based on measurement in 20 m × 100 m plots. A mixture of non-destructive and destructive sampling was employed, with estimates checked by **satellite monitoring** using Landsat imagery for 2 years and further **GIS analysis**. This study did not include soil carbon, but that can be added.

Perspectives

Finally, this last section treats problems of present-day **conservation strategies** and the future course of the Earth's landscapes and perhaps of land cover and vegetation study in general. This involves, among other things, **biodiversity management** and analysis of ecological integrity. Biodiversity is often construed by decision makers and some managers simply as species richness, i.e., the number of species present. **Ecosystem integrity**, on the other hand, is hard to define but refers to the "wholeness" of systems, i.e. the degree to which all the natural components and processes are present and functioning naturally or nearly naturally. This has practical advantages, since more or less naturally functioning systems are largely self-managing and do not require large inputs of money and manpower in order to prevent undesirable consequence of system dysfunction. Unfortunately, biodiversity and ecosystem integrity have sometimes been seen, perhaps rightly, as conflicting policy goals (Angermeier and Karr 1994; cf. Pimentel et al. 2000; Westra and Lemons 1995).

The chapter by Colin Meurk (of Landcare, in New Zealand) treats "Vegetation History and Dynamics in New Zealand" but with an eye toward present and future **trajectories** and threats. As a long-isolated micro-continent, New Zealand evolved quite different life forms from other areas. Ancient native elements, though, have been joined over the past 5–10 million years by trans-oceanic arrivals that radiated in mountain environments or, in the absence of mammalian predators, evolved some bizarre adaptations and lost redundant functionality, such as bird flight. As a result, perhaps 85% of native plant species are endemic to New Zealand, many influenced profoundly during evolution by the lack of native mammals. Of course both the native flora and fauna were devastated by the predatory and herbivorous mammals brought by humans over the past thousand years — and even more so by the exotic plant species brought more recently. Another loss identified by the authors is what can be called the "extinction of experience" that has put great strain on the ecological integrity of the biota, especially in the lowlands. This paper summarizes key factors of the condition of New Zealand landscapes and ecosystems and considers their trends, possible future trajectories, and opportunities to recover some of the lost integrity of natural patterns.

Finally, facing loss of biodiversity, of self-managing natural landscapes, and of ecological integrity in general, what should vegetation science and geobotanical research focus on? That is the question addressed by Richard Pott in this last chapter, on "Fundamentals and Perspectives of Geobotanical Research in the 21st Century." **Geobotany**, or vegetation science, attempts to document and understand spatial and temporal patterns of biodiversity, which has become a key word in human society as well as current science. Biodiversity involves structural diversity of life forms, functional biodiversity of ecosystems and processes, and diversity of patterns in long-term evolution and short-term development. Perhaps between 10 and 100 million species are thought to exist, but many will go extinct before ever being identified. Services provided free by nature, so-called **ecosystem services**, are necessary for our daily lives, but these are being undermined by the overexploitation and outright destruction of self-managing, at least quasi-natural habitats, due to the activities of more humans than the Earth can support over longer periods of time. Rapid recent increase in the rate of species losses has led to the term "The Sixth Extinction" (in allusion to the five major extinction events known from Earth's geological history). This last chapter discusses some aspects of global problems in the 21st century and the role of geobotanical research in addressing some of these problems.

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Part I
Global Scale

World Bioclimatic Zonation

Elgene O. Box

Abstract Attempts to regionalize world climates began in the early 1800s, based partly on natural landscapes. The first attempts were empirical, but better understanding of global atmospheric circulation led eventually to 'genetic' approaches, based on the mechanisms that generate different climate types. It was recognized early that climatic zones follow mainly from temperature, at least in lowlands, but the duration of wet and dry seasons also characterizes many climate types quite distinctly. This paper expands the familiar genetic climate classification of Walter to provide a simple, globally consistent, more complete classification that also recognizes subtypes and transitions explicitly, and facilitates understanding of world soil and vegetation types. This genetic approach is preferable to empirical systems, such as Köppen, because it:

- has fewer main types
- recognizes types tied more directly to dynamic mechanisms that cause different climate types
- has a more general and flexible set of subtype descriptors
- unifies some climatic concepts better
- matches natural vegetation and landscapes better, and
- is more flexible under changing global climatic conditions than are empirical limits.

Zonal climate types are easier to understand and to teach, since they are tied directly to atmospheric dynamics and reflect visible geographic regions and landscapes. The resulting global geographic framework also provides a basis for testing the validity of putatively general ecological models.

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Introduction

The concept of bioclimatic zonation appeared with the first treatments of world vegetation in the early nineteenth century and was developed into a modern concept, with greater understanding of atmospheric circulation, in the early twentieth century. The idea of zonal soil types to match zonal climates was added by Dokuchayev (1899, 1900), and the idea of zonal vegetation types was formalized by Walter (1954), along with his global system of climate types (cf. Walter and Lieth 1960–67; Walter 1968, 1970, 1973, 1976). The Walter system, with its familiar Roman-numeral notations and useful climate diagrams (Walter 1955), is the most widely known and probably best of the global climate classifications based on so-called "genetic" principles, i.e. based on the mechanisms of global atmospheric circulation that generate recognizably different climate types.

The principle of global zonation is now well accepted, not only for climates, soil and vegetation, but even for aspects such as speciation mechanisms (in animals as well as plants) that enhance tropical diversity (Kozak and Wiens 2007; cf. Janzen 1967). Even so, existing global zonation systems are still incomplete, without explicit recognition of all zones, transitions, exceptions and zonal vegetation. The Walter system, for example, has only ten types—plus one major flaw, namely the lack of distinction between east-side and west-side "warm-temperate" (type V) climates, which result from quite different atmospheric mechanisms. The purpose of this chapter, then, after some background information, is to expand the Walter system, representing these west-side and east-side situations separately; to add subtypes and recognize transitions, building on Walter's familiar notation; to check the consistency of the various climate types and subtypes by examining their geographic occurrences in different regions; and to formalize zonal vegetation types (biomes) for all climates. The main regional exceptions to the general global zonation pattern are also identified and discussed. The result is a consistent, more detailed, mechanism-based global bioclimatic system that should also be more flexible under climate change than are empirical systems.

Background

The idea that climates occur in somewhat recognizable east-west "zones" was suggested already by the ancient Greeks, who divided the world into torrid (tropical), temperate and frigid (polar) regions [perhaps first suggested by Parmenides as early as the fifth century BC; see historical summaries by Ukert (1816), Kiepert (1878), Tozer (1897), and Berger (1903)]. The tropical zone was construed as frost-free but hot and "uninhabitable", the temperate zone as having freezing temperatures seasonally, and the polar zone as cold (also uninhabitable), with freezing temperatures throughout the year. The Greeks understood latitude quite well, and Aristotle (see Ward 1905) was able to delimit the tropical zone by the Tropics of

Table 1 Basic climatic divisions of the world

Region	Frost occurrence	General temperature levels
Tropical	Never	Always warm, little if any temperature seasonality
Subtropical	Almost never	Warm but with cooler period, with very occasional slight frost in only a few years
Temperate	Seasonally every year	Significant difference between summer and winter
Warm-temperate		Warmer summer, milder winter
Cool-temperate		Cooler summers
Sub-polar		Shorter, even cooler, marginal summers
Polar	Always possible	Cold, even in the short "summer"

These basic divisions are based only on temperature. Frost occurrence and temperature levels are for lowlands; conditions will be colder in mountains

Cancer and Capricorn and the polar zones by the Polar circles, with temperate zones in between. As transitions, one can imagine a subtropical zone with almost no frost, a subpolar zone with a cool, very marginal summer, and warmer and cooler variants of the temperate zone. Such a scheme is outlined in Table 1 and still represents the first level of essentially all world climate classifications.

Perhaps the first to delimit climate zones by temperature was the Austrian geographer Alexander Supan (Rubel and Kottek 2011), although isotherms had already been drawn on global maps by Humboldt (1817) and by Dove (1852). At first Supan (1879) used the 20 °C and 0 °C mean annual isotherms, respectively, to delimit the tropics and polar regions, with subdivisions that yielded 6 zonal types and a total of 11 zones (see summary by Ward 1905). Supan (1884) placed the polar treeline at the 10 °C isotherm for the warm-month mean, a value still widely used (cf. Andersson 1902; Brockmann-Jerosch 1919; see review by Tuhkanen 1980, p. 66). These limits were accepted by Wladimir Köppen (1884), who added specified durations of critical temperatures. These first zonations by Supan and Köppen are summarized in Table 2 (see also Ward 1905; Mather 1974; Tuhkanen 1980). Modification led to the first fairly complete global climate classification, by Köppen (1900), based on particular temperature levels plus temperature-precipitation ratios. In his next version, Köppen (1918) changed the tropical limit from 20° to the 18 °C isotherm for the coldest month; he also lent further support to the occurrence of polar treeline at the 10 °C warm-month isotherm (Köppen 1919, 1920, 1923). The Köppen system was refined into a final version (Köppen 1931) that involved five basic subdivisions. Since this system is largely quantitative (see, for example, the summary in Oliver and Hidore 1984), it lends itself well to drawing boundaries between climate types. As a result, the Köppen classification has remained the basis for almost all climatic wall maps and maps in atlases and textbooks, albeit sometimes with (proprietary) variations.

Table 2 Early evolution of temperature-based limits for world climatic zonation

Tropical	Tmin ≥ 20 °C (all months ≥ 20 °C)	Supan (1879)
	Tmin ≥ 20 °C (all months ≥ 20 °C)	Köppen (1884)
	Ty ≥ 20 °C (limit of palms and trade winds)	Supan (1896)
	Tmin ≥ 18 °C (all months ≥ 18 °C)	Köppen (1918)
Subtropical	Between 20 °C isotherms for Ty and Tmin	Supan (1879)
	4–11 months ≥ 20 °C, 1–8 months 10–20 °C	Köppen (1884)
Temperate	Between Ty = 20 °C and Ty = 0 °C	Supan (1879)
Warm	Between Ty = 20 °C and Tmin = 0 °C	
Cold	Between Tmin = 0 °C and Ty = 0 °C	
(Temperate)	4–12 months 10–20 °C, >20 °C not >4 months	Köppen (1884)
Oceanic	All months between 10 and 20 °C	
Warm-summer	Tmax ≥ 20 °C, at least 1 month <10 °C	
Cold-winter	Tmax < 22 °C, 4–11 months 10–20 °C	
(Temperate)	Tmin < 18 °C (Tmax ≥ 10 °C)	Köppen (1918)
Mesothermal	Tmin ≥ −3 °C	
Microthermal	Tmin < −3 °C	
Cold	1–4 months 10–20 °C (other months <10 °C)	Köppen (1884)
Polar	Ty ≤ 0 °C (permafrost)	Supan (1879)
With summer	Between Ty = 0 °C and Tmax = 0 °C	
Ice-cap	Tmax ≤ 0 °C	
	Tmax ≤ 10 °C	Supan (1884/1896), Köppen (1884), cf. Andersson (1902), Köppen (1920)

Supan (1879) seems to have been the first to suggest the use of isotherms instead of latitudes to delimit climate zones. Köppen (1884) adopted these limits originally but then modified them continuously into his final classification in the 1930s. All values represent mean temperatures, and all limits are based, empirically, on relationships to apparent natural vegetation and landscapes

Tmax = mean temperature of warmest month, Tmin = mean temperature of coldest month, Ty = mean annual temperature

During the same early years, other ideas of climatic zonation were also developing. The idea that global atmospheric circulation, with its rain-producing wind systems, would generate different wetter and drier climate types was presented in a classification by Davis (1894; cf. de Martonne 1909; Hettner 1911). This idea was expanded especially by Tor Bergeron (1928, 1930), who analyzed weather and circulation in terms of air masses; and by Hermann Flohn (1950), who pioneered the development of a general theory of atmospheric circulation. This latter provided the basis for global classification of climates based on the mechanisms of atmospheric dynamics that produce the main climatic regions. These mechanisms include, in particular, the seasonal north-south migrations of:

- the Inter-Tropical Convergence zone and Subtropical High-Pressure belts, which bring the tropical wet and dry seasons, respectively; and
- the tropical Trade Winds (tropical easterlies) and mid-latitude Westerlies, which bring wet oceanic air masses inland, especially in the temperate zone.

The first complete classification based on atmospheric circulation was probably by Alisov (1936), which laid the groundwork for a long Russian tradition in study of climatic and other natural zonation, including soils and vegetation [see Dokuchayev (1948), Borisov (1955), Grigor'yev and Budyko (1956), Armand (1965, 1970); cf. review of Classical and Medieval concepts by Ditmar and Chernova (1967), and summary of Soviet climatology by Lydolph (1971)]. This "genetic" approach to climate classification was also pursued in Germany (cf. Kupfer 1954; Hendel 1960) and became the basis of later classifications by Gaussen and Walter (see below). A brief but good summary of the genetic approach was given by Butzer (1968), and a genetic classification based on air masses was formulated by Hidore (1969; cf. Oliver and Hidore 1984).

Subsequent climatic description and classification sought ways to relate zonation to measureable climatic elements, including indices to relate temperature and moisture in expressions of wetness and dryness. The first published notion of a moisture index relating precipitation and (potential) evaporation may have been by Linsser (1867, 1869; cf. Thornthwaite 1943), followed by Penck (1910). Probably the most influential early index, however, was the *indice d'aridité* of de Martonne (1926a, b), which related more readily available annual temperature and precipitation, and was used to estimate boundaries between wetter and drier climatic regions. A somewhat similar *indice pluviometrique* by Emberger (1930a, b, 1932) was used to map potential vegetation regions, and a world map of the Martonne index was eventually published also (de Martonne 1941). The index of de Martonne actually expresses humidity rather than aridity, but it is still in use, perhaps due largely to its simplicity. A thorough review of the various parameters and indices developed and used in climatic description and classification was provided by Tuhkanen (1980). In a very useful but much shorter historical summary of climatic indices, Lauer (1953) pointed out quite correctly that "Die großen Klimagürtel … sind aber zunächst thermisch bedingt", i.e. that indices cannot replace classifications or delimit climatic zones, because the basic climatic zones are determined by temperature.

A major step in relating temperature and moisture was provided by C. Warren Thornthwaite, who classified the climates of North America (Thornthwaite 1931) and then the world (Thornthwaite 1933) based on indices of “precipitation effectiveness” (similar to de Martonne) and “thermal efficiency”. These formulations were complex, and in a second classification, Thornthwaite (1948) replaced his P-E index with the concept of potential evapotranspiration (PET), defining it as the amount of water that could evaporate or transpire under the prevailing energy conditions. Using PET as a basis, Thornthwaite also provided:

- a global climate classification system, with indices of aridity and humidity related to climatic water deficit and surplus (Thornthwaite 1948);
- a procedure to estimate the complete climatic water balance, based on precipitation, PET, soil water and actual evapotranspiration (Thornthwaite and Mather 1955); and
- a method to estimate PET from temperature, based mainly on temperate-zone data (Thornthwaite and Mather 1957).

The Thornthwaite classification was an improvement and was tested in several places (e.g. Chang 1955; Fukui 1958), but calculation of PET was complicated and the Thornthwaite system was never used for maps as much as the simpler Köppen system. A simpler method for estimating PET, based also only on air temperature (but mainly neotropical data), was offered by Holdridge (1959), to complement his system of “life zones” (Holdridge 1947, 1967). Since these PET estimators were both based on regional data, they both have geographic biases. Comparison of the two PET formulas showed higher estimates by Thornthwaite for much of the Northern temperate and higher latitudes (north of about 40° N) and by Holdridge elsewhere, i.e. throughout the tropics and much of the Southern hemisphere (Box 1979, 1986).

More modern concepts for climate classification and zonation were based at least partly on global atmospheric circulation (e.g. Flohn 1950) and relations with natural landscapes and vegetation. At the International Geographical Congress in Lisbon, botanist Henri Gaussen (1949) presented his ideas for a moisture index based on daily temperatures and the number of dry days, thus the length of the dry period. The concept of ‘growing season’ and the duration of conditions warm enough for plant growth goes back at least to Grisebach (1838). Köppen (1884) had also recognized the importance of durations through his criteria of 1, 4 and 12 (consecutive) warm months, respectively, for his cold, temperate and tropical climates. In the 1920s, Rubinstein (1924) noted that oaks in northern Europe appear to require 4 months of mean temperature of at least 10 °C, and Enquist (1924, 1929, 1933) mapped such requirements for various trees, focusing also on the duration of extreme temperatures (cf. Dahl 1951). The importance of the duration of cold, wet and dry periods in China was recognized by Wang (1941), and the duration of wet and dry seasons was shown by Lauer (1951, 1952) to be related to tropical vegetation types, in a unifying way, in both Africa and South America. A simple measure to express the degree of growing-season warmth, called ‘biotemperature’, was provided by summing only monthly mean temperatures above 0 °C and dividing by 12 (Holdridge 1959).

The Gaussen index was presented more formally as the *indice xérothermique* (Gaussen and Bagnouls 1952, 1953; see summary by Lauer 1953) and was used as the basis for a global climate classification (Gaussen 1955). In a truly seminal paper, Bagnouls and Gaussen (1957) went on to define:

- warm (mean temperature ≥ 20 °C) and cold (mean temperature ≤ 0 °C) months and periods (consecutive months), assuming frost possible if mean temperature is below 15 °C;
- an *indice xérothermique* to express the degree of dryness by counting the number of biologically dry days within the dry period; and
- wet and dry months (and periods), based on an *echelle double* that considers a month to be dry if its precipitation is less than twice the temperature, i.e. $P < 2T$ (in °C).

This last relationship became known as the Bagnouls–Gaussen ratio and was the basis for the *diagrammes ombrothermiques* (see Bagnouls and Gaussen 1957) used to represent the different, essentially genetic, climate types recognized. This approach was adopted in the 1950s by ecologist Heinrich Walter, who presented a similar global system of (genetic) climates and represented them by ‘climate diagrams’ (Walter 1955; modified only slightly from Bagnouls and Gaussen 1957, cf. p. 217). The Walter system had nine basic climate types, denoted by Roman numerals, plus a type X for highlands. Climate diagrams for about 8000 meteorological stations worldwide, classified by his global system, were presented in a *Klimadiagramm Weltatlas* (Walter and Lieth 1960–67). These diagrams show wet and dry seasons quite elegantly, as well as general temperature and precipitation levels, and have been used very widely ever since as the standard concise way to represent local climatic conditions, especially for ecological purposes. More detailed descriptions of the Walter climates were presented in his *Vegetation und Klimazonen* (Walter 1970, 1977) and his remarkable books on world vegetation (Walter 1968, 1973; cf. Walter 1985, condensed but in English). Zonation in mountains and relationships with world biomes were considered more completely by Walter (1976; cf. English summary by Walter and Box 1976).

Climates may be recognized and classified based on whatever criteria may be of interest, including more particular considerations such as storm frequency or human comfort. For more general classification, though, three main approaches have developed:

(1) an **empirical** or **quantitative** approach (e.g. Köppen, Thornthwaite), based on numerical values of basic climatic elements such as temperature and precipitation;
(2) a **genetic** approach (e.g. Flohn, Walter), based on the mechanisms of global atmospheric circulation, the air masses involved, and the resulting seasonal patterns; and

(3) a **duration** approach (e.g. Lauer), based on the duration or degree of the warm, wet and dry seasons that affect geographic patterns of natural vegetation.

The quantitative approach has been developed in perhaps most detail by Rivas-Martínez (1994), from a Mediterranean perspective. The genetic system of Walter is well known and has a partially quantitative basis in the Gaussen ombrothermic relationship, which permits representing the degree and duration of warm, wet and dry seasons. These approaches were combined to some extent in the world map of *Jahreszeiten Klimate der Erde* (Seasonal Climates of the Earth) by Troll and Paffen (1964). It was Wilhelm Lauer in particular, though, who recognized the importance for vegetation of the duration of wet and dry seasons, and finally presented a complete, more quantified global classification based on durations (Lauer and Rafiqpoor 2002).

In many ways, a genetic approach yields more intuitive results, since it is tied directly to understandable mechanisms. Whereas quantitative approaches focus automatically on boundaries, genetic classifications focus tacitly on core climatic regions. The genetic approach is not good for representing boundaries, but in the real world most climates change gradually into the next anyway, through broad transition regions. Genetic classifications began to appear in some English-language geography textbooks by the 1960s, and summaries relating climate types to dynamic mechanisms such as winds and air masses were presented, among others, by Trewartha (1954; with Horn 1968, cf. p. 227 of 1980 printing) and Hidore (1969) (cf. Gersmehl et al. 1980; Oliver and Hidore 1984). Even so, the best known genetic system is still that of Walter, which covers the world with only ten basic climate types. These also match natural biome and landscape types better than do the roughly 15 types and subtypes of Köppen and its variants.

The concept of bioclimatic zonation appeared with the first treatments of world vegetation in the nineteenth century (e.g. von Humboldt 1807; Schouw 1823; Grisebach 1866, 1872; Drude 1890; Warming 1895; Schimper 1898; Diels 1908; see summary by de Laubenfels 1975). The first global attempt to relate vegetation types to actual climatic values (temperature and precipitation) was by Rübel (1930), in his book on *Pflanzengesellschaften der Erde*. The basic symmetry (and asymmetry) of Northern versus Southern zonation was demonstrated on the "average continent" of Troll (1948). This asymmetry includes a boreal zone, with long severe winters and mild but short summers, which occurs over the large land area of Northern high latitudes (cf. Hare 1950; Bryson 1966) but has no Southern equivalent. To this general zonation, the traditional Russian system added the concept of "sectors" to represent the strong east-west gradient from ultra-continental interior Siberia to the milder Pacific climates (see Krestov 2003). It is not easy to represent east-west sectors in latitude-based zonations, but the continentality gradient is unavoidable on large, higher-latitude land masses (cf. Alekhin 1951; Suslov 1961; Hämet-Ahti et al. 1974; Lydolph 1971).

Basic Principles

From the beginning, climate classifications were related to landscapes and general vegetation types. This is reasonable since vegetation determines landscape appearance and constrains many of the raw materials available for human activity, including agriculture. Even so, there has always been significant disagreement in the terminology of the various climatic classifications, largely because most schemes are based on local or regional perspectives. For example, the "far northern" perspective of the Russians describes some 'taiga' as temperate and the southern Turanian Basin as subtropical (e.g. Alisov 1956). This perspective, adopted by the Chinese, sees Shanghai as "subtropical" (December mean temperature 3.2 °C) and Manchuria as "warm-temperate" (January mean −19 °C at Harbin, extremes to around −40 °C). In most countries, atlases and introductory climate textbooks are based on variants of the Köppen system and may call areas "subtropical" as far north, for example, as Boston (January mean −3 °C, with extremes below −25 °C). Even the marine west-coast climate (e.g. Vancouver, with a July mean of 17 °C) was originally called 'warm-temperate' by Walter. Basic climatic terminology could be improved greatly and perhaps even unified by: (1) respecting the meanings of basic words, such as 'sub' (which suggests a smaller subregion); (2) taking a more global view; and (3) focusing on mechanisms that separate landscape responses to climate.

The number of basic physiological mechanisms that limit plants and vegetation is not large, involving mainly aspects of temperature and water availability. In drier but sufficiently warm climates, evergreenness (except in succulents) ceases when the plants can no longer extract soil water when needed. Plant size decreases generally with decreasing water availability in the driest season, unless the plants can reduce their water-losing surface area by such adaptations as deciduousness. Water-balance factors are hard to quantify, especially at broad scale, but drastic differences between wet and dry seasons often make climate types distinct.

Direct limitation by extreme cold is relatively understandable and may be quantifiable. Since their buds and foliage are less protected, tropical and subtropical plants may be damaged by even short-term exposure to "cold" temperatures. Damage to unprotected buds (or other growth points) may start at short-term exposures of around −3 °C for subtropical plants and below about +5 °C for equatorial and some other truly tropical plants. In higher latitudes, ice formation in the fluids between plant cells represents a normal aspect of the cold-hardening that lowers the freezing temperature of fluids in general. Ice formation within cells, however, is lethal, since the ice breaks cell walls, killing cells and plant tissues. Intra-cellular ice begins to form in evergreen broad leaves at even short-term exposure to temperatures below about −15 °C (e.g. Woodward 1987). Freezing of fluids within tree boles and branches may not figure in broad-scale zonation, but it does set a poleward limit of about −40 °C for most truly temperate-zone tree species (with ring-porous wood) versus trees such as boreal birches and willows (with diffuse-porous wood), which may tolerate −70 °C (George et al. 1974).

Limitation by extreme temperatures has been described in detail by various authors, especially by Sakai (1971), Larcher (1973), Levitt (1980) and Sakai and Larcher (1987). Such limitation is summarized in the concept of 'cardinal temperatures' (Woodward 1987, p. 81).

In addition to direct damage, threshold temperatures or durations may limit as follows:

- *Water uptake* is not possible from frozen soil and may be insufficient from cold soil above freezing, so all growing seasons require some period with at least daytime temperatures above 0 °C. Broad-leaved trees with deeper root systems are generally precluded by the occurrence of permafrost, and evergreen broad-leaved trees are usually precluded where soil is frozen even for short periods.
- *Wood production* (by plants larger than tundra dwarf shrubs), appears to require at least 30 days of mean temperatures of 10 °C or above (see summary by Tuhkanen 1980, p. 12, with further references).
- Production of *viable fruit and seeds* by the main trees and shrubs of mid-latitudes appears to require 4 months or more of mean temperatures of at least 10 °C (cf. Rubinstein 1924; Enquist 1924; Walter 1968).

Limitation by temperature becomes most important in temperate and higher latitudes, and a basis in limitation mechanisms can yield more quantitative concepts of climatic zones, as appreciated already in the earliest zonations (cf. Table 2). Geographic zonation by frost limitation is seen especially clearly in south-central Florida, where the subtropical flora is replaced almost completely by a temperate flora within a south to north distance of about 100 km, near a town called Frostproof (Crumpacker et al. 2001).

From very early it was clear that landscapes and vegetation depend heavily on water availability but that climatic zonation depends mainly on aspects of temperature (cf. Lauer 1953). Cardinal temperatures and duration requirements associated with the above limitation mechanisms provide numbers for an initial delimitation of the main zones, as follows:

Polar zone	Fewer than 30 days ≥ 10 °C, if any at all
Boreal zone	At least 30 days of mean temperature ≥ 10 °C
Temperate zone	≥120 days (4 months) ≥ 10 °C mean temperature
Warm-temperate zone	Tmin ≥ 0 °C and Tabmin ≥ −15 °C (and at least 4 months warm, i.e. with mean ≥ 10 °C)
Subtropical zone	Tmin ≥ −3 °C
Tropical zone	No temperature ever below 0 °C, perhaps not < 5 °C

Tmin is the mean temperature of the coldest 30-day period and Tabmin is the absolute minimum temperature, i.e. the lowest temperature ever measured (over a sufficient number of years) or reasonably expected. The warm-temperate zone must also have at least 4 warm months (mean ≥ 0 °C) and probably more, while the subtropical zone may approach and the tropical zone should attain mean temperature ≥10 °C for all 12 months.

Poleward boundaries of forest zones and most tree species are generally set by these temperature limits, but equatorward boundaries are much less well defined, posed probably by such subtle mechanisms as the point at which higher respiration demands in the warmer conditions exceed the photosynthetic capacities of the trees involved, thus weakening the trees until they eventually die. Before this point is reached, however, warm-side limits are more likely posed by the greater competitive abilities of trees from the respective adjacent warmer zones. In many cases these more thermophilous trees may replace other trees by being more shade-tolerant, as in replacement of summergreen deciduous trees by evergreen laurophyll trees (both geographically and in successional sequences). In other cases, the more thermophilous trees may out-compete the trees from cooler climates simply because the thermophilous trees are able to grow faster in the warmer conditions. All of the above leads to more precise, mechanism-based concepts for basic climatic terms, as shown in Table 3.

Table 3 Basic climate-zone concepts and terminology

Equatorial	Near the equator: no frost or other "cold" temperature ever (except in mountains); very little temperature seasonality
Tropical	Low latitudes, generally between the Tropics of Cancer and Capricorn: no frost ever (except in mountains), but low-sun months may be distinctly cooler than high-sun months
Subtropical	Nearly tropical: light frost or near-frost only very occasionally
Temperate	Mid-latitudes (generally about 30–60° N/S)
Warm-temperate	Warm summers with light frost or near-frost every year; significant frost only occasionally (not below about −15 °C)
(Typical) Temperate	Significant frost every year, with occasional temperatures below −15 °C, except in very maritime areas; winters too cold for evergreen broad-leaved trees
Cool-temperate	Cool summers, as in maritime areas (or higher latitudes), with frost every year (extremes above or below −15 °C); growing-season warmth may be marginal for many temperate-zone trees and crops
Boreal (N Hemisphere only)	Cool to mild but short summer, with long, severely cold winters (with deep soil freezing), as over large high-northern continents; summer warmth insufficient for most crops and temperate trees
Austral (S Hemisphere only)	More maritime cool-temperate (milder winters), as small high-southern land areas such as Tasmania and New Zealand; an ultra-maritime counterpart to the Northern boreal climates
Subpolar	Nearly polar: very cool summers, with long severe (continental) or milder (maritime) winters, still with significant frost; total warmth marginal for tree growth
Polar (non ice-cap)	Very cool, short summers (frost possible in any month) and very long, cold winters; may be continental or maritime but with summer warmth insufficient for any tree growth
Polar (ice-cap)	Permanently frozen: summer warmth insufficient to melt accumulated ice

These terms represent an expansion of Table 1, with some limiting temperatures and better resolution of tropical and high-latitude zones

The dearth of new global classification schemes over the past 50 years suggests no need for them, unless there is a fundamentally different approach, like that of Lauer and Rafiqpoor (2002) based on durations of warm, wet and dry seasons. The classification presented herein is useful precisely because it is not "new" but rather an enhancement of an existing, well known classification. Even so, for a useful but also flexible classification and zonation system, some basic principles are needed:

- Types should be recognized based on conditions over the *whole year*, not just periods of particular interest, such as growing seasons.
- Types should be recognized based on *genetic mechanisms* of atmospheric circulation, geographic position, latitudinal effects on energy inputs, etc.
- Types should describe obvious *seasons*, including wet and dry, as well as levels and durations of temperature, precipitation and other relevant factors.
- Types should involve boundaries recognizable by climatic "breaks", i.e. locations of *steep gradients* (if not discontinuities) in important climatic factors.
- *Subtypes* should also be recognized for finer distinctions, but only as necessary to recognize truly different situations (without increasing the number of main types).
- *Transitions* between adjacent types should also be recognized explicitly, with some formal notation for describing their characteristics.
- Only *truly distinct* types should be recognized, with no duplications (cf. subtypes vs transitions), in order to keep the system as simple as possible.
- Types should be recognized as far as possible based on *readily available data*, in order to permit eventual global quantification.

No other formal modification or enhancement of the Walter system has ever been published, although Breckle (cf. Walter and Breckle 1991) and others have recognized the need to separate the east and west-side variants of Walter's original warm-temperate (V) climate.

Data and Methods

Data for this exercise in global-scale generalization include previous descriptions and classifications of climate, worldwide climate data, global and regional vegetation descriptions, taxon range maps, and worldwide field experience in sampling vegetation and interpreting it in relation to climatic conditions. The main climate data are long-term monthly means of temperature and precipitation (up to about 1980, when global warming accelerated), from a world data-base compiled over 40 years by the author. This data-base also includes absolute minimum temperature for at least half the sites and estimates for the other sites, made by locally constrained three-dimensional triangulation (program TXTRAP: Box, unpublished, from early 1990s). Where measurement periods are short, the estimates of absolute minima are generally better than the available data. Climates for a very few mountain sites were also included, reconstructed by another triangulation program

(POLATE, also unpublished). A brief description of this data-base was given by Box and Fujiwara (2010).

The methodology involved identifying types and subtypes (from literature and data); generalizing them to global scale; and comparing regional occurrences to insure global consistency. This involved standardization of already recognized climate types, aided greatly by 30-plus years of teaching the genetic approach to undergraduate and graduate students. Global standardization sometimes involved mapping the climate data (e.g. Box and Choi 2003; Box, unpublished) and testing by predictive mapping of climate types represented as climatic envelopes (e.g. Box 2014). Further quantification of climate classifications will probably also require envelope modeling but is complicated by the quantitative similarity of some lowland and mountain climates.

Main Climate Types and Regions

In a genetic approach some climate types are obvious, being tied directly to latitude and atmospheric circulation. These types include everwet equatorial, tropical with wet and dry seasons, subtropical arid, mediterranean, marine west-coast, boreal, and polar. Mid-latitude climates are less tied to global circulation but may still be distinct. Walter (1954) divided these into types called warm-temperate (V: with evergreen forests), nemoral (VI: cooler, with deciduous forests), and temperate continental (VII: with grasslands and cold-winter deserts). The problem with this is that Walter did not recognize the different nature of the ultra-oceanic climate of windward west coasts and combined it with the warm-temperate climate that occurs near east coasts, at lower latitudes, due to totally different atmospheric mechanisms. As a result, Walter's type V is divided here into the already well recognized Marine West-Coast type (called Vm below) and the much warmer Warm-Temperate type (called Ve) occurring on continental east sides (cf. Walter and Breckle 1991). The result is the following set of 10 basic climate types, denoted by Walter's original Roman numerals:

I. Equatorial	Ve. Warm-temperate (east side)
II. Tropical summer-rain	VI. Typical temperate
III. Subtropical arid	VII. Temperate continental
IV. Mediterranean	VIII. Boreal
Vm. Marine West-Coast	IX. Polar

These types form the basis for a global genetic classification, which is depicted, with genetic mechanisms, in Table 4. Relative locations of these climate types on a hypothetical "Ideal Continent" are shown in Fig. 1 (cf. Box 2002). Consistently apparent subtypes, such as temperate deserts (which Walter did not distinguish within VII), are also recognized and are denoted by appending a single letter to the Roman numeral (see Subtypes section below).

Table 4 Main world climatic zones, their genetic mechanisms and zonal vegetation types (Biomes)

Climate type	Notation	Main characteristics	Genetic mechanisms		Zonal vegetation types
			Summer	Winter	
Equatorial	I	Warm and wet year-round; no frost in lowlands	Inter-Tropical Convergence Zone (low pressure, esp. equinoxes)		Tropical rainforests
Tropical summer-rain	II	Distinctly wet summer and dry, cooler low-sun season	ITC	STHP	Raingreen forests, woodlands, and scrub; derived savannas
Subtropical arid	III	Dry year-round, with cooler winter; various rain patterns	Subtropical high pressure		Deserts and semi-deserts
Mediterranean	IV	Dry summer, winter rainfall (mild winter, spring growth)	STHP	Windward westerlies	Sclerophyll forests, shrublands and dwarf scrub
Marine west-coast	Vm	Oceanic conditions year-round (wet, cool summer and winter)	Westerlies on windward coasts		Temperate rainforests
Warm-temperate (east sides)	Ve	Warm/hot summer, mild winter, no true dry season	Convectional rainfall	Frontal rainfall	Evergreen broad-leaved and mixed forests
Typical temperate (cf. nemoral)	VI	Warm summer, frosty winter, no true dry season	Convectional rainfall	Frontal rain/snow	Summergreen broad-leaved forests
Temperate continental	VII	Warm summer with rainfall early; colder, dry winter	Convectional rainfall	Frontal rain/snow	Tall and short grasslands
a. Temperate arid	VIIa	Drier, with sporadic rainfall; cold winter	Convectional rainfall	Frontal rain/snow	Cold-winter deserts and semi-deserts
Boreal	VIII	Cool/mild summer, severely cold winter; summer rain	Frontal rain plus convection	Dry cold polar air	Boreal coniferous forests, including larch woods
Polar	IX	Cold summer, severe winter	Dry cold polar air masses		Polar tundra and moss-lichen cold deserts

The climatic types (and Roman numerals) represent the expanded Walter system (see also Fig. 1; cf. Box and Fujiwara 2013; Walter 1970, 1977). Zonal vegetation (biome, landscape) is that which would potentially occur, on zonal soils (euclimatopes, *sensu* Walter 1976; cf. Walter and Box 1976) and "normal" lowland topography, under full control by the zonal climate

ITC = inter-tropical convergence zone, *STHP* = subtropical high-pressure belt

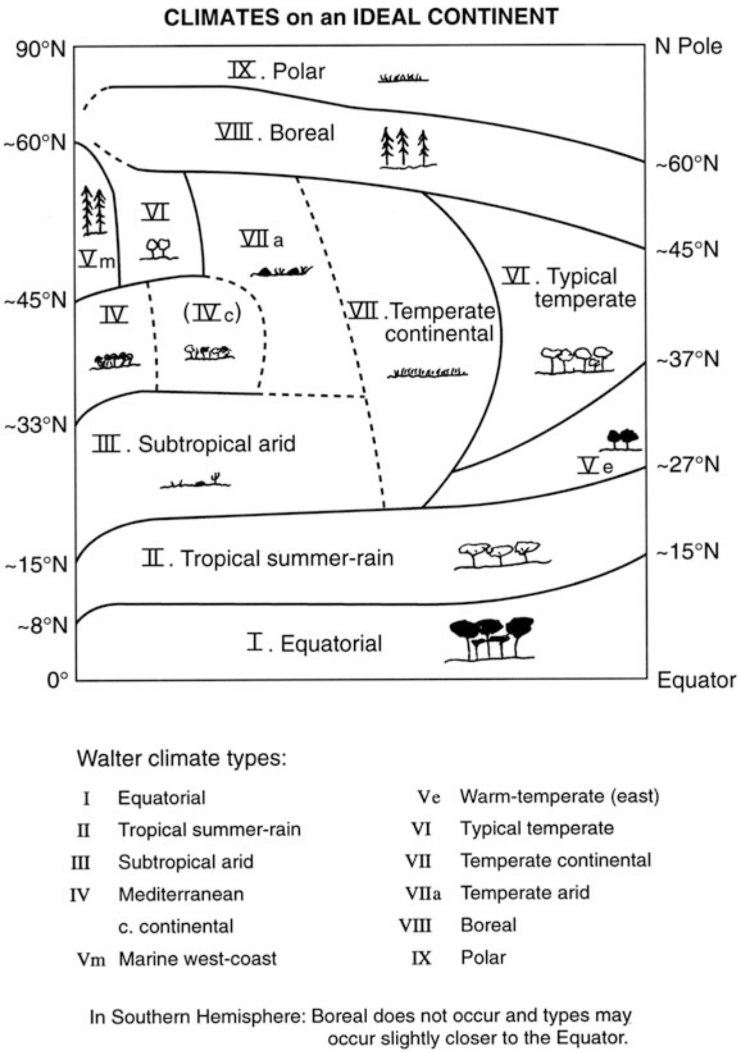

Fig. 1 Climatic regions on an ideal continent. The climates are the genetic climate types of Heinrich Walter (1970, 1977; cf. 1968, 1973, 1985; Walter and Lieth 1960–67), as modified herein by splitting the original Walter V climate into marine west-coast (Vm) and warm-temperate east-coast (Ve) types, due to the quite different atmospheric mechanisms that produce them. Two subtypes are also shown, represented by ‘a’ for arid (VIIa: Temperate Arid) and ‘c’ for continental (IVc: Interior Mediterranean)

Equatorial climates (I), with tropical rainforests, are warm and wet all year, due to the proximity of the inter-tropical convergence zone of low pressure, rising air, and frequent rainfall. Tropical summer-rain climates (II) have green (wet) and brown (dry) seasons, due to alternating dominance by the ITC (wet) and the subtropical high-pressure belts (dry). Landscapes may range from forest to savanna, depending on the total precipitation. On continental west sides, subtropical arid climates (III), dominated by subtropical high pressure, have semi-deserts and deserts with hot summers and only light if any winter frost. Further poleward, Mediterranean climates (IV) have these same dry conditions in summer but some rainfall from autumn to spring, brought to their winter-windward coastal positions by wet air masses from the adjacent ocean. The subtropical high pressure does not reach further poleward, so windward oceanic conditions prevail there all year, resulting in cool, wet marine west-coast (Vm) climates.

In the mid-latitudes (except near west coasts) climates are not related directly to Hadley circulation. The three main climate types all have summer precipitation maxima and differ mainly by winter temperatures and by geographic position (periphery versus interior of a landmass). On continental east sides, within reach of maritime air masses, warm-temperate (Ve) climates (usually with evergreen forests) have warm summers, mild winters, and no dry season. Toward the poles, typical temperate (VI) climates have colder winters and temperate deciduous forests; these climates may also occur on continental west sides (at higher latitudes), if winter temperatures are low enough to distinguish them from Vm climates (as in Europe). Temperate continental (VII) climates, with wider temperature ranges and grassland landscapes, occur in continental interiors where total precipitation is reduced by distance from the ocean.

At high latitude, boreal (VIII) climates with pleasant summers but long, severe winters are distinguished from polar (IX) climates that have cold summer, with frost possible at any time. These types are separated fairly well by the 10 °C isotherm for mean temperature of the warmest month. The boreal climate (from *Boreas*, god of the north wind), which is fundamentally continental, is the only main type in the system that does not occur in both the Northern and Southern Hemispheres. Even so, it may be moderated greatly along oceanic coastlines. The polar climate includes the permanently frozen ice-cap regions but refers more normally to areas that do thaw in summer, as across the northern coastal plains of the two large Northern Hemisphere land masses and on subpolar islands of both hemispheres.

Subtypes in Global Climatic Systems

Subtypes represent variants that are not due mainly to zonation (latitude) but which may be due to relative position on a land mass (geographic position). The most common subtypes are maritime and (more) continental, but six kinds can be distinguished (see Table 5) and are denoted by adding a one-letter code after the Roman numeral:

- *Arid* (a) or other drier variants, as in the Temperate Arid (VIIa) semi-desert and desert climates of mid-latitude rain shadows, such as the Cascade rain shadow in the northwestern USA (Palouse region).

- *Continental* (c) for drier, more extremely continental subtypes with wider temperature ranges, as in the ultra-continental boreal climate (VIIIc) of eastern Siberia.
- *Maritime* (m) for more oceanic variants, with narrower temperature ranges and higher humidity (even if not more rainfall), as found for example in the coastal and island climates of boreal latitudes (VIIIm), e.g. Iceland, Tierra del Fuego.
- *Controverse* (x) for apparently self-contradictory situations, in particular dry but rather maritime temperate climates such as southern Argentina and other rain-shadow areas of the Southern Hemisphere.
- *Winter-rain* (w), especially where a winter rainfall maximum is unexpected, as in the tropical wet-dry climate of Tamil Nadu (east side of southern India).
- *Frozen* (f), for the permanently frozen polar and other ice-cap climates, such as in Antarctica, in order to denote them separately in the system.

These subtypes, following the above guidelines, are described further below, with examples. Some of these subtypes represent clear exceptions to the normal zonation pattern and are treated further in the section on Exceptions (below). The full system of climate types and subtypes is also seen in the Appendix, in an inventory of world vegetation regions.

Table 5 Subtypes in the global system of genetic climate types

Main types		m. Maritime	c. Continental	a. Drier	Other
Equatorial	I			Dry equatorial (e.g. East Africa)	
Tropical wet-dry	II	Windward wet-dry (e.g. monsoon S Asia)			w. Tropical winter-rain (e.g. Tamil Nadu)
Subtropical arid	III	Coastal Fog Desert (e.g. Peru, Namibia)			
Mediterranean	IV	Coastal mediterranean (e.g. California)	Interior mediterranean (e.g. Iran, W USA)		
Marine west-coast	Vm				V. Island warm-temperate (e.g. NZ North Island)
Warm-temperate	Ve		Dry warm-temperate (e.g. Texas, Australia)		

(continued)

Table 5 (continued)

Main types		m. Maritime	c. Continental	a. Drier	Other
Typical temperate	VI	Maritime temperate (N + central Europe)	Monsoon temperate (e.g. Eastern China)		
Temperate continental	VII	Maritime steppe (e.g. Patagonia)		Temperate arid (W USA, Mid-Asia)	x. Maritime arid (e.g. Patagonia)
Boreal	VIII	Maritime Boreal (e.g. Iceland)	Ultra-Continental Boreal (NE Siberia)		
Polar	IX	Maritime Polar (e.g. Aleutians)			f. Frozen permanently (e.g. Antarctic icecap)

Subtypes represent variants that are not due to zonal position (latitude). The most common subtypes are maritime (m) and continental (c). All climate types have a maritime subtype except those that are inherently near-coastal (Vm, Ve) or everwet (I). Such maritime subtypes have reduced seasonal and usually diurnal temperature ranges, and usually more precipitation and higher humidity. Most extra-tropical climates have continental subtypes, with wider temperature ranges and less precipitation, unless already arid (III) or continental (VII). Drier (a) variants are drier for reasons other than continentality, such as rain shadows (VIIa) or unusual regional circulation patterns (Ia). Other variants (see particular notation) include the Tropical winter-rain (w), the Island warm-temperate (V) of small islands, the Maritime arid (x) of extreme rain shadows on small land masses, and the permanently Frozen (f) icecap climate. Definitions and climatic distinctions of all of these subtypes are described in the main text.

In equatorial East Africa, coastline orientation and interaction of the Asian and African monsoons combine to produce an unusual circulation pattern and reduced precipitation, such that the normal rainfall minima near the solstices (when the ITC is farthest away) actually become dry seasons. This climate is called Dry Equatorial (Ia) and has two rainy seasons, one usually longer than the other. A somewhat similar anomaly occurs in near-equatorial latitudes of the southern Caribbean Sea. These anomalies are treated a bit more below, in the section on Exceptions.

In the tropical summer-rain (II) region, the most common variant is in windward coastal locations affected by trade winds or monsoon systems. The dry season is less extreme and summer rainfall is especially heavy, especially in monsoon areas. This resulting Windward Wet-Dry (IIm) climate can be especially wet if mountains lie perpendicular to the path of incoming wet air masses, as at Cherrapunji (eastern India, with 10.8 m of average rainfall—and a 2-month dry season) and on the northeastern slopes on Kauai (Hawaiian Islands, with about 10–11 m of rainfall estimated). An unusual tropical winter-rain climate (IIw) can also be recognized, in Tamil Nadu (southeastern India), where dry outward-flowing monsoonal winter air masses must cross the Bay of Bengal before reaching India, thereby becoming wet air masses. In summer, the incoming monsoonal wet air is blocked somewhat by the Western Ghats Mountains, producing a dry season.

In the subtropical arid regions of continental west sides (latitudes roughly 15–35°), there is always a cold ocean current just off oceanic coastlines. In the case of South America, and to some extent southern Africa, the zonal subtropical desert is extended toward the equator by the stabilizing effect of the cold ocean surface on the local atmosphere. This results in a more "maritime" subtropical arid climate that is still almost completely rainless but is often foggy and can be quite cool. The result can be called a Subtropical Fog-Desert climate (denoted IIIm) and occurs not only along coasts with the strongest cold currents (the Peruvian and Benguela) but also, in less extreme form, along the coasts of Baja California, Morocco and even to some extent northwestern Australia.

This cold-current effect extends also into mediterranean latitudes (about 30–45°) and may result in cooler but still dry summers. The resulting climates can be called Maritime Mediterranean (IVm), the extreme case perhaps being San Francisco, where summers are cool and foggy and the warmest month is actually September, with a mean just under 17 °C. Some non-oceanic mediterranean coastal areas may also be less dry in summer, due to stray local disturbances that produce localized summer showers, as along the Tyrrhenian coast of Italy. More extensive are regions of a drier, more continental Interior Mediterranean (IVc) climate, in which summers are arid and winters usually drier and distinctly colder, with significant frost (and more deciduous vegetation elements), enhanced in some areas by somewhat higher elevation. Such IVc climates occur well into the interior Middle East (e.g. parts of Iraq and Iran), in uplands of the Great Basin (western USA), and in smaller areas of central Chile, southwestern Australia, and perhaps even eastern Spain.

Further poleward along windward west coastlines (about 40–60°) are the coastal strips of marine west-coast climate (Vm), which do not have any significant subtypes because the areas are narrow, delimited inland by mountains, except in Europe. On some islands, however, such as the North Island of New Zealand (35–42° S), it is difficult to separate an oceanic west-side Vm climate from the east-side Ve climate, with plentiful but less extreme rainfall. Summers are cooler than in more typical Ve situations, which are usually at lower latitudes. One can recognize this humid oceanic climate, with its moderated temperatures both summer and winter, as an Island Warm-Temperate climate and denote it simply by V. Such a climate is often called cool-temperate and may have cool-temperate laurel forests, but winter temperatures are not far below freezing. So it is not the cool-temperate VIm climate described below.

Mid-latitude climates tend to be more continental and their temperate zones broader on east sides than on the west. In the usual warm-temperate (Ve) latitudes on continental east sides (27–37° N/S, see Fig. 1), there may also be more interior, drier locations that are somewhat continental, such as the "hill country" of central Texas and parts of interior, mainly southeastern Australia. Such areas can be called Dry Warm-Temperate (Vc) and still have mild winters and enough rainfall to support (less dense) woody vegetation.

In the typical temperate climate (VI), both maritime and continental subtypes can be recognized. Climates often called "cool-temperate" (e.g. northwestern Europe) are usually more oceanic and occur at higher latitudes on windward continental west sides. These can be interpreted as a Cool-Maritime Temperate

(VIm) climate, with significant winter frost (extremes below −15 °C), as occurs not only in Europe but also in some small, somewhat inland areas of Oregon, Washington and British Columbia and even in some lower-elevation belts in the southern Andes. The distinguishing feature of this VIm climate is its cooler summers than in the usual VI climates of continental east sides (East Asia and eastern North America). Winters may be milder near the coast or significantly colder inland. On the other hand, under the monsoon system of East Asia there is also a distinctly more continental temperate climate, with a short summer wet season of 4–5 months and dry conditions from autumn through spring. This Monsoon Temperate (VIc) climate occurs mainly in northern to eastern China, where winters are consistently colder and drier than at comparable latitudes and geographic position in eastern North America.

In East Asia, humid temperate climates have traditionally been divided into cool-temperate and warm-temperate (e.g. Kira 1945, 1949, 1991; Physical Regionalization Committee 1958–59). In eastern North America, however, only New England and southeasternmost Canada have the cool summers suggestive of a cool-temperate climate, while the mild winters of a warm-temperate climate do not appear southward until one reaches the inner southeastern coastal plain. This leaves a large region of somewhat subcontinental “typical temperate” climate in between and suggests a division into three parts:

- a cool-temperate region with cooler summers (due to higher latitude or oceanic influence), usually with significant admixtures of conifers in the otherwise deciduous forests;
- a generally subcontinental ‘typical temperate’ zone, with four seasons of roughly equal expression and more completely deciduous forests; and
- a warm-temperate zone with milder winters, quite warm-sultry summers, and generally evergreen broad-leaved forests as the zonal vegetation.

Logic suggests that the middle part, i.e. the typical temperate, should be the widest portion, with cool and warm-temperate as smaller zones or sub-zones possessing some transitional character. The warm-temperate is thus zone Ve, and the typical temperate is zone VI, including much of the VIc climate of northern and eastern China. The cool-temperate occurs mainly on windward continental west sides and is best represented as the maritime subtype VIm—or even as a part of the VI-VIII transition where winters are colder and mixed forests involve boreal conifers. This three-part scheme fits both eastern North America (cf. Greller 1989) and East Asia (cf. Box and Fujiwara 2012).

The most important subtype in the entire system is probably the climate of the driest temperate continental areas, with their cold-winter steppe or desert landscapes. These Temperate Arid (VIIa) climates, with annual precipitation sometimes below 200 mm, occur in two situations: the innermost areas of large land masses and extreme rain shadows of high mountains that remove the water from west-to-east-moving oceanic air masses. The first situation occurs especially in parts of Middle Asia and Central Asia. In western North America, the temperate arid climates occur in the Great Basin, which is well inland but also lies in the rain shadow of the Sierra Nevada Mountains to the west (and of the Rocky Mountains to the east). The rain shadow of the Cascade Range, which lies further north, creates a less extremely dry region called the Palouse (from French *pélouse*: grassland), some of which has steppe vegetation and can still be seen as Temperate Continental (VII), albeit with different precipitation seasonality. Since such rain-shadow areas often lie in Mediterranean or nearby latitudes, much of the scant precipitation may come as snow. This provides an early-summer snowmelt-based growing season somewhat analogous to that of more typical VII grassland areas, in which a quasi-monsoonal mechanism brings the early-summer rainfall maximum. On the other hand, the dry rain-shadow climate on the east side of the Patagonian Andes has a much narrower, less continental temperature range, due to the oceanic effect on the narrow land mass. In this case, the apparent self-contradiction between dryness and cool, maritime influence is denoted by subscript ‘m’ for the less arid Maritime Steppe (VIIm) climate and by ‘x’ for the more extreme Maritime Arid climate (VIIx).

Boreal climates are inherently continental, but one can also recognize an even more Ultra-Continental Boreal (VIIIc) climate in the coldest parts of interior northeastern Siberia, where mean winter temperatures may be below −30 °C and evergreen conifers are replaced by deciduous larches. The VIIIc climate is also drier than typical boreal climates, with average precipitation sometimes below 200 mm annually. Such areas usually have pleasantly warm, albeit short summers but winter extremes to around −70 °C. These areas are also underlain by permafrost, which effectively “rations” available groundwater to the usually open-woodland vegetation by means of its slow melting throughout the summer. On the other hand, winters are not as long and severe in coastal and island locations of boreal latitudes, such as Iceland, northern Norway and even coastal areas of Alaska. In this Maritime Boreal (VIIIm) climate, there is usually no permafrost, the potential growing season is a bit longer (even if cooler), and there is usually significantly more precipitation, much of it coming as rain rather than snow. In VIIIm climates, conifers are often replaced by short-summer deciduous trees such as birches. There is no boreal climate in the Southern Hemisphere, but the VIIIm climate does have a kind of Southern counterpart in the “austral” climate of the subpolar forest areas of New Zealand, Tasmania and southern South America.

Finally, one can also recognize a Maritime Polar (IXm) climate in which winters are less severe (with no permafrost) but summers are only slightly above freezing. Such situations occur on both isolated, oceanic subantarctic islands (e.g. Falklands, South Georgia, Macquarie, and even Kerguelen) and on northern islands such as the Aleutians and Kurils. Temperature ranges are quite narrow, but the resulting stenothermal growing seasons are relatively long and can have surprisingly high biological productivity. Permanently frozen Icecap (IXf) climates have been of less interest but will be reduced significantly with global warming, exposing large amounts of buried soil carbon.

Among the main climate types, only the Marine West-Coast climate (Vm) has no subtypes, although it is involved in the Island Warm-Temperate variant (V), which combines some attributes of both east-side and west-side situations. Mediterranean, Typical Temperate and Boreal climates have both maritime and (more) continental subtypes. Tropical Wet-Dry, Subtropical Arid and Polar climates have maritime subtypes only, while the Equatorial has only a drier subtype. Temperate Continental has both maritime and drier subtypes, but the latter is often due more to rain shadows than to greater distance from the ocean.

Zonal Climates, Soils and Vegetation

Apart from the always-cold polar climates, the different climate types can be grouped into broader classes based on their patterns of wet and dry seasons. This grouping (below) provides a basis for interpreting zonal soil and vegetation types.

Wet Climates (no dry season)	FOREST landscapes (cf. montane, subalpine)
Circulational	I, Vm
Positional	Ve, VI
Latitudinal	VIII
Dry Climates (no wet season)	DESERT (or semi-desert) landscapes
Circulational	III
Positional	VIIa (VIIx)
Wet/Dry Climates (wet and dry seasons)	Landscape GRADIENTS, based on total rainfall
Circulational	II, IV (Ia)
Positional	VII (VIIm)
Cold Climate	DWARF vegetation (tundra; cf alpine)
Latitudinal	IX (IXm)

In this scheme, the term ‘circulational’ refers to types resulting directly from global atmospheric circulation; ‘positional’ refers to types resulting largely from their geographic position (i.e. relative position on a land mass); and ‘latitudinal’ refers to the boreal and polar climates that result mainly from their high latitude, low sun angle, low solar energy input, and short, cool growing seasons. The wet/dry climates are especially interesting, since they present broad gradients of total precipitation and growing-season length.

The idea that natural soil types correspond to the main climatic zones and can also be called *zonal* appeared in the Russian literature at least as early as Dokuchayev (1899, 1900). For example, the zonal soil of the equatorial climate is a deep, extremely leached, nutrient-poor tropical latisol, while the zonal soil of a boreal climate is a stratified podzol. Similarly, the zonal soil of typical temperate climates is a moderately humus-rich ‘brown forest soil’, while the zonal soil of temperate continental climates ranges from deep, quite humus-rich chernozems (black earths) on the wetter side of these regions to shallower, lighter, tan soils on the drier side. It is not possible to treat zonal soils in detail here, but please refer to Lang (1915), Jenny (1929), and Dokuchayev (1948).

The idea of zonal vegetation types also appeared early (e.g. Grisebach 1872) and was formalized by Walter (1954). Zonal vegetation is the expected natural vegetation in a particular climate zone, on sites with “normal” topography and soil (called ‘eu-climatopes’) that permit full expression of the climatic potential (Walter 1954, 1977; Walter and Box 1976; cf. Box 2002; Box and Fujiwara 2013). Zonal vegetation types for the different climate zones are shown in Table 4 and are discussed below, along with some ideas on the zonal vegetation of climatic subzones. In zones with wide ranges of total precipitation (climates II and IV), there may be a range of zonal vegetation types, from forest at the wet end of the range to shorter, open vegetation at the dry end. Regional occurrences of zonal vegetation, including subzones, are shown in more detail in the Appendix.

The natural biotic response to the five wet climate types (no dry season), plus the V hybrid, is forest, at least at maturity. The forests of these main zones are evergreen except for the deciduous forests of typical temperate (VI) climates and the larch woods of the ultra-continental boreal climate (VIIIc) of central and eastern Siberia. The forests of northern New Zealand (V) are ‘cool-temperate laurel forests’ and have no trouble being evergreen, despite the cool summers, as long as winter temperatures are not limiting. On the other hand, the boreal (conifer) forest is mainly evergreen, despite severe winters, because of the ability of conifers to go dormant in winter, recover quickly from dormancy, and thus use the entire short growing season. Even so, in the Ultra-Continental Boreal climate (VIIIc) of the coldest parts of interior northeastern Siberia, mean temperatures may be below −30 °C and extremes have reached −70 °C. Conifers still dominate, but the evergreen conifers are replaced by deciduous *Larix* (larch), usually in rather open stands with dense lichen ground covers. In Maritime Boreal climates (VIIIm), on the other hand, conifers are often replaced completely by short-summer deciduous trees such as birches (*Betula*), willows (*Salix*) and alders (*Alnus*), as in Iceland, northern Norway, and parts of Alaska. Although there is no real Boreal counterpart in the Southern Hemisphere, these more maritime high-latitude forests do have “austral” counterparts in the more southern (or upland) *Nothofagus* forests of New Zealand and Tasmania (evergreen only) and of southern South America (evergreen and deciduous species, rarely mixed).

The two main wet/dry climates present a wide range of potential vegetation and landscapes, depending on total precipitation and the relative lengths of the wet and dry seasons. In the Tropical Wet-Dry (II) region, for example, zonal vegetation ranges from Moist Deciduous Forest at the wet end, though shorter Dry Deciduous Forest/Woodland, to raingreen Thorn Scrub and Savanna. These last two may both occur zonally in the II-III transition, but there are some climatic and topographic affinities. Scrub occurs more on rougher terrain and where precipitation is less reliable, since the deeper-rooted woody plants can still get soil water there. Savanna tends to occur more on gentler terrain with finer-textured soils and where the rainy season is more reliable. Even so, both may occur on patchy topographies, and both now occur far outside their original locations, as degradation forms where more robust woody vegetation has been destroyed. Vegetation types along a climatic gradient spanning climates I and II were shown quite early by Beard (1944), along with some edaphic gradients.

A similar pattern is seen in Mediterranean (IV) regions, where zonal vegetation runs from Sclerophyll Forest at the wet end, through Sclerophyll Scrub (maquis, chaparral, etc.), to dwarf scrub that may be evergreen (e.g. Australia) or mainly summer-deciduous (e.g. California)—and may also occur extensively as a degradation form (garrigue). Evergreen sclerophylls are a consistent response to the combination of short spring growing seasons followed by dry summers, as long as the woody plants involved have root systems that can obtain some soil water during the summer. Even so, the case has been made for deciduous vegetation as "natural" in some mediterranean-type situations (Blumler 1991, 2014) and for marcescence as an adaptation by summergreen deciduous trees to the transitional submediterranean conditions (Abadía et al. 1996; Sánchez de Dios et al. 2009; García et al. 2014). Vegetation may also become more deciduous in drier, more inland Interior Mediterranean (IVc) areas, with their colder winters. This is seen in the "deciduous chaparral" of montane belts in the Great Basin of western USA and in parts of Iraq, Iran and Turkey (cf. Blumler and Plummer 2014).

For the two arid climates (III and VIIa, with no wet season) the zonal vegetation is of course semi-desert or desert. The zonal vegetation of polar (IX) climates is treeless tundra, which can however be mainly grassy or have small shrubs where the growing season is longer. The shrubs may be smaller versions of boreal tree species, other species in the same genera (mainly *Betula*, *Alnus* and *Salix*), or in some cases evergreen shrubs from genera such as *Rhododendron*.

The main climates of the mid-latitudes (Ve, VI and VII) often change only gradually over long distances, and vegetation can become more important in delimiting them. For potential forest (Ve and VI) versus non-forest (VII), it seems reasonable to recognize the transition ("boundary") where the moisture-balance gradient is changing most rapidly. In North America this sharper gradient occurs along a (north-south) line from western Minnesota, through western Iowa and easternmost Kansas, and then a bit further west in eastern Oklahoma and Texas. In East Asia the gradient occurs relatively close to the coast in northern and eastern China, with Beijing in the subhumid transition region. In Europe, on the other hand, the transition occurs mainly southward (especially in Ukraine, see Walter 1974) as potential evaporation surpasses decreasing precipitation (cf. Walter 1968, p. 677).

The zonal vegetation of the Temperate Continental (VII) regions is grassland, because the warm season is not wet long enough to permit trees to produce viable fruit, except along streams and on other favorable sites. There is, though, a distinct gradient from tall prairie or meadow-steppe on the wetter side (VII-VI) to shorter, more open steppes (VII) and even 'desert grasslands' (VII-VIIa) in places like New Mexico, Kazakhstan, and southern Mongolia. In North America, tall grassland extended farther east (VI-VII), across Illinois and into western Indiana, but was probably a result of recurrent fire, natural and anthropogenic.

For the warm-temperate zone (Ve), the zonal vegetation is evergreen broad-leaved forest, as occurs (or occurred) in southern China and southern Japan, in southern Brazil, and parts of eastern Australia and New Zealand. In the southeastern USA, the zonal Ve vegetation occurs only in more humid topographic situations, due to the prevalence of rapidly draining sand substrates and the sharp vertical gradient between dryness and high groundwater on the low-lying topography (Fujiwara and Box 1994; cf. Christensen 1988; Wells 1942). For extra-tropical evergreen broad-leaved trees, absolute minima below about −15 °C appear to be a more important limitation than mean winter cold (Woodward 1987; Box 1995). The importance of such extremes can be seen, for example, in the inadequacy of mean temperature in delimiting regions of deciduous versus evergreen broad-leaved forest at corresponding locations in East Asia and eastern North America. The −15 °C isotherm for absolute minimum temperature would place the Ve-VI transition in eastern North America roughly at the boundary of the southeastern coastal plain (Box 1988; cf. Greller 1989), where the transition from deciduous to at least partly evergreen broad-leaved forest actually does occur. This is much further south than on the many Köppen-based maps, which are based on mean temperatures. The zonal vegetation of drier, more inland warm-temperate areas (climate Vc) is shorter and more open but still woody and mainly evergreen (despite somewhat lower winter extreme temperatures), as in the live oak (*Quercus virginiana*) woodlands of central Texas, the more evergreen areas (with *Schinopsis quebracho-colorado*, *Aspidosperma quebracho-blanco*, etc.) of the eastern Chaco in northeastern Argentina), and perhaps large areas of sclerophyll woodland in interior Australia, involving many different *Eucalyptus* species.

The zonal vegetation of the typical temperate zone (VI), with its colder winters, is deciduous (summergreen) forest, as occurs across large areas of eastern North America, northern Japan, most of Korea, parts of northern China and into Russian Manchuria, and in much of western to eastern Europe. There are, however, some subtle differences. Mean winter temperatures in eastern North America are consistently higher but extremes are lower than at comparable locations in East Asia (Box 1995). Furthermore, the piedmont of southeastern North America has no lasting snow cover (night-time minima usually slightly above freezing), and temperatures below −15 °C come only infrequently (but reliably). The result of the infrequent extreme minima is deciduous forest, at latitudes (and geographic position) where East Asia has evergreen broad-leaved forest. Tatsuō Kira (1949) recognized a similar situation in East Asia and proposed the term ‘warm-temperate deciduous forest’ for deciduous forests that occur in areas that appear otherwise to be warm enough for evergreen (broad-leaved) forest. In Europe, the richer deciduous forests in warmer southern areas are often called ‘thermophilous’ (e.g. Čarni et al. 2009) or ‘submediterranean’ (e.g. Meusel and Jäger 1989), although summer temperatures in these areas are not as high as in East Asia or eastern North America. This concept of ‘warm-temperate deciduous forests’ in the VI-Ve (or even Ve-VI) transition was explored recently in a book (Box and Fujiwara 2014), which includes a world map of potential humid-temperate forest zones (Box 2014a). In mainland East Asia the monsoon system provides an additional factor, assuring that autumn, winter and spring are dry. The zonal vegetation of the resulting Monsoon Temperate (VIc) climate is still deciduous forest, but with a greater role for trees that complete their reproductive cycles more quickly, such as *Populus* and *Betula*.

The climates and zonal vegetation of humid continental east sides have been treated, within a global context, by Kira (1945, 1977, 1991), Wolfe (1979), Box (1995), Box and Choi (2003), Kolbek et al. (2003), and Box and Fujiwara (2012, 2013, 2014), among others. A special warning is needed, though, for the terminology used in China, where the national zonation scheme focuses on growing seasons and not the climate of the whole year (see summary by Fang et al. 2002). This system was developed in the 1950s (see Physical Regionalization Committee 1958–59; cf. China Natural Geography Editorial Committee 1984), influenced by the northern perspective of the Russian system of that time (e.g. Alisov 1956). The Chinese system includes zones called *liáng wên* (凉 温, = cool-warm) and *nuăn wên* (暖温, = warm-warm), and is not necessarily bad for what it was intended to do. The problem comes when *liáng wên* is translated as 'cool-temperate' and used for the zone of boreal conifer forests, and *nuăn wên* is called 'warm-temperate' and applied to the zone of temperate deciduous forests (e.g. Zhao 1986). This latter includes much of interior Chinese Manchuria, where January mean temperatures are around −20 °C and extremes drop annually to around −35 °C. There is nothing "warm" about this winter, and it is not the mild winter required for any reasonable concept of warm-temperate; it may not even seem very "temperate" at all, although summers are quite warm. Furthermore, the northernmost Chinese zone of evergreen broad-leaved forests, involving largely Fagaceae and other taxa of mainly temperate affinities, is already called "subtropical". Although this zonation may be useful in China, especially for agricultural purposes, its uses of basic terms are misleading and invalid in a global context (cf. Box 1995; Box and Choi 2003; Box and Fujiwara 2013).

As this chapter is being written, one is also hearing constantly about the Winter Olympics in "subtropical Sochi" along the Russian Black Sea coast. As of mid-2013, extreme low temperature in Sochi had reached −15 °C, over a measurement period of 111 years (from www.climatebase.ru). For Yalta, on the south coast of the Crimea, Walter (1974, p. 363) gave the absolute minimum as −14.5 °C, which may represent measurement over at least 62 years (see www.climatebase.ru). Thus, neither of these locations is "subtropical", and they are barely even warm-temperate, although palm trees and common mediterranean plants (e.g. *Sparteum junceum*) may develop well between extreme-cold events, along a narrow coastal strip.

One problem is clear: climatic terms are used very loosely, for local consumption, and with little consideration for global consistency. For zonal as well as other vegetation, it is also clear that the relationship between potential vegetation and climate is complicated—although not impossible to discern. For vegetation that is determined mainly by climatic conditions, there is a place for everything within an adequate global bioclimatic zonation system. Even so, the zonal vegetation types shown in Table 4 answer only some questions. Some other "natural" vegetation types and climatic exceptions to the global zonation scheme are treated in the next section and shown in the Appendix.

Exceptions to the Expected Zonation

Due mainly to the shapes of the world's land masses, there are some areas that do not follow the rules of the global zonation pattern suggested on the Ideal Continent (Fig. 1). Most of these were recognized as "problem climates" by Trewartha (1961,

Table 6 Main exceptions to regular global climatic zonation

Region	Latitude	Phenomenon	Resulting climatic conditions
Northern Scandinavia, especially Norway	55–70° N	Much milder winter than normal at such high latitudes, due to the warm Gulf Stream ocean current	No true boreal climate except well inland; instead: cool boreo-nemoral climate (VIm-VIIIm) with birch instead of conifer forests
Somalia to N Tanzania	15° N–10° S	Less precipitation in normally wet latitudes, due to coast orientation, high altitude and interaction of the Asian and African monsoons	No everwet equatorial climate (I); instead: dry-equatorial climate (Ia) with equinoctial rainfall and dry seasons near the solstices
Northern South America including Southern Antilles	15–5° N	Less precipitation in normally wet latitudes, due to coast orientation, consequent upwelling and cooler sea surface; less ITC influence	No wet equatorial climate (I); instead: Wet/dry (II) climate over most of Venezuela Desert-like climates (Ia) on Aruba and other S-Caribbean islands
West coast of South America, especially Peru	5–30° S	Lack of precipitation in normally wet/dry latitudes, due to atmosphere stabilization by the cold Humboldt ocean current	Extension of subtropical arid climate to southern Ecuador, albeit as cool fog desert (IIIm)
Eastern Patagonia and pampa region	30–50° S	Unusual lack of precipitation in normally humid latitudes, due to Andes rain shadow wider E-W than the continent	No humid temperate climate (VI) on/near mid-latitude east coast; instead: maritime dry-temperate climate (VIIx)

"Problem climates" were recognized and described by Trewartha (1961, 1981). Above are the most important of these exceptions, as compared with the normal zonation on an Ideal Continent (see Fig. 1). Roman numerals represent the (expanded) Walter climates (cf. Table 4) and some subtypes (see Table 5).

1981). Table 6 summarizes the five most important regions of disagreement, some of which were recognized already as climatic subtypes.

Three of these major discrepancies are in South America. In the north, trade winds along the east-west Venezuelan coastline produce upwelling and a cooler sea surface, reducing precipitation, especially during the high-sun period that would be the wet season. A further anomaly is that much of the rainfall occurs at night, when the coastal land-sea breezes blow offshore (Martis et al. 2002). The Azores segment of the subtropical high-pressure belt is also extended westward. As a result, islands of the southern Caribbean (Aruba, Bonaire, Curaçao) have a Dry Equatorial (Ia) climate, and most of Venezuela has a tropical summer-rain (II) climate, even in latitudes that approach the Equator (cf. Troll and Paffen 1964; Walter and Lieth 1960–67). Although the climate is somewhat out of place, the natural landscape of lowland Venezuela is largely a quasi-zonal wet-dry savanna (*llanos*), including areas of seasonal flooding and palm savannas (e.g. Hueck 1966, p. 389).

The west side of South America is oriented north-south and is quite straight from Tierra del Fuego (near 55° S) to southern Peru, then inclined north-northwestward to southern Ecuador (about 5° S). This shape produces the Peruvian (Humboldt) Current, the world's strongest cold ocean current, which brings cold, subantarctic water almost to the equator before it is shunted out into the Pacific Ocean. The cold ocean surface makes the atmosphere very stable along this entire stretch of the South American coast, preventing precipitation and permitting the cool version of a subtropical arid climate (IIIm) to extended northward, well beyond its zonal location, to southern Ecuador. As a result, the tropical summer-rain climate occurs only as part of a transition (from III through II to I) compressed into only five degrees of latitude along the coast of Ecuador. In the normal II position, the coast of Peru remains quite dry (about 30 mm annual precipitation in Lima)—except in El Niño years.

Southern South America (south of about 30° S) is in the belt of prevailing westerly winds for much of the year and would be expected to have typical humid temperate climates. It also, however, includes the wide rain shadow of the southern Andes, which extends past the narrow land mass and out into the Atlantic Ocean. As a result, although the west-coast zonation is normal, the only climate east of the Andes is a dry but maritime temperate climate, i.e. there is no VI climate. This dry but not really continental climate of Argentine Patagonia can be placed in the global system only as a maritime (VIIm) or arid-maritime (VIIx) variant of a temperate continental climate, in this case with a much narrower temperature range.

There is really only one other large area in the world that presents such a drastic departure from the expected zonation, and that is eastern Africa. Here, as in northern South America, rainfall is reduced by a combination of atmospheric circulation and the coastline orientation (north of the equator) (see Hastenrath et al. 2011). Wet air masses brought from the Arabian Sea by Trade Winds hit almost parallel to the coastline, thus receiving little lift (as needed for precipitation). During part of the year, this wet air may even go to Asia instead, due to the pull of the Asian monsoon system. The resulting Dry Equatorial (Ia) climate of southern Somalia, Kenya, and northern Tanzania (about 15° N to almost 10° S) has the bimodal precipitation pattern of an equatorial location, but the lows (near the solstices) become dry seasons. The two wet seasons are of similar length only near the equator; otherwise they represent the "long rains" and the "short rains". The zonal vegetation of this unusual wet-dry seasonality is generally a broad mosaic of savanna and scrub, with varying degrees of evergreenness in the woody component.

Finally, one more discrepancy is quite important for northern Europe. The shape of eastern North America propels the warm, northward-moving Gulf Stream northeastward across the Atlantic, where it keeps northwestern Europe less cold in winter than would be expected so far north. Even Murmansk on the White Sea coast of northern Russia remains ice-free for much of the winter, and coastal northern Norway has no true boreal climate at all but rather a 'maritime boreal' (VIIIm) climate similar to that of Iceland, parts of windward southern Alaska, and Tierra del Fuego. The mean January temperature at Tromsø, in a coastal fjord at 69° N, is no colder than about −5 °C, and natural landscapes in lowland northern Norway are mainly low birch woods rather than boreal conifer forest. See Tuhkanen (1984) for a summary of climatic conditions in Fenno-Scandia, as well as for further references.

These situations all represent exceptions to the expected zonation, but they also validate the system to some extent since each is an understandable aberration and can be represented in the system, either as a subtype or as an unusual extension of an adjacent type.

Transitions Between Zones

Climatic transitions are usually broad and gradual, unless there is a sharp surface discontinuity such as a land-water boundary or the crest of a mountain range. Even on flat terrain, steeper climatic gradients are often related to abrupt surface changes. For example, as one goes westward across the southeastern USA, precipitation suddenly decreases steeply in eastern Texas and Oklahoma as the source region for southerly winds changes from the Gulf of Mexico to the dry continental land mass of northern Mexico. With strong mid-latitude cyclones, this geography often results in an air-mass boundary called a “dryline”, along which squall lines and tornadoes are most frequent. Other relatively steep climatic gradients on flat terrain occur, for example, as one goes inland in eastern China (toward and beyond Beijing) and in Namibia and other areas with a cold offshore ocean current. Even so, the gradients involved extend over at least 100 km, so a transition region can be recognized. An exception is found in Manchuria, where the climate is so ultra-continental that areas with 4 warm months and temperate deciduous forests are truncated, patchily but abruptly, with no transition, by the sudden appearance of permafrost where mean annual temperature falls below about −1 °C (cf. Box et al. 2001).

Transitions between climate types are represented, as Walter did, by pairing the Roman numerals of the adjacent types involved. These climatic transitions also involve transitions in natural vegetation, which Walter (1976) called zono-ecotones (cf. Walter and Box 1976). The transitions between adjacent main climate types and their corresponding landscapes are summarized in Table 7. One can also denote finer distinctions by the order of the Roman numerals, not only different climatic situations but also different potential landscape or vegetation types. For example, the transition from equatorial to tropical summer-rain climate involves forests grading from more evergreen to more deciduous. Tropical seasonal evergreen and tropical semi-evergreen forests are commonly recognized variants of humid tropical forest along this gradient of increasing dry season (cf. Beard 1944, 1955; Richards 1952; Whitmore 1975). These can be seen as corresponding to transition subzones I-II (seasonal evergreen) and II-I (semi-evergreen). Similarly, in the transition from nemoral (VI) to mediterranean (IV) climates in southern Europe,

Table 7 Main transitional climates, locations, distinctness and landscapes

Transition	Locations	Sides	Distinguishing feature(s)	Landscapes
I-II	TRF margins	I-II	Wet with short dry period	Tropical seasonal evergreen forests
		II-I	Wet but 2–3 months dry	Tropical semi-evergreen forests
I-III	Somalia to N Kenya	I-III	Bimodal precipitation (cf. Ia)	Equatorial semi-deserts
		III-I	More unimodal precipitation	Tropical semi-deserts and deserts
I-Ve	SE Asia	I-Ve	Essentially frost-free	Subtropical rainforests
		Ve-I	Light frost possible	Subtropical laurel forests
II-III	Sub-Sahara	II-III	Dry longer than wet	Savanna (with trees)
		III-II	Sparse summer rain	Shrub or other drier savanna
II-Ve	S China	II-Ve	Essentially frost-free	Subtropical monsoon forests
		Ve-II	Occasional light frost	Subtropical laurel forests
II-VII	Argentina, S Texas	II-VII	Mostly frost-free	Shrub savannas (e.g. *Prosopis*)
		VII-II	Warm but significant frost	Subtropical grasslands
III-IV	N Sahara margin	III-IV	Sparse winter rain	Semi-desert shrub steppe
		IV-III	Short spring GS	Garrigue, coastal sage (kwongan if rain irregular)
III-VIIa	Upland W USA (e.g. Las Vegas?)	III-VIIa	Occasional frost	Warm-temp. deserts with few tall succulents
		VIIa-III	More frost	Warm-temp. deserts with no tall succulents
IV-Ve	S coasts of S Africa and SE Australia	IV-Ve	Moderate summer drought	More sclerophyllous EG-BL forests
		Ve-IV	Fairly even seasonal precipitation	EG-BL forests with some laurophylls
IV-Vm	Northern California, SW Australia karri	IV-Vm	Moderate summer drought (< IVm)	Tall sclerophyll forests
		Vm-IV	Less summer drought	Tall, more mixed evergreen forests
IV-VI	Southern Europe (esp. western)	IV-VI	Less summer precipitation	Mediterranean deciduous forests
		VI-IV	More summer precipitation	Submediterranean deciduous forests
Ve-VI	Interior SE USA	Ve-VI	Occasional T just below −15 °C	Warm-temp. decid. forests with EG elements
		VI-Ve	More frequent, lower temperatures	Warm-temp. decid. forests, mostly deciduous

(continued)

Table 7 (continued)

Transition	Locations	Sides	Distinguishing feature(s)	Landscapes
Ve-VII	Central Texas, Australia	Ve-VII	Too dry for closed forest (cf. Vc?)	Warm-temperate evergreen woodlands
		VII-Ve	Too dry for forest at all	Warm-temperate evergreen scrub
VI-VII	E prairie margin, across S Russia	VI-VII	GS marginal for woods (cf. VIc)	Temperate savanna
		VII-VI	GS marginal for trees	Tall-grass prairie, forest steppe, meadow steppe
VI-VIII	NE USA–SE Canada, Manchuria	VI-VIII	Cool, short summer (cf. VIm)	Cool-temperate mixed forest
		VIII-VI	GS marginal for temperate trees	Sub-boreal mixed forest, with more boreal conifers
Vm-VI	NW Europe, NW USA	Vm-VI	Milder winter (Tmin, Tabmin)	Cool-temperate deciduous forest
		VI-Vm	Colder winter (Tmin, Tabmin)	Cool-temperate deciduous forest
Vm-VIII	Lower slopes of windward Brit. Col.	Vm-VIII	VIIIm is deciduous	Sub-boreal coniferous rainforest
		VIII-Vm	Colder winter, shorter GS	Boreal coniferous rainforest
Vm-IX	S Chile to Tierra del Fuego	Vm-IX	Very cool-oceanic (Tabmin > -15 °C)	Subpolar rainforest (evergreen)
		IX-Vm	GS marginal for EG-BL trees	Subpolar evergreen BL woods (short)
VI-IX	Tierra del Fuego	VI-IX	VIm: winter not as cold	Subpolar deciduous BL forest
		IX-VI	GS marginal for BL trees	Subpolar deciduous BL woods (short)
VII-VIII	Canadian and Russian prairie margins	VII-VIII	Water marginal for trees	Grove belts: aspen, Mongolian oak
		VIII-VII	Water marginal for conifers	Aspen woodlands with conifers
VIII-IX	Subpolar N America and Siberia	VIII-IX	Summer somewhat warmer	Open forest-tundra woodlands
		IX-VIII	GS marginal for NL trees	Sparse woodland-tundra transition

Roman numerals denote the basic (expanded) climate types, based on Walter (see Fig. 1, Table 4). Each transition is shown with two "sides" represented by the two possible different orderings of the Roman numerals (e.g. I-II vs. II-I)

BL = broad-leaved, *NL* = needle-leaved, *EG* = evergreen, *GS* = growing season, *Tmin* = mean temperature of the coldest month, *Tabmin* = absolute minimum temperature

one can distinguish 'submediterranean' deciduous forests (VI-IV) with more precipitation and more typically nemoral summergreen tree species from more truly mediterranean deciduous forests (IV-VI) with less precipitation, drier summers, and more pronounced dominance by more xeromorphic deciduous taxa such as *Quercus*. A distinction may also be made in places like southern China between subtropical monsoon forests with more deciduous taxa, occurring where winter is drier (II-Ve), versus subtropical laurel forests that are still overwhelmingly evergreen where the seasonally drier winters receive somewhat more precipitation (Ve-II). This is perhaps especially useful since the Walter system did not distinguish a “humid subtropical” climate (very occasional, very light frost) as distinct from a (humid) warm-temperate climate with light to modest frost in most years. In southern China such a difference is significant for the flora, if not for the dominant evergreen broad-leaved physiognomy.

Not all transitions can be treated here, but Table 7 provides some basic logic. In continental areas, almost all of the adjacent climate pairs in Fig. 1 show clear transition regions. In maritime areas of continental west sides, however, the boreal climate may almost disappear, even in its maritime form, as the windward oceanic Marine West-Coast (Vm) climate grades slowly poleward, with decreasing summer temperatures, into the Maritime Polar (IXm) climate. As a result, the Southern Hemisphere has no true boreal climate and perhaps not even a Maritime Boreal VIIIm climate in its Northern form. Instead, the Valdivian rainforest climate (Vm) grades through areas of deciduous *Nothofagus* woods (perhaps VIm-IXm) into maritime polar (IXm) on the subantarctic islands. Especially interesting is the area around Ushuaia (south coast of Argentine Tierra del Fuego), where evergreen (broad-leaved) *Nothofagus betuloides* forest occurs at mean warm-month (January) temperature of only about 9.5 °C and mean winter temperature just slightly above freezing.

Upland Climates and Belts

All global climate classifications are based, at least tacitly, on relationships in lowlands. Uplands, on the other hand, are typically cooler, often cloudier and windier, generally more humid, and receive more precipitation (at least up to the cloud layer). Higher elevations receive more intense solar radiation, which causes them to heat and cool faster than in the lowlands, especially near the surface. In mountains, the ground surface is also usually rougher (rockier) and more inclined, and both of these features increase upward. As a result, soils are shallower, patchier, and more rapidly drained than in the lowlands. Finally, uplands generally have more equitable daylength regimes than their lowland analogs, which are at higher latitudes.

Uplands can often be separated from lowlands by topographic “breaks”, such as foothills or escarpments, where elevation increases more rapidly than elsewhere. Climatic delimitation of uplands is more difficult but could involve some of the phenomena in the preceding paragraph. In particular, uplands can be seen as beginning, climatically, where gradients of temperature decrease or water-balance amelioration show significant thresholds or are steeper than elsewhere. Uplands may also involve an atmospheric inversion layer, as on islands (e.g. Tenerife) and along coastlines with cold offshore ocean currents that produce relatively permanent fog. Lowlands may include piedmont terrain, even low foothills and lower tablelands (e.g. Australia, Iberian Peninsula), but not montane belts or higher, where landscapes are clearly different. Inclusion of upland zonation in a global system first requires identification of the lowland climate zone or zones within which the particular upland rises (cf. Walter 1976). Walter used X to denote mountain climates in general, so mountain climates in a Temperate Continental climate, for example, could be denoted X(VII). Beyond the separation of uplands from lowlands, though, further upland zonation requires delimitation of the different altitudinal belts, which are normally recognized by differences in vegetation. The region above treeline, up to the line of more or less permanent snow (if the mountains are high enough), is normally called the alpine belt and has treeless vegetation somewhat analogous to polar landscapes. The first belt below treeline (or dry-climate equivalent) is the subalpine belt, and the first quite different landscape up from the lowland, such as woodland occurring above grassland, is called the montane belt. For example, in the VII climate of the central Rocky Mountains in Colorado:

- the montane belt (above short-grass steppe) is dry pine forest (mainly *Pinus ponderosa*);
- the subalpine belt is a less-dry, mainly non-pine conifer forest (mainly *Picea* and *Pseudotsuga*); and
- the alpine belt is dry alpine “tundra” dominated by *Kobresia* at maturity.

In middle and higher latitudes, conditions and vegetation in subalpine belts may be somewhat similar to the lowland boreal (VIII) zone; humid montane belts may have mixed or deciduous forests similar to those in the nemoral-boreal (VI-VIII) transition zone.

Bioclimatic belts normally occur at higher elevation in more continental areas (*Massenerhebung* effect), since belts (outside the tropics) are determined largely by summer temperatures. Outside the tropics, treeline and the beginning of the alpine belt (ignoring local topography) may occur near a 10 °C isotherm for mean temperature of the warmest month, as for polar treeline. This threshold may be lower in more oceanic areas. In the tropics the critical factor may be mean soil temperature, perhaps a 0 °C isotherm (which varies less over a year than in higher latitudes). On the other hand, the montane and subalpine belts seem to be distinguished more by water-balance factors, such as the degree of soil dryness in summer or the occurrence and relative elevation (above mountain base) of a cloud belt. Some of these climatic characteristics for the different altitudinal belts, in the different climate zones, are suggested in Table 8.

Finally, topography and other substrate factors would probably confound any attempt to identify any regular pattern of zonal soil types in mountains. Since altitudinal belts are recognized mainly by vegetation, though, an attempt was also made in Table 8 to identify the zonal vegetation types of the altitudinal belts in the main climate zones. In a tropical summer-rain (II) climate, for example, the

Table 8 Zonal bioclimatic belts and corresponding vegetation in mountain areas

Zone	Belts	Temperatures	Water balance (GS)	Zonal vegetation
I	Alpine	>0 °C daytime, frost at night	No dry season	Páramo scrub, with tuft treelets
	(Dry subalpine)	(Frost or near frost at night)	(Drier than cloud belt)	(Transitional scrub)
	Cloud belt	Cool but above freezing	Wet: persistent cloudiness	Cloud forest: short, stunted, many epiphytes
	Montane	Cooler than lowland	Wetter than lowland	Montane rainforest: tall but fewer epiphytes
II	Alpine	>0 °C daytime, frost at night	Wet and dry seasons	Moist puna grassland: often large tussocks
	Subalpine	Cool, frost/near frost at night	Dry season disappearing	Low, generally evergreen subalpine forest
	Montane	Cooler than lowland	Moderated dry season	Raingreen to semi-evergreen forest
II-III			Dry season still significant	Montane to subalpine grassland
III	Alpine/ subalpine	>0 °C daytime, frost at night	Dry all year	Dry puna grassland: bunchgrass steppe
	Montane	Cooler, seasonally cold	Slightly more rainfall	Semi-desert scrub, succulents often common
IV	Alpine	Seasonally cool/cold	Dry summer persists	Thorn scrub, cushion forms common
	(Subalpine)	(Seasonally warmer/ cold)	(Dry summer persists)	(More mesic conifer woods/ forest)
	Montane	Seasonally warmer/ cold	Dry summer persists	Dry conifer forest/woods, especially pines
IV-Vm			Moderately dry summer	Giant foothill/montane forests (e.g. redwoods)
Vm	Alpine	Very cool summer, winter frost	Very wet	Wet alpine tundra
	Subalpine/ montane	Cool summer, winter frost	Very wet	Montane rainforest
Ve	Alpine	Very cool summer, winter frost	Wet, especially in summer	Moist alpine tundra
	Subalpine	Cool summer, winter frost	Generally wet	Mostly evergreen mixed forest (BL + NL)
	Montane	Moderated summer and winter	Frequent rainfall	Montane laurel forest: often smaller leaves
VI	Alpine	Very cool summer, quite cold winter	Generally moist	Alpine tundra
	Subalpine	Cool summer, cold winter	Generally moist	Conifer forest, with “boreal” species
	Montane	Moderated summer, cold winter	Generally moist	Mixed forest: BL-decid + conifers, incl. temperate

(continued)

Table 8 (continued)

Zone	Belts	Temperatures	Water balance (GS)	Zonal vegetation
VII	Alpine	Very cool summer, severe winter	Somewhat subhumid	Dry alpine tundra: often “grassier”
	Subalpine	Cool summer, quite cold winter	Generally subhumid	Conifer forests, mainly with boreal-like species
	Montane	Moderated summer, cold winter	Still somewhat subhumid	Dry conifer forests/woods: especially with pines
VIII	Alpine (“montane”)	Very cool, polar-like; severe winter	Generally moist	Polar-like tundra but with more dwarf shrubs
IX	Subnival	Very short, cold summer	Persisting snowmelt	Snow-valley herbs; moss-lichen cold-desert

Roman numerals denote the main climate types, based on Walter (1970, 1977) and expanded (see Fig. 1, Table 4; cf. Box and Fujiwara 2013). The altitudinal belts in mountains are distinguished mainly by their different vegetation types, as determined by climatic conditions. The alpine belt is above treeline, subalpine is at and just below treeline, and montane represents belts above and different from the zonal lowland vegetation

BL = broad-leaved, *NL* = needle-leaved, *decid* = deciduous, *EG* = evergreen, *GS* = growing season

montane belt is usually a denser but still at least partly deciduous woodland or forest, occurring where the dry season is already ameliorated relative to the adjacent lowland. The subalpine belt may be semi-evergreen forest—or evergreen (laurophyll) if the montane belt is already semi-evergreen. The alpine belt is usually a bunch or tussock grassland, called ‘puna’ in South America (cf. Walter 1973). A somewhat analogous pattern of dry-season amelioration was described for mediterranean (IV) climates, but with the added factor of growing-season truncation by frost (Miller and Hajek 1981). More description of the zonal vegetation of altitudinal belts in the main climate zones was also given by Box (2014b).

Applications

Genetic climate types and global climatic zonation are useful concepts for both research and teaching. Among other things, types tied to atmospheric mechanisms are more intuitive than empirical types (e.g. Köppen) and can be learned more easily. After only 2–3 weeks of study, even first-year students at the University of Georgia can select locations at random on a world map, look at the latitude and geographic position (relative position on a land mass), and reason out the climate type by using a mental image of the Ideal Continent. More specifically, the enhanced genetic system presented here is useful and preferable to other systems because it:

- has fewer main types and can thus be learned and communicated more easily
- links climate types more directly and intuitively to causative dynamic mechanisms

- has a flexible and more general set of subtype descriptors
- unifies some climatic concepts better, especially in temperate latitudes, and
- matches natural soil, vegetation and landscapes better.

This system, based on Walter but expanded, thus provides a geographic framework for identifying, teaching and understanding world climates, soils and natural vegetation types within a single globally consistent system. It also provides a basis for recognizing and explaning exceptions to the general global zonation pattern.

Mechanism-based genetic climate systems will also be more robust under global climate change than are quantitatively delimited types based empirically on recent climate. In particular, a genetic system of bioclimates is more flexible under climate change because:

- it has no empirically estimated limiting temperatures or precipitation-temperature ratios, which may become invalid under different temperature levels and geographies;
- the zones and regions in a genetic system shift automatically with shifting rainfall patterns, low temperatures and seasonal durations; and
- boundaries remain tied to limitation mechanisms that have biological significance and thus are expressed in natural vegetation and landscape potentials.

For example, southern portions of boreal (VIII) climates may become typical temperate (VI) with global warming, not because some threshold summer temperature was passed but rather due to longer duration of the summer warmth needed for temperate-zone trees.

A complete global bioclimatic system, including zonal vegetation types and biomes, also provides a basis for geographic validation of global or other large-area geographic models (cf. Box and Meentemeyer 1991)—most of which are never validated geographically if at all. To this end, a list of the main biome occurrences resulting from bioclimatic zonation is given in the Appendix and is summarized in Table 9. This geographic inventory produces 26 basic zonal vegetation types, such as tropical savanna or boreal larch woods, and a total of 126 occurrences as regional biomes or vegetation formations. Complete geographic validation of global models would use this as a checklist, testing the particular model in each zone and regional occurrence.

Finally there is the question of whether a system of conceptually based climate types can be quantified, as would be necessary for mapping and modeling. One possible approach to quantification was suggested by the system of Lauer and Rafiqpoor (2002), based on the lengths of the warm, wet and dry periods of the year. To these quantitative descriptors one could add significant values for other phenomena, such as the cardinal temperatures that represent apparent physiological limits for various plant types. An initial attempt, for the most typical expression of the main climate types in lowlands only, was given by Box and Fujiwara (2013). More general estimates of climatic limits, expressed in a quasi-envelope format, are shown in Table 10.

Table 9 Numbers of regional occurrences of the main zonal climates and biomes

Climate type		Biome types	Biomes	Macro-regions	No. of main regions
Equatorial	I	1	Humid tropical forests	4	12
Tropical summer-rain	II	3	Moist raingreen forest	2	3
			Dry raingreen forest/woods	4	13
			Semi-EG/raingreen scrub	3	3
Short-rain	II-III	1	Savanna	4	8
Tropical mountains			Rainforest, cloud forest, laurel forest, semi-evergreen forest, alpine scrub, alpine grassland	4	
Subtropical arid	III	3	Semi-deserts with arborescents	3	4
			Semi-desert scrub/steppe	4	6
			Extreme arid deserts	4	5
Maritime	IIIm	1	Cool subtropical deserts	2	2
Mediterranean	IV	3	Sclerophyll forest	4	4
			Maquis/chaparral scrub	4	6
			Microphyll dwarf scrub	4	8
Mediterr. mountains			Conifer, hard-cushion scrub	4	
Submediterranean	IV-Vm	1	Tall sclerophyll forests	2	2
Marine West-Coast	Vm	1	Temperate rainforests	3	4
Warm-temperate	Ve	1	Temperate BL-EG forests	4	7
Typical temperate	VI	1	Temperate deciduous forests	3	5
Temperate continental	VII	1	Temperate grasslands/steppe	3	8
Temperate arid	VIIa	2	Cold semi-desert with trees	1	1
			Cold-winter semi-desert/desert	2	7
Boreal	VIII	2	Boreal conifer forest (evergreen)	2	2
			Boreal larch forest/woods	1	1
Maritime subpolar	VIIIm	1	Subpolar birchwoods	2	5
	Vm-IX	1	Subpolar *Nothofagus* woods	1	1
Polar	IX	2	Tundra	3	3
			Moss-lichen cold deserts	3	3
Maritime	IXm	1	Maritime tundra	3	3
	Totals	26			126

Regions are counted as occurrences within four basic macro-regions: the Americas, Africa, Eurasia and Australia-New Zealand-Antarctica. Far-northern and far-southern regions in the Americas were counted separately. Global and other large-area ecological models are inherently *geographic* models and should be evaluated geographically (cf. Box and Meentemeyer 1991), i.e. in a stratified manner, by such ecologically distinct geographic regions as shown here. The actual occurrences of the biomes are shown in the Appendix, within this same geographic framework. Roman numerals denote the main climate types (cf. Fig. 1, Table 4), and lower-case letters (except for Ve and Vm) denote climatic subtypes (see Table 5).

Table 10 Main quantitative limitations on the main world climate types (in lowlands)

		Numbers of months				Monthly temperature		Abs. Min. Temp. (°C)
		Warm	Wet	Dry	Summer/winter precipitation	Tmax (°C)	Tmin (°C)	
Wet climates								
Equatorial	I	12		≤1			≥18°	>5°
Warm-temperate	Ve	≥6		≤1	Usually >1	>19°	≥1°	>−15°
Typical-temperate	VI	≥4		≤2			<10°	<−15°
Marine West-Coast	Vm	4–10		<2	Usually <1	<15°	>−1°	
Boreal	VIII	1–3		≤1			<−1°	≪0°
Dry climates								
Subtropical arid	III		≤1				≥5°	>−5°
Temperate arid	VIIa		≤1				<7°	≪0°
Wet/dry climates								
Tropical wet/dry	II	≥10	≥2	≥2	≫1		≥13°	>−5°
Mediterranean	IV	≥6	≥3	≥3	<1		>1°	
Temp. continental	VII	≥4	≤4	≥4			<10°	<0°
Cold climate								
Polar	IX	0				<10°		<0°

The climates and their Roman numerals are the (enhanced) Walter types, as shown on Fig. 1 and explained in Table 4. Typical limits for these climates, with gaps for transitions, were given in Box and Fujiwara (2013); the value ranges here are more general. Months represent consecutive, non-calendar 30-day periods. Warm months are periods with mean temperature (T) > 10 °C. Months (T > 0 °C) are considered 'wet' if precipitation exceeds potential evapotranspiration and 'dry' otherwise. Tmax and Tmin denote the mean temperature of the warmest and coldest (non-calendar) months, respectively; absolute minimum temperature is the lowest every measured or expectable (based on longer-term nearby measurements). Only necessary limits are shown.

Some climates are wet throughout the year and represent potentially forested landscapes; climates that are dry all year (or cold all year) represent semi-desert and desert landscapes. Climates with both wet and dry seasons generally represent a range of landscape potentials, from forest if wet enough (not Temperate Continental), through open woodlands and scrub, to taller or shorter grassland or dwarf scrub at the dry end of the range of total precipitation.

Temperate-zone trees generally require four consecutive warm months in order to produce viable seeds. Evergreen broad-leaved trees may occur where summer is only cool or mild, as long as winter is not too cold; thus a low Tmax threshold is given for the Warm-Temperate climate in order to include the oceanic climates of the Southern Hemisphere. Boreal and Polar climates normally involve extreme winter cold but may also include highly oceanic variants with winter temperatures not far below freezing (or even above, e.g. Kerguelen).

Unfortunately, such a simple set of delimiting values would not work everywhere, especially in coastal areas with their modified temperatures, and in mountains, since some mountain climates can be quite similar in their overall temperature and water-balance values to lowland climates. For example, the climate of the drier tropical alpine puna, as in Peru, grades continuously into a very similar climate in lowland Argentine Patagonia, with similar dry landscapes dominated by bunch grasses and cushion shrubs. Models involving quantified climatic limits can perhaps be made, as was done for temperate climates around the Northern Hemisphere (see map in Box 2014a). For reliable global models, though, mountain climates must be delimited in such a way that they do not overlap (much) with similar lowland climates but are still delimited by climatic criteria rather than just latitude or elevation (cf. Box 2014b). A dichotomous approach to this kind of modeling has also been attempted but was frustrating and showed that the problem of similar upland and lowland climates is not trivial.

Appendix: World Vegetation Regions Within a Zonal Framework, as Needed for Geographic Validation of Global Models

	Americas	Africa	Eurasia	Australia-NZ-Oceania-Antarctica
I. **Tropical Humid Forests** (rainforest and seasonal EG forest)	Amazon Basin Atlantic Brazil Chocó to windward Central America Caribbean islands	Congo Basin Guinea coast Madagascar coast	Malay Peninsula windward S Asia East Indies Philippines	New Guinea and archipelagos Melanesia, Micronesia and Polynesia
Subtropical	SE Brazil		Assam-N Myanmar	Montane Queensland
a. Dry Equatorial Scrub	S Caribbean	East Africa		
I-II. Semi-Evergreen Forests	Campeche-Yucatan Colombia-Venezuela Sub-Amazon Brazil	TRF periphery E Madagascar	Windward S Asia Eastern E Indies N Philippines?	(northern and coastal Queensland)
Dry EG Forest			Inland SE Asia	
II. **Tropical Wet/Dry Woods**				
Moist deciduous Forest	Cuba-Hispaniola (Yucatan)		E India-Vietnam eastern Java	
Dry Deciduous Forest/	Meso-America, incl. Caribbean	N Afr below savannas	Interior Deccan India	N-interior Australian

(continued)

	Americas	Africa	Eurasia	Australia-NZ-Oceania-Antarctica
Woodland plus Thorn-Scrub	dry sides Venezuela-Colombia Caatingas Chaco	S-central Africa Leeward Madagascar	Interior SE Asia Leeward Sri Lanka Sumbawa-Timor Upland W Persia	thorn-tree scrub
Semi-EG Scrub/Woods	Cerrado	East Africa		N Austr sclerophyll
II-VII. Thorn-Steppe	Mexico-W Texas Argentine *monte* scrub			
II-III. **Tropical Savanna**	Mexico: Tamaulipas and central valley Cuba Venezuelan llanos and Caribbean Colombia	Sub-Saharan belts E Africa Interior southern Africa Madagascar	Hejaz thorn savanna N India-Pakistan	N and NE Australian grassy woodlands N Australian thorn savanna
Palm Savannas	Llanos Mesopotamian Argentina			
Pine Savanna	Mexico Nicaragua			
Tropical Mountains	Montane TRF, cloud forest, subalpine scrub, páramo (I) or puna (II)	Montane TRF, cloud forest, subalpine ericaceous scrub, páramo	Semi-EG to laurophyll forest, mixed subalpine	Montane rainforest, cloud forest, páramo
III. **Subtropical Deserts**				
Semi-deserts with arborescents	Sonoran + Baja California	W Kalahari		
	Mojave Desert			Interior Austr mulga
Shrub Semi-Desert	Chihuahua Desert			Interior and west Australia
Dwarf-Shrub Desert		Sahara Desert	Sinai-N Arabia Persian halophyte basins Thar Desert	
m. Fog-coast deserts with succulents	Atacama Desert	Namib Desert		
(no vegetation)	Atacama (inland)	Central Sahara	Rub al-Khali Arab-Iran-Pakistani rock desert	W-central Australia
III-IV. Semi-Desert Steppe (shrubs/hard grass)	Central Chile	N Sahara margins	Syria-N Mesopotamia	

(continued)

	Americas	Africa	Eurasia	Australia-NZ-Oceania-Antarctica
IV **Mediterranean Woods/Scrub**				
Sclerophyll Forest	California coast and foothills	Atlas Mtns	Mediterranean borderlands	SW + SE Australia (e.g. jarrah)
Sclerophyll Scrub/Shrublands	Calif. chaparral + Ariz. encinal central Chile	Maghreb uplands Cape fynbos	Mediterranean maquis	SW + SE Australian kwongan
Dwarf Shrublands	S California (coastal sage)	Maghreb Cape fynbos	Mediterranean garrigue, phrygana	
c. Continental Scrub (mainly conifer)	Upland Great Basin (mtns: decid. chaparral)	Western Cape S Maghreb	Interior Turkey N Afghanistan	
Mountains	Calif: montane *Pinus*, subalp conif, scrub Chile: mont mixed, subalp *Araucaria*, etc.	NAfr-EMed: *Cedrus*, alpine hard cushions Cape: Cupressaceae	Med: montane *Pinus*, subalpine conifer, alpine hard cushions	Australia: Cupressaceae + *Eucalyptus*
IV-Vm Submediterranean Tall EG Forests	Calif. coast + Sa. Nevada central Chile (*Fitzroya*)			Australia: SW (karri) and SE (*Euc. regnans*)
V. **Oceanic Forest** (EG-BL)				NZ North Island
Vm. **Temperate Rainforests** (tall broad-evergreen)	Valdivian Chile			W Tasmania (*Nothofagus*) NZ W coast (mixed)
Coniferous	Coastal NW N America		Japan Alps, Yakushima (Norway, Alps)	
Vm-VI. Cool-Oceanic	S Chile to Ta.del Fuego (EG/decid *Nothofagus*)			New Zealand
Ve. **Warm-Temperate Forests**				
Laurophyll Forest	SE Brasil uplands (SE USA: topogenic)	S African montane Canarias montane	Across S China S Japan-Taiwan SE Asian mtns to E Himalaya	E and SE Australia, incl. mountains
Semi-EG Sclerophyll Forest (mixed)	SE USA (*Quercus*) Sa. Madre Oriental		Yunnan? Himalaya?	E and SE Australia (*Eucalyptus*)
Ve-IV. Submediterr. EG Forests (opposite rainfall seasonalities)		Knysna (S Africa)		Coastal Victoria (*Eucalyptus*)

(continued)

	Americas	Africa	Eurasia	Australia-NZ-Oceania-Antarctica
VI. **Temperate Forests** Deciduous Forests	Eastern N America (NW USA: scattered)		Manchuria-Korea-Primorye-N Japan	
Cool-Temperate	S Andes-Ta.del Fuego		Europe: Scandinavia and Britain to Russia	
c. Low decid. woods	S-central USA		N China	
Warm-Temperate (deciduous)	Interior SE US		N Balkan-Caucasus-Hyrcanian N China and interior Japan	
VI-IV. Submediterranean Deciduous Woods	Interior California		S Europe: N Iberia, S France, Italy, S Balkan	
VI-VII. **Forest-Steppe** (summergreen)	Grove Belt (N America) Cross Timbers (S USA)		Eurasian belt: Roman-Ukr-China N China elm grasslands Hungarian Basin Iranian uplands	
VI-VIII. Mixed Forest (sub-boreal)	Great Lakes to NE USA and Maritime Canada		Fennoscandia-N Russia Manchuria-Dahuria	
VII. **Temperate Grasslands** (tall, mixed, short)	Great Plains Palouse (NW USA)	S African Veld (upland)	Russian-Ukrainian-Kazakh steppe Mongolian steppe	
m. Tussock Grasslands	Pampa Patagonian steppe			NZ Canterbury Plain (interior Victoria)
Montane Steppe			Anatolian plateau Azerbaijan-Iran Western China	
a. **Cold-Winter Deserts** (non-summer rain)				
Tree Semi-Desert			Mid-Asian sand deserts	
Shrub Semi-Desert	Great Basin		Middle Asia Persia-Afghanistan	
Monsoonal (summer rain)			Gobi Desert Tarim Basin	
Cold High Plateau			Tibetan Plateau	
x. Cool-Maritime Semi-Desert	Patagonian semi-desert			

(continued)

	Americas	Africa	Eurasia	Australia-NZ-Oceania-Antarctica
Temperate Mountains				
(a) Humid	Montane mixed forest, subalp conif, alp tundra		Mont pine/laurel, mixed, subalp conif, tundra	SE Australia: *Eucalyptus*
(b) Dry	NAm: montane *Pinus*, subalp conif, dry tundra		Montane *Pinus*, subalpine conif, dry steppe/tundra	NZ: mont/subalp BL-EG, tundra
VIII. **Boreal Forest**	Canada–Alaska		Scandinavia-Russia-Siberia-Kamchatka	
c. Decid Larch Woods (ultracontinental)			Interior E-NE Siberia (+ Manchurian mtns)	
m. Deciduous Broadleaf Woods and Scrub (maritime)	Labrador-Newfoundland W and coastal Alaska Ta.del Fuego (*Nothofagus*)		N Sweden-Kola peninsula Iceland Kurils-Sakhalin-Hokkaidō	
VIII-IX. **Forest-Tundra** (sparse conifers)	Across subpolar N America		Across subpolar Eurasia	
IX. **Polar Tundra** (low, upland)	N Canada–Alaska coastal Greenland		Across Arctic Eurasia	Antarctic peninsula
m. Maritime Tundra	W Alaska + Aleutians		Iceland Kuril-Komandr Isls.	Falklands (+ Isla Estados) S Georgia, S Orkneys, S Shetlands
Vm-IX. Everwet Oceanic Moors (EG)	Outer islands of southern Chile			Wet subantarctic islands (Macquarie, Kerguelen)

(continued)

	Americas	Africa	Eurasia	Australia-NZ-Oceania-Antarctica
IX-IXf. Polar Cold Deserts	N Canadian islands Coastal Greenland		Novaya Zemlya and Siberian Arctic islands	Antarctic peninsula and periphery

Boldface signifies the main divisions of the table, i.e. the main climatic zones

The idea that global and other large-area ecological models are inherently *geographic* models and should be evaluated geographically was emphasized by Box and Meentemeyer (1991). This implies validation in a stratified manner, by bioclimatically and ecologically distinct geographic regions, not just by statistical pixel counts over a whole mapped area. This Appendix lists different occurrences of the world's main vegetation types, within a climatic framework, as a basis and checklist for geographic validation of models. Roman numerals denote these main climate types (cf. Fig. 1, Table 4); lower-case letters (except V and temperate mountains) denote climatic subtypes (see Table 5): a = arid, c = continental, m = maritime, x = controverse (e.g. rain-shadow but oceanic).

EG = evergreen, *SG* = summergreen, *BL* = broad-leaved, *NL* = needle-leaved, *conif* = coniferous, *alp* = alpine belt, *subalp* = subalpine belt, *mont* = montane belt

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Vegetation Functional Types and Traits at Multiple Scales

Andrew N. Gillison

Abstract Purpose and scale are the two main drivers that influence the description and classification of vegetation. Whereas the former can be relatively well defined, the latter is far more challenging where attributes that carry useful information at one scale often lack utility at another. Issues of scale dependency are widely discussed in theory but much less attention is given to their resolution in practice. This chapter considers how the advent of plant functional types and traits has added a new dimension to the study of scale dependence by replacing traditional, broad structural, species-based attributes with finer-scale trait characteristics and trait assemblages or 'syndromes' that reflect response-effect relationships of individuals and communities more explicitly along environmental gradients. Traditional scale-related aspects of vegetation classification are compared with recent advances involving plant functional types and traits, especially those expressed in holistic plant strategies. Case studies using global data sets illustrate a critical need for uniformity in data collection and analysis and address the question of scale dependency among specific sets of singular traits and trait syndromes at local, regional and biome scales.

Introduction

Purpose and scale are the two main drivers that influence the description and classification of vegetation. Whereas the former can be relatively well defined, the latter is far more challenging where attributes that carry useful information at one scale often lack utility at another. Issues of scale dependency are widely discussed in theory (Waide et al. 1999; Messier et al. 2010; Chakraborty et al. 2012; Chalcraft 2013; López-Martínez et al. 2013; Šímová et al. 2013), but much less attention is given to their resolution in practice. Most theoretical and empirical approaches invoke scale dependence between species richness and productivity, and for this reason there is a need for explicit consideration of scale in

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analytical studies of productivity and diversity (Waide et al. 1999). Yet such studies are rare. The advent of plant functional types and traits has added a new dimension to the study of scale dependence by replacing traditional, broad structural, species-based attributes with finer-scale trait characteristics and trait assemblages or 'syndromes' that reflect response-effect relationships of individuals and communities more explicitly along environmental gradients.

A key question concerns whether the relatively new trait-based ecology is better placed than traditional methods to cast light on how functional characteristics interact across varying environmental scales and whether functional types and traits can be exploited to improve our understanding of ecosystem dynamics. The aim of this chapter, therefore, is to review briefly the more traditional scale-related aspects of vegetation classification and then to compare these with recent advances involving plant functional types and traits, especially those expressed in holistic plant strategies. Case studies then address the question of scale dependency among specific sets of singular traits and trait syndromes at local, regional and biome scales.

Origins and Definitions

The nomenclature surrounding plant function is confused. 'Functional type', 'functional trait', 'functional group', 'structure-function group', 'plant type', 'adaptive syndrome', 'strategy' and 'species group' are but a few terms used to describe ecological groupings of species. Plant 'function', a term most often used to reflect adaptive behaviour, has its roots among the early ecologists, notably Alexander von Humboldt (1806), Eugenius Warming (1895, 1909) and his student Christen Raunkiær (1934). It was Andreas Schimper (1898) however, who established the connection between the physical environment and its physiological influence on vegetation at various global scales. Schimper reasoned that, across progressively finer scales, heat primarily controlled the flora, humidity the vegetation, with soil as a modifying factor. This hierarchical approach formed the basis for Schimper's vegetation '**formations**' within which he described groups of plants "of quite different modes of life", namely '**guilds**' ('*Genossenschaften*') or plants that depend on others for their existence. Schimper's guilds were restricted to lianes, epiphytes, saprophytes and parasites. Much later, Root (1967) extended the application of 'guild' to methods of resource use among birds (Rootian guilds), an essentially trophic concept that was modified by Wilson (1999) with further divisions (Alpha and Beta guilds) classified according to differences in resource use and environmental strategies respectively. More recently, Giordani et al. (2012) have allocated lichenized and lichenicolous fungi and bryophytes to "**functional guilds**", based on growth form, reproductive strategy and photosynthetic traits.

Synusiae are frequently regarded as guild analogues but with a definite structural-functional connotation (e.g. moss layers). According to Pedrotti (2013), synusiae possess a dual significance: structural, as a concrete part of a phytocoenosis, and adaptive or functional, since they unite species with similar adaptations (See also Barkman 1973). Much wider and less functional use of synusiae is applied to structural layers or strata, for example in rain forests (Williams and Adams 2010), although this usage lacks practical application in most structurally complex vegetation types. While guilds continue to be applied in faunal ecology, plant ecologists now are moving away from the use of guilds simply as trophic entities to a more complex response-effect 'functional' typology—a move presaged by Fosberg (1967). Much present-day functional ecology has its origins in the '**life form**' (*livsform*) of Raunkiær (1934) (described below)—a 'response' type functional trait, based on the condition of the perennating organ during the most unfavourable season.

The need for mechanistic models of global classifications of structural-functional plant functional types (PFTs) was first recognized by Box (1981, 1996), who constructed a set of pheno-physiognomically defined plant types associated with ecophysiological functional traits that could be related directly to climate variables such as water balance and evapotranspiration. The first of its kind, the model proposed by Box provided a framework for subsequent finer-scale investigations of functional typology by Lavorel et al. (1997), who proposed four main types of functional classifications of plant species): (1) **emergent groups**—groups of species that reflect natural correlations of biological attributes; (2) **strategies**—species within a strategy have similar attributes interpreted as adaptations to particular patterns of resource use; (3) **functional types**—species with similar roles in ecosystem processes that respond in similar ways to multiple environmental factors; and (4) **specific response groups**—containing species that respond in similar ways to specific environmental factors. To these may be added specific **effect groups**—containing species that influence ecosystem performance either directly or indirectly (Díaz et al. 2002, 2007a, b; Lavorel et al. 2007). More recent applications now focus on functional traits as they apply to plant functional strategies that have attracted a diverse array of proposed models.

Plant Functional Strategies and Scale Dependency

Overview

When ecologically important plant traits are correlated, they may be said to constitute an ecological 'strategy' dimension when matched against trade-offs in investment (Westoby et al. 2002; Wright et al. 2007). More specifically, '**plant strategy**' is usually taken to mean a combination of plant characteristics that optimize trade-off in resource allocation patterns in order to achieve maximum growth rate, maximum size and maximum age along with the plant's growth response to different combinations of light and water availability (cf. Smith and Huston 1989). The different strategies manifested among species also contribute to the maintenance of diversity and hence ecosystem performance (Kraft et al. 2008; Bonser 2013), so that understanding plant ecological strategies and their application

Table 1 Summary of key plant functional strategies described in this chapter

Strategy	Main characteristics	Functional traits	Scale of application	Source
Leaf, Height, Seed size (LHS)	Parsimonious model of key elements of resource acquisition and return expressed primarily as tradeoffs between three main axes: SLA, H, S	SLA, LLS, seed mass (S) and fecundity, potential plant height at maturity (H), leaf size, shading, water use and response to disturbance, (LS) and twig size (TS)	Community to Biome. Excludes most succulent vegetation types	Westoby et al. (1998, 2002)
Leaf Economics Spectrum (LES)	Parsimonious model of quick-to-slow return on investments of nutrients and dry mass in leaves	LMA, Photosynthetic assimilation (A_{mass}), Leaf nitrogen (N), Leaf Phosphorus (P), dark respiration (R_{mass}), and leaf lifespan (LL).	Community to Biome. Excludes succulent vegetation types	Wright et al. (2004)
C-S-R	Characteristic developmental traits can be expressed within a triangular framework of competitor (C), stress-tolerator (S) and ruderal (R) strategists	Shoot morphology, leaf form, litter, max. potential RGR, leaf longevity, leaf phenology, flowering phenology, proportion of animal production devoted to seeds	Mainly herbaceous communities; limitations in complex woody vegetation	Grime (1977, 1979)
Life-form	Key adaptive strategies are indicated by the position of the perennating organ during the most unfavourable season	A set of Raunkiærean life-forms.	Local to biome; all vegetation types	Raunkiær (1934)
Vital attributes	Predicts successional changes in vegetation based on specific life history traits following disturbance	Propagule type, life stage, species presence	Communities subject to recurrent disturbance	Noble and Slatyer (1980)
Leaf, Life-form, Root (LLR)	Whole-plant combinations of functional traits are used to assess vegetation performance along biophysical gradients	36 generic functional traits based on leaf, life-form and above-ground root systems, combined according to a formal assembly rule	Any environment with potential for plant growth and survival. Local to biome	Gillison and Carpenter (1997), Gillison (2002, 2013)

across multiple scales has become one of the central facets of ecological research. This section introduces some of the better known plant strategies, the most significant of which are summarized in Table 1.

Three main directions of adaptive specialization are evident in the world flora, reflecting fundamental trade-offs between economics (conservative vs. acquisitive investment of resources) and size (Pierce et al. 2013). It is also argued (Lososová and Láníkova 2010) that two key processes affect the structure of trait values within communities, namely competition and habitat filtering. Combined with traditional knowledge, these and other new insights are improving our ability to generalize broad strategic patterns and outcomes of competitive interactions among plants at various scales and to understand better the way functional traits and trait syndromes facilitate interactions among plants (Butterfield and Callaway 2013; Pierce et al. 2013). Across multiple scales, pattern and process remain elusive nonetheless.

Within the broad constraints of resource acquisition, four axes of specialization are considered pivotal to plant strategies (Westoby et al. 2002; Lavorel et al. 2007). These are contained within a well known strategy: the **Leaf, Height, Seed size** (LHS) model involving trade-offs between functionally independent traits. The related **Leaf Economics Spectrum** (LES) strategy (Wright et al. 2004) focuses on similarly parsimonious functional traits concerned with a quick-to-slow resource acquisition and return where functional relationships can be expressed along a biome-invariant scale (described later in this section). As well as the strategic dimensions outlined above, according to Craine (2009) all seed-plant diversity can be represented by four somewhat analogous central resource strategy axes: strategies for low nutrients, low light, low water, and low CO_2—with modifications for increases in resource supply. In the light of the above, for most practical purposes, a problem facing ecologists is the identification of a minimal set of factors among whole-plant trait syndromes and individual traits that best explain causal links within such an array of strategies and how these relate to scale. Most plant strategy models are fuelled by community-weighted means of species-related variables, with little attention to functional characterization at finer community or individual scale. At the level of the individual, the functional significance of leaf traits within the context of the entire plant becomes increasingly evident where plant responses along gradients of environmental adversity require coordinated responses of both whole plant traits and leaf traits alike (Bonser 2006).

The functional and strategic significance of leaf traits has analogues among root traits (Jackson et al. 1996; Craine et al. 2005; Roumet et al. 2006; Cornwell and Ackerly 2009; Liu et al. 2010; Laughlin et al. 2010), indicating clearly that not all trade-offs are above ground. Investment trade-offs between specific root length—the ratio of root length to root biomass (SRL)—and root nitrogen and lignin concentrations, indicate co-varying plant response (e.g. potential growth rate) along environmentally limiting gradients for overall plant growth (Comas and Eissenstat 2002; Craine and Lee 2003; Craine et al. 2005). Root structural and anatomical traits known to constrain relative growth rate and plant height at maturity are also considered potential links with hydraulic conductance, support and longevity (Hummel et al. 2007) and exert a feed-forward effect on stomatal conductance. Traits of woody roots in Neotropical tree species show, for example, close alignment with stem but not leaf traits. In their study of leaf, stem and woody-root traits in lowland South American forests Fortunel et al. (2012) identified two orthogonal axes of functional trade-offs: a first axis defined by leaf traits, corresponding to the LES, and a second axis defined by co-varying stem and woody-root traits, corresponding to a '**wood economics spectrum**'. These axes remain consistent when accounting for species evolutionary history with phylogenetically independent contrasts. A related study in subtropical forests in eastern

China, by Kang et al. (2013), found that leaf and wood traits varied differently across ecological scales, suggesting that trait variability is tissue-specific. More importantly, they concluded that these decoupled trait axes may increase the dimensionality of niche space and thus facilitate species co-existence in forest communities—until now a feature not regarded as significant.

Consistency between above-ground and below-ground trait strategies observed by Mokany and Ash (2008) suggests that below-ground traits may be predictable from above-ground traits, reducing the need to quantify root traits, at least in controlled conditions. On the other hand, Liu et al. (2010) have shown that, across multiple scales, while both root and leaf traits exhibited most of their variance among individuals and species within communities, variance in leaf traits tended to be relatively higher at coarser spatial scales than in root traits.

Among the more significant plant ecological strategies involving whole-plant functional types and individual traits is the **‘resource-ratio’ model** of Tilman (1982, 1985; cf. Clark et al. 2007) that views the spatial heterogeneity of resources as selecting for optimal foraging in chronically unproductive habitats. However, Tilman’s model requires precise ordering of trade-offs, for example, between life history and competitive ability in which data for the ability of multiple coexisting species may be limiting (Pierce et al. 2005). It is also argued by Miller et al. (2005) that additional validation is needed in many circumstances, although this is partly contested by Wilson et al. (2007). It is here that ecological context may play a significant role, as it is argued by Jabot and Pottier (2012) that the resource-ratio and **CSR theories** (Grime 1979) make different predictions regarding competition on poor soils, not because of their differing schemes of plant strategies, but because of the different disturbance types that they consider. In such cases Tilman’s predictions apply to marginally disturbed natural habitats, whereas Grime’s predictions target more disturbed conditions. Both approaches are based largely on temperate herbaceous communities and are yet to be tested in structurally and floristically rich communities such as those in humid lowland tropical forests.

In forecasting plant functional response along gradients of increasing abiotic stress, the **‘stress-gradient hypothesis’** (SGH) predicts that the frequency of facilitative and competitive interactions will vary inversely across abiotic stress gradients, with facilitation being more common in conditions of high abiotic stress relative to more benign abiotic conditions. Limitations in the way SGH had been studied led Maestre et al. (2009) to suggest differentiating between the original idea of how ‘common’ interactions might be along stress gradients and the ubiquitous empirical approach of studying shifts in the strength of pair-wise interactions. In line with this approach, a study of vegetation response (Gross et al. 2013) along a major aridity gradient in Spain at multiple scales (regional, community, neighbourhood) revealed that, despite their opposing influence, habitat filtering (trait convergence) and niche differentiation (trait divergence) acted simultaneously on species where competition and facilitation interacted with aridity in determining community structure. A key consequence of this finding is evidence that opposing traits (trait convergence and trait divergence) can interact effectively along regional gradients, suggesting further examination of the relative trait contributions to plant performance at individual trait level and with traits combined as a whole-plant syndrome (see also Armas et al. 2011; Maire et al. 2012).

The '**mass ratio hypothesis**' (MRH) of Grime (1998) predicts that the effect of species or groups of species on ecosystem properties will depend on their proportional abundance in a community. The hypothesis is supported by empirical evidence (Díaz et al. 2007a; Garnier et al. 2004; Mokany et al. 2008; Laughlin 2011) and implies that the ecosystem function is determined to a large extent by the trait values of the dominant contributors to the plant biomass. According to the MRH, ecosystem properties should be predictable from the community-weighted mean of traits with proven links to resource capture, usage, and release at the individual and ecosystem levels. Díaz et al. (2007a) point to overwhelming evidence that the more abundant traits are major drivers of short-term ecosystem processes and their scale-related feedbacks onto global-change drivers. On the other hand, McLaren and Turkington (2010) argue that the effects of losing a functional group do not depend solely on the group's dominance and that functional group identity plays a critical role in determining the effects of diversity loss—an argument that plays directly into the debate on functional redundancy.

Other, relatively well known but now less widely applied strategies include the '**Vital attribute**' strategy of Noble and Slatyer (1980), which is based on the residence time of specific life-history traits following disturbance. This is one of the very few plant strategy models specifically geared to predict community outcomes in disturbance-related vegetation successional sequences. The strategy is better suited to community level rather that higher assembly scales where logistic and computational requirements unfortunately limit practical application. In a similar way, the well-known **r-K model** of MacArthur and Wilson (1967) (r indicating high rate of reproduction at low cost and K low rate of reproduction at high cost), while conceptually attractive, tends to oversimplify interaction between strategists. The r-K model also presents methodological limitations in many complex vegetation-successional sequences at local and regional scale where the indeterminacy of an r versus K characteristic detracts from its utility. This in turn reflects a general condition that the successful application of different strategies has as much to do with environmental context as it does with spatial scale. Other, less well known strategies are reviewed elsewhere (Westoby 1998; Lavorel et al. 2007; Gillison 2013).

Perhaps the most persistent and most successful plant strategy over the last century is that of Raunkiær's (1934) '**life-form model**'. Raunkiaer defined life form (*livsform*) theoretically as "The sum of the adaptation of the plant to the climate" (Du Rietz 1931) but in practice selected one of the most fundamental adaptations as a base for his systems of life forms, namely the survival of the perennating organ during the most unfavourable season. Although based primarily on sensitivity to winter temperatures, Raunkiær's strategy is applicable to 'unfavourableness' under other periodic or episodic, thermal, light, and moisture regimes including flood, fire and strong winds. The method (especially his 'life-form spectrum') has been applied widely across the globe with varying results, and a global physiognomic-ecological vegetation classification that includes the Raunkiær model (Mueller-Dombois and Ellenberg 1974) is rarely applied in practice. It can be argued nonetheless that, as a plant ecological strategy, Raunkiær's system is consistent with a theoretical trade-off of carbon investment per individual against tissue loss and reproductive and regenerative capacity under regimes of cyclic environmental extremes. Thus a gradient can be shown to exist between a dominance by woody phanerophytes in 'optimal' environments with corresponding decreases towards less optimal habitats accompanied by an increasing relative percentage of structurally reduced chamaephytes, geophytes and hemicryptophytes (Gillison 2013). Although frequently confused with the more physiognomic 'growth forms', Raunkiær's system remains attractive in its simplicity and its general application across many spatial and temporal scales. The system is greatly limited however, through an inability to account for critical adaptive elements related to plant physiological response to environmental change, in particular photosynthesis—a characteristic considered further in the '**LLR strategy'** described below.

The following four strategies (CSR, LHS, LES and LLR) (Table 1) are described here in greater detail, as they share some common traits that are recognized determinants of plant growth, persistence and productivity. Together with primarily leaf-based features, they reflect a paradigm shift towards measureable evidence of cause and effect between functional traits and environment beyond the more loosely defined adaptive or 'epharmonic' Raunkiær descriptors. With the possible exception of CSR, a feature in common with all of these strategies is their applicability across multiple scales.

The C-S-R Strategy

Apart from the Raunkiær model, CSR is one of the best known plant strategy theories, which considers the interaction between competition (limitations to biomass production imposed by other species), stress (direct limitations to biomass production imposed by the environment) and disturbance (biomass removal or tissue destruction) in shaping phenotype. According to CSR theory, characteristic developmental traits are inherent to competitor (C), stress-tolerator (S) and ruderal (R) strategists, with apparent intermediate strategies (Grime 1977, 1979; Caccianiga et al. 2006). A fundamental aspect of CSR suggests that stress and indeterminate resource availability favour conservative phenotypes (Pierce et al. 2005). Although most theoretical support for CSR is derived from extensive studies on herbaceous vegetation in the UK, methodological limitations constrain its application in other countries containing especially species-rich, structurally and functionally complex woody vegetation (Gillison 2013). A partial solution to the methodological impasse (Hodgson et al. 1999; Hunt et al. 2004) is to allocate a functional type to an unknown subject using a few, simple predictor variables. Traits such as leaf weight, specific leaf area (SLA) and leaf dry matter content (LDMC) can be linked statistically with productivity traits that are relevant, for example, to the S type (slow-growing, stress-tolerant species of chronically unproductive habitats). An ordination of these more readily measurable traits then allows the taxa under study to be placed within CSR coordinate space.

A potential solution to the problem in applying standard CSR methods to vegetation complexes containing both woody and herbaceous plants is proposed by Pierce et al. (2013), who employed Principal Components Analysis and a spreadsheet procedure that returns ternary coordinates and tertiary CSR strategies for target subjects based on leaf area (LA), dry-matter content (LDMC) and specific leaf area (SLA). The method by Pierce et al. (2013) allows classification of target species within a triangular space corresponding to Grime's theoretical CSR triangle and is arguably sufficiently precise to distinguish between different strategies of species within genera and within populations of species. While various authors argue that rapid CSR classification of woody and herbaceous vascular plants is thus possible over landscape scales via ordination procedures, the application has yet to be tested in wide-ranging, complex habitats such as tropical land-use mosaics.

According to Westoby (1998), the CSR triangle defines the axes with reference to concepts, for which there is no simple protocol for positioning species beyond the reference datasets within the scheme; consequently, benefits of worldwide comparison have not materialized. Both theoretical and practical limitations are evident where, under studies of grazing impact and shoreline successional sequences, CSR types cannot be applied readily (Oksanen and Ranta 1992; Ecke and Rydin 2000; Moog et al. 2005). Problems with the CSR format have been noted elsewhere (Austin and Gaywood 1994; Onipchenko et al. 1998; Körner and Jeltsch 2008), although certain studies show promise along environmental gradients including grazing intensity (cf. Cerabolini et al. 2010; Kilinç et al. 2010; Frenette-Dussault et al. 2012; Kelemen et al. 2012; Schmidtlein et al. 2012). Nonetheless, as a scale for environmental assessment, Grime's (1979, 2001) ruderality (R) also has the relatively unsatisfactory feature that some species with high ruderality are mainly associated with perennials that are not ruderal (Hill et al. 2002). Despite improved numerical procedures, the capacity of CSR theory to predict variation in species composition and interaction along environmental gradients remains problematic across differing community and landscape scales.

The Leaf-Height-Seed Size Strategy

The almost infinite array of co-varying plant functional types and traits constrains the search for a 'core' set of orthogonal (functionally independent), parsimonious traits that facilitates the construction of plant strategies in a way that avoids the tyranny of scale. Such an approach, based on specific Leaf area (SLA), mature plant Height (H) and Seed mass (S), i.e. the LHS system of Westoby (1998), represented a significant breakthrough in quantifying plant response to environment, with capacity for generic application worldwide. The LHS system represents a tightly defined functional concept using orthogonal (independently functioning) parsimonious traits and as such indicates a paradigmatic shift towards the understanding and application of plant functional traits. As described by Westoby (1998), the LHS plant ecology strategy scheme employs three axes: SLA (light-capturing area deployed per unit of dry mass allocated), height of the plant's canopy at maturity, and seed mass in which the strategy of a species is described by its position in the volume formed by the three axes. The benefits of the LHS scheme can be understood by comparing it to Grime's CSR scheme over which it has several advantages. Whereas certain elements of the CSR scheme (e.g. the C–S dimension) are overtly conceptual, and as such present methodological limitations (Westoby 2007), these limitations are essentially overcome by the more readily quantifiable LHS approach that can be arguably applied at a world scale to any vascular plant species in any terrestrial environment. Apart from these positives, the advantage of the axes defined through a single, readily measured variable needs to be weighed against the disadvantage that single plant traits may not capture as much strategy variation as CSR's multi-trait axes (Westoby 1998).

Apart from its evident application at biome scale, there is evidence that the success of the LHS system is supported at community scale, for example in North American pine forests (Laughlin et al. 2010) and elsewhere, but not necessarily at species level, as described under grazing systems by Golodets et al. (2009). Spatial scale and environmental context clearly influence the utility of LHS where differences in detecting community response can be detected when CSR and LHS strategies are compared in managed grasslands (Moog et al. 2005). Detailed studies in alpine vegetation based on LHS traits (de Bello et al. 2012a, b) emphasized the hierarchical nature of ecological forces in shaping local species assemblage where coarse-scale environmental filters have a primary effect in selecting the pool of species adapted to a site, followed by filters at finer scales that determine species abundances and local species coexistence. According to de Bello et al. (2012a, b), different components of functional community structure respond differentially to environmental change, so that predicting plant community responses will require a hierarchical multi-faceted approach. From a practitioner's viewpoint, and despite established theory, the largely 'laboratory-based' LHS approach constrains the practical acquisition of specific trait data in poorly documented, complex vegetation types. As well, no study so far appears to confirm the utility of LHS as a bioindicator, as illustrated for example in its failure to predict dispersal guilds of birds (Jardim and Batalha 2008) (see section below on bioindicators).

The Leaf Economics Spectrum Strategy

There are evident common trends and functional linkages between the LHS strategy and the LES scheme proposed by Wright et al. (2004) that describes, at global scale, a universal spectrum of leaf economics consisting of key chemical, structural and physiological properties. The spectrum reflects a quick-to-slow return gradient on investments of nutrients and dry mass in leaves that are reflected in six key attributes: LMA (leaf mass per area), photosynthetic assimilation rates (A_{mass}), leaf nitrogen (N), leaf phosphorus (P), dark respiration rate (R_{mass}), and leaf lifespan (LL). Unlike many other strategies, LES is frequently regarded as independent of growth form, plant functional type or biome, a feature not without implications for ecological applications requiring vegetation classification at multiple scales. According to Wright et al. (2004) categories along the spectrum would, in general, describe leaf economic variation at the global scale better than plant functional types, because functional types overlap substantially in their leaf traits.

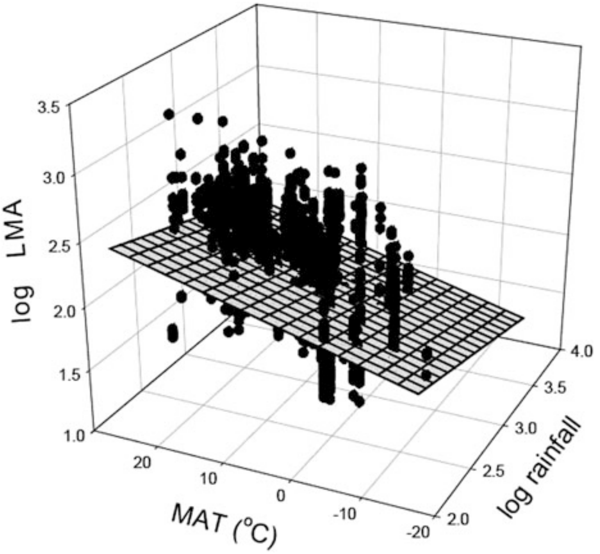


Fig. 1 Leaf mass per unit area (LMA) (SLA) response to mean annual temperature (MAT) and Log rainfall. Reproduced from Wright et al. (2004) with permission from *Nature*

It is argued by Shipley et al. (2005) that functional linkages between leaf traits and net photosynthetic rate provide a mechanistic explanation for the empirical trends relating leaf form and carbon fixation, and predict that SLA and leaf N must be quantitatively co-ordinated to maximize C fixation, thus lending support to the scale-invariant nature of the LES scheme.

Current evidence suggests nevertheless that the pattern of universality demonstrated by the LES at predominantly global scale (Fig. 1) remains to be confirmed effectively at community or habitat scale. Greenhouse experiments conducted by Wright and Sutton-Grier (2012) on a suite of co-occurring wetland species showed that, apart from significant relationships between specific leaf area and photosynthetic rate under some treatments, there was little support for the relationships predicted by the LES. When examined for their potential connection with ecosystem processes, Jackson et al. (2013) also found that LES traits and litter decomposability were decoupled at infra-specific and whole-community levels in temperate New Zealand forests—a finding that contrasts with studies in a Bolivian lowland forested land-use mosaic by Bakker et al. (2011), in which leaf and litter traits were closely associated. In line with the LES, the Bolivian study also showed a slow-fast continuum over which both individual traits of living leaves and species' position on the LES persisted in litter, indicating that leaves lead influential afterlives, affecting decomposition, nutrient and carbon cycling—a possibility also considered by Freschet et al. (2012).

Other evidence suggests that the biome-invariant LES model may not perform as well as expected across different floras. Differences in leaf-trait allometries among global floristic regions were examined by Heberling and Fridley (2012) who evaluated biogeographic effects on bivariate relationships between LES traits, including relationships of photosynthetic capacity and dark respiration rate

(A_{mass}–Rd_{mass}), leaf lifespan and mass per area ratio (LL–LMA), and photosynthetic capacity and nitrogen content (A_{mass}–N_{mass}). Their results indicate that evolutionary histories of different floras clearly mediate the scale-invariance implied in the LES model where independent floras can exhibit different tradeoffs in resource-capture strategies.

At the genetic level, Vasseur et al. (2012) tested the evolutionary assumptions of metabolic scaling theory (MST) and the LES using a cross of two genetic variants of *Arabidopsis thaliana*. They found that a small set of pleiotropic genes underlies many plant functional traits and life histories, potentially unifying MST and LES within a common genetic framework. Vasseur et al. (2012) suggest further that observed intermediate size and longevity in natural populations originate from stabilising selection to optimise physiological trade-offs. Despite these findings it remains to be seen whether pleiotropic infraspecific relationships based on a herbaceous winter-annual species can be extended across different life forms to confirm scale-invariance of both MST and LES from species to biome. Although attractive, the prospect of a universal gene-based schema is yet to be demonstrated at the inter-specific and community level among very different trait syndromes involving, for example, woody perennials in forest canopies that exhibit a differential response to habitat filtering and physiological trade-offs along photon flux-density gradients (cf. Posada et al. 2009).

The scale-invariant LHS and LES models are driven primarily by leaf-based traits that ignore significant elements of the world's succulent and semi-succulent vascular flora (~10,000 species, Oldfield 1997), in which the photosynthetic organs and tissues are not readily amenable to quantification of SLA (1/LMA). Further, while SLA is not the only functional trait used in these models, the potentially uncritical application of SLA in plant ecology sounds a note of caution where, for example, SLA values can be similar among otherwise functionally highly dissimilar PFTs, for example the subalpine fir *Abies lasiocarpa* (39.3), the lingonberry *Vaccinium vitis-idaea* (41) and the tropical mangrove *Lumnitzera littorea* (41.2) (SLA values from Wright et al. (2004) and I. J. Wright, pers. comm.).

The Leaf-Life-Form-Root Strategy

Both the LHS and LES strategies are based on parsimonious, arguably independently functioning traits that, although exhibiting a clear case for a biome-invariant pattern, pay only limited attention to other potential trait-interactions or the possibility of a potential 'functional Gestalt' where the totality of functional trait combinations at a 'whole-plant' level represents more than just the apparent sum of the functional parts. Arguments for parsimony assert that orthogonal traits achieve an economy of scale in expressing ecological performance that is otherwise unattainable in "overlapping" or co-varying functional types. Across multiple scales it is yet to be confirmed however, that parsimony is a more effective in predicting response-effect relationships along environmental gradients within and

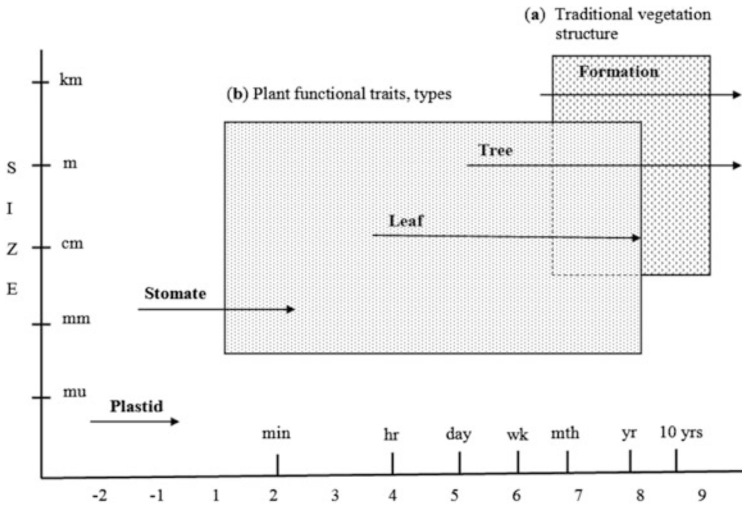


Fig. 2 Approximate log response time (s) of above-ground plant elements including spatio-temporal domains of PFT and individual trait sensitivity. (**a**) Formation class and (**b**) Generalized zone of plant functional classifications (adapted from Gillison 2002)

between plant species than functional 'whole-plant' syndromes containing co-varying traits. To this extent the LLR approach considers ways in which multiple traits can be used to construct plant functional types (PFTs) or trait syndromes via an assembly system that addresses whole-plant performance rather than economically-acquisitive, single traits such as LMA. This is achieved in part by coupling photosynthetic traits with life form and above-ground rooting structures, and is consistent with observed stem-root interaction (cf. Fortunel et al. 2012). When coupled with additional information that describes vegetation structure, the methodology facilitates comparative analysis across a range of environmental scales (Fig. 2) (Gillison 1981, 2002, 2013). The LLR strategy complements significant gaps in the CSR, LHS and LES systems that otherwise exclude critical photosynthetic traits such as leaf inclination (Falster and Westoby 2003; Posada et al. 2009), leaf phyllotaxis or insertion pattern such as rosettes (Withrow 1932; Lavorel et al. 1998, 1999a, b; Díaz et al. 2007a; Ansquer et al. 2009; Bernhardt-Römermann et al. 2011) and green-stem photosynthesis, all notable plant adaptations to irradiance, nutrition and water availability.

As discussed, one strategy that has stood the test of time is the Raunkiaer life-form system, partly because it is built on a fundamental survival adaptation to cyclic environmental and edaphic (nutritional) extremes and partly because it is simple, with mostly readily observable traits. In its basic form, however, and despite external reference to a table of leaf size classes, the Raunkiær model excludes photosynthetic traits. In a move to help redress this issue but to retain the essential Raunkiær format, Gillison (1981) devised a whole-plant classification system based on plant functional attributes in which a plant individual is classified as a ‘functionally coherent’ unit composed of a photosynthetic ‘envelope’ supported by a modified Raunkiaer life form and an above-ground rooting system presented as the Leaf-Life form-Root’ or LLR spectrum (Gillison 2013).

A fundamental tenet of the LLR is that a single attribute, such as leaf size class, takes on additional functional significance when combined with leaf-inclination and other morphological (e.g. leaf stomatal distribution) and temporal (e.g. deciduous) descriptors of photosynthetic tissue. In this case the photosynthetic attributes describe a ‘functional leaf’ that includes any part of the plant (including the primary stem cortex) capable of photosynthesis. Unlike LHS and LES, this includes succulent vegetation (ca. 10,000 species, Oldfield 1997) that involves significant elements of world flora. For convenience, and to indicate the unique type of PFT, specific LLR combinations are termed functional *modi* (from *modus* Latin SM II, meaning mode or manner of behaviour) (compare also the “modality” of Violle et al. 2007). This initial model (Gillison 1981) appears to be the first coordinated use of plant functional attributes (PFAs) or functional traits to relate whole-plant PFTs to environmental conditions. The method was subsequently formalized (Gillison and Carpenter 1997) using an assembly-rule set and syntactical grammar to construct *modal* PFTs based on 36 generic plant functional elements (PFEs) (Table 2). In this method, a typical PFT *modus* for an individual of *Acer palmatum* might be a mesophyll (*me*) leaf size class with pendulous (*pe*) inclination, dorsiventral (*do*) (hypostomatous), deciduous (*do*) leaves with green-stem (cortex) (*ct*) photosynthesis supported by a phanerophyte (*ph*), the resulting *modal* PFT combination being *me-pe-do-de-ct-ph*.

Within the same species on the same or other site, variation in any one functional element, such as leaf size class, results in a new *modus*, thereby facilitating comparison of intra-as well as inter-specific variability at a described location. This can be especially useful where phenotypic expression within a species may be expressed in different modal combinations along an environmental gradient ranging, for example, from a dry ridge (e.g. small vertically inclined leaves) with skeletal soil to a river margin on alluvium (larger, laterally inclined leaves). With the public-domain VegClass software package (Gillison 2002), quantitative and statistical comparisons within and between species and plots are facilitated via a predetermined ‘costing’ of lexical distances between different PFTs (Gillison and Carpenter 1997). The system comprises a many-to-many mapping whereby more than one modal PFT can be represented within a species and *vice versa*. While ~7.2 million combinations are theoretically possible, a data set compiled using a standard recording proforma (Table 3) from 1100 field sites worldwide covering all major latitudes and climates (Fig. 3) indicates the ‘real’ number of unique modal PFTs approximates 3500 for the world’s approximately 300,000 vascular plant species. For vascular plants, Fig. 4 illustrates whole-plant LLR functional syndromes arranged along two key environmental gradients or axes (irradiance and moisture—see also Lavers and Field 2006).

The distribution of species and PFTs can be seen to vary with latitude (Fig. 5) and, while a strong linear relationship exists between them at global scale (Fig. 6), regression slopes between species and PFT correlations can vary predictably

Table 2 VegClass data variables recorded for each 40 m × 5 m transect

Site feature	Descriptor	Data type
Location reference	Location	Alpha-numeric
	Date (dd-mm-year)	Alpha-numeric
	Plot number (unique)	Alpha-numeric
	Country	Text
Observer/s	Observer/s by name	Text
Physical	Latitude deg. min. sec. or decimal deg. (GPS)	Alpha-numeric
	Longitude deg. min. sec. or decimal deg. (GPS)	Alpha-numeric
	Elevation (m.a.s.l.) (aneroid or GPS)	Numeric
	Aspect (compass. deg.) (perpendicular to plot)	Numeric
	Slope percent (perpendicular to plot)	Numeric
	Soil depth (cm)	Numeric
	Soil type (US Soil taxonomy)	Text
	Parent rock type	Text
	Litter depth (cm)	Numeric
	Terrain position	Text
Site history	General description and land-use/landscape context	Text
Vegetation structure	Vegetation type	Text
	Mean canopy height (m)	Numeric
	Canopy cover percent (total)	Numeric
	Canopy cover percent (woody)	Numeric[a]
	Canopy cover percent (non-woody)	Numeric[a]
	Cover-abundance (Domin)—bryophytes	Numeric
	Cover-abundance woody plants <2 m tall	Numeric
	Cover-abund. lichens (crustose, fruticose, foliose)	Numeric
	Basal area (mean of 3) (m^2 ha^{-1})	Numeric
	Furcation index (mean and cv % of 20)	Numeric
	Profile sketch of 40 m × 5 m plot (scannable)	Digital
Plant taxa	Family	Text[b]
	Genus	Text[b]
	Species	Text[b]
	Botanical authority	Text[b]
	If exotic (binary, presence-absence)[a]	Numeric
Plant functional type	Plant functional elements (36) combined according to published rule set.	Text
Quadrat listing	Unique taxa and PFTs per quadrat (for each of 8 (5 m × 5 m) or more quadrats)[a]	Numeric
Photograph	Hard copy and digital image[a]	JPEG

[a] Preferably a radial view from plot centre and with embedded date and GPS reference
[b] Where identified, usually with voucher specimens, used directly in numerical analysis

Table 3 Plant functional attributes and elements

Attribute	Element	Description	
Photosynthetic envelope			
Leaf size	nr	no repeating leaf units	
	pi	picophyll	$<2\ \text{mm}^2$
	le	leptophyll	2–25
	na	nanophyll	25–225
	mi	microphyll	225–2025
	no	notophyll	2025–4500
	me	mesophyll	4500–18,200
	pl	platyphyll	18,200–36,400
	ma	macrophyll	36,400–18×10^4
	mg	megaphyll	$>18 \times 10^4$
Leaf inclination	ve	vertical	>30° above horizontal
	la	lateral	±30° to horizontal
	pe	pendulous	>30° below horizontal
	co	composite	
Leaf chlorotype	do	dorsiventral	
	is	isobilateral or isocentric	
	de	deciduous	
	ct	cortic	(photosynthetic stem)
	ac	achlorophyllous	(without chlorophyll)
Lf. morphotype	ro	rosulate or rosette	
	so	solid 3-D	
	su	succulent	
	pv	parallel-veined	
	fi	filicoid (fern)	(Pteridophytes)
	ca	carnivorous	(e.g. *Nepenthes*)
Supporting vascular structure			
Life form	ph	phanerophyte	
	ch	chamaephyte	
	hc	hemicryptophyte	
	cr	cryptophyte	
	th	therophyte	
	li	liane	
Root type	ad	adventitious	
	ae	aerating	(e.g. pneumatophore)
	ep	epiphytic	
	hy	hydrophytic	
	pa	parasitic	

between widely separate biogeographic regions (Fig. 7) as well as at progressively finer scales, for example along gradients of land-use intensity in tropical forested landscape mosaics and in extreme habitats such as arctic tundra (Gillison 2012, 2013). PFT syndromes reflecting position along these gradients together with

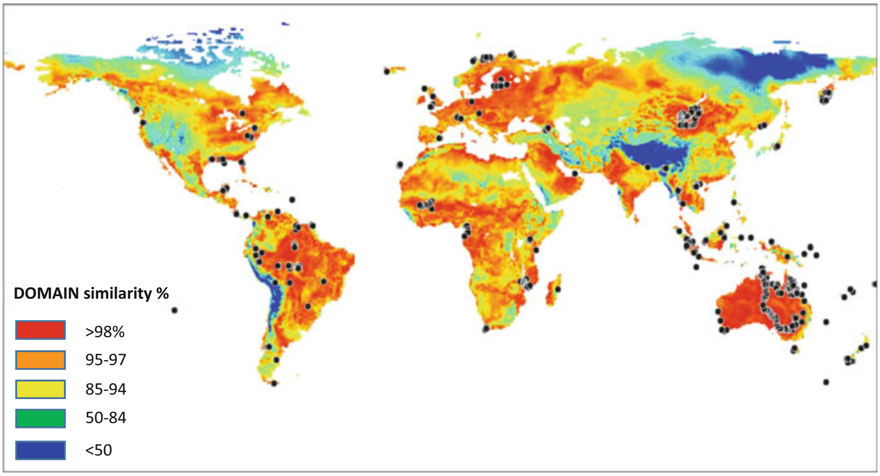


Fig. 3 DOMAIN similarity mapping of key climate variables based on mean annual precipitation (mm), mean annual actual evapotranspiration (mm), mean minimum temperature of coldest month (°C) and elevation (m) above sea level. Legend indicates percentage representation of these environmental domain values derived from 1138 (40 m × 5 m) VegClass transects (*black points*)

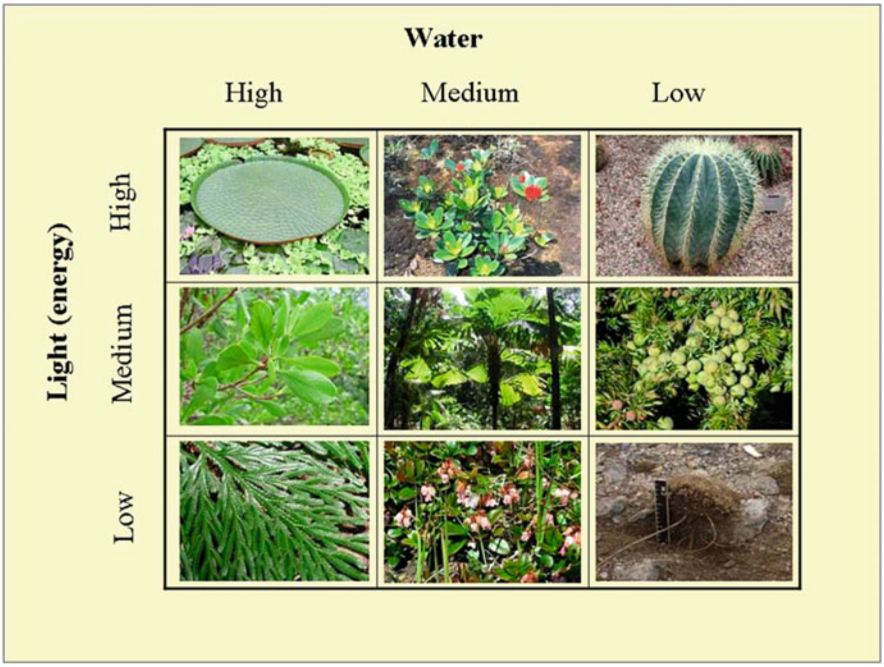


Fig. 4 Different whole-plant PFT syndromes, positioned subjectively along gradients of light (energy) and moisture. L to R: *Victoria regia* (Amazon basin), *Metrosideros sp*. (Philippines), *Echinocactus* sp. (Mexico), mangrove *Lumnitzera littorea* (Indomalesia), phanerophytic swamp fan palm *Licuala ramsayi* (tropical N. Australia), *Juniperus communis* (Fennoscandia), fern *Selaginella* sp. (Indomalesia), *Vaccinium vitis-idaea* (boreal region), and cushion plant *Azorella macquariensis* (subantarctic Macquarie Isl.). Each example can be described as a *modal* PFT according to the VegClass method described under the LLR strategy (after Gillison 2002)

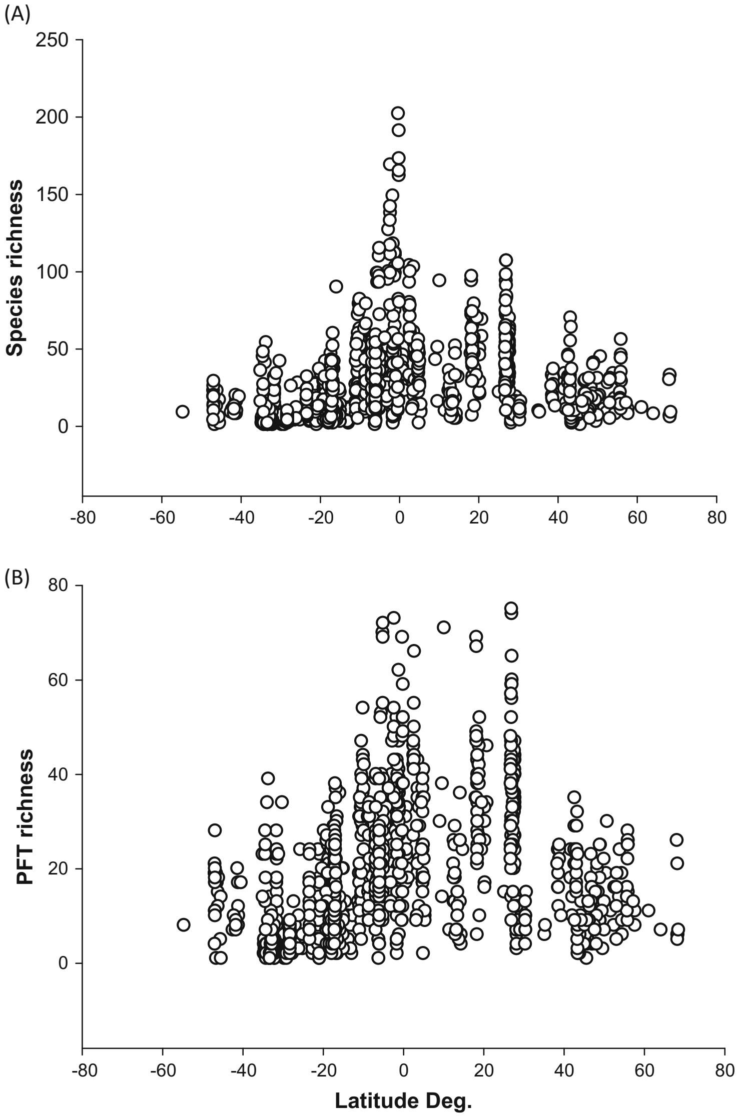


Fig. 5 Variation of vascular plant species and *modal* PFT richness with latitude. Data from 1138 (40 m × 5 m) transects (see Fig. 3)

disturbance are readily described according to the modal schema and at global scale. Unlike the log-transformed linear relationships indicated in Fig. 1 for LES, untransformed LLR values such as individual PFTs and PFEs can exhibit two-dimensional, mostly non-linear responses to mean minimum temperature of the coldest month (Fig. 8a, b) as well as three-dimensional responses with minimum temperature of the coldest month, mean annual precipitation and mean annual

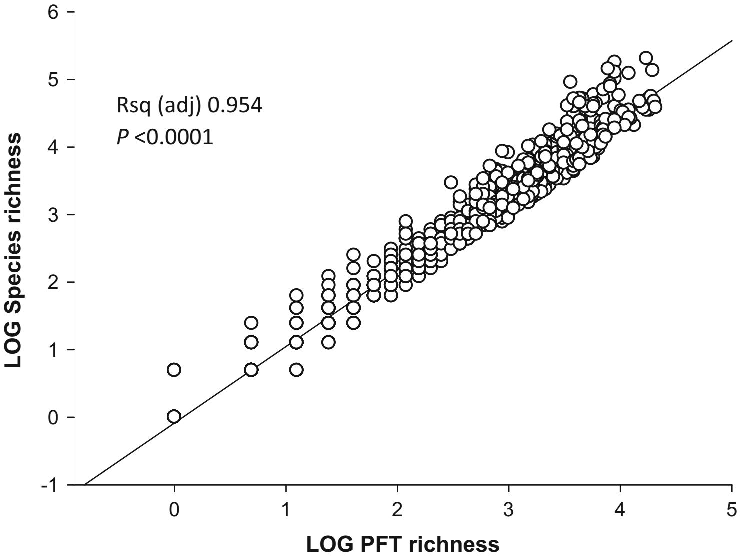


Fig. 6 Counts of vascular plant species regressed against counts of unique (distinct from species) *modal* PFTs from 1138 (40 m × 5 m) transects as indicated in Fig. 3

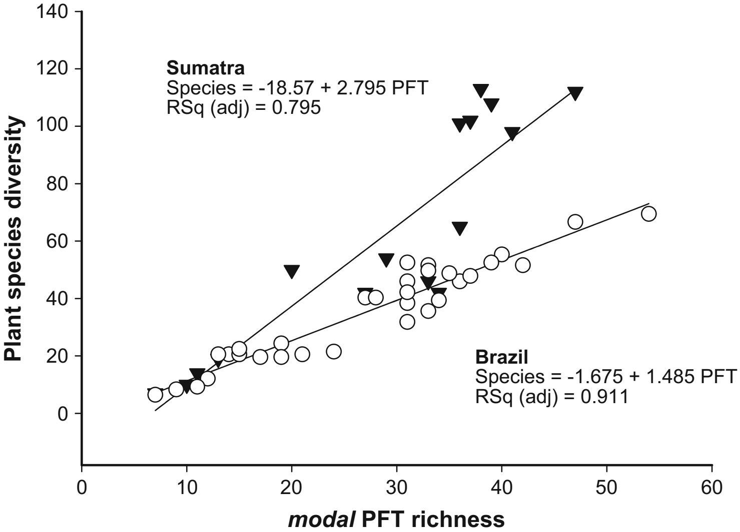
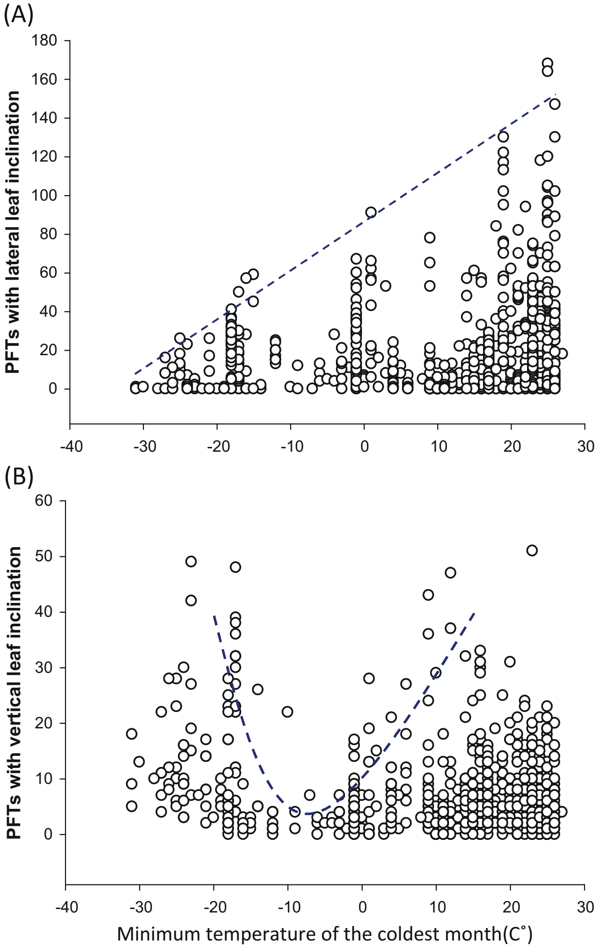


Fig. 7 Different regional 'signatures' in species diversity (species richness)-to-modal PFT richness ratios along similar land-use intensity gradients and vegetation mosaics in Sumatra (*triangles*) and Brazil (*circles*) may reflect evolutionary separation of floras and functional characteristics. Data points are 40 m × 5 m transects from which species and modal PFT counts were recorded (after Gillison et al. 2013)

Fig. 8 Leaf inclination shows divergent response to minimum temperatures within PFTs in 1138 (40 m × 5 m) transects at global scale (*circles*). (**a**) Leaf lateral inclination; (**b**) Leaf vertical inclination (*lines hand-drawn*)



actual evapotranspiration (Figs. 9, 10). Unlike meta-data sets based on community-weighted means of traits, the LLR data used in VegClass are based on original counts.

Functional diversity measures based on the abundance of species per PFT (Shannon H', Simpson's D and Fisher's Alpha) can also be generated on demand in VegClass, with the inverse of the PFT Simpson measure equating to Rao's quadratic entropy (Botta-Dukat 2005; Lepš et al. 2006; Mason et al. 2012; Vandewalle et al. 2014). A separate measure of plant functional complexity (PFC), based on a minimum spanning-tree distance of PFT values within a transect, also provides a useful comparator between sites where the number of PFTs is the same but where their identities differ. The PFC measure has been found useful as a bioindicator, as it is also independent of species—a useful feature where species identification is problematic. An indication of the application of the LLR at global

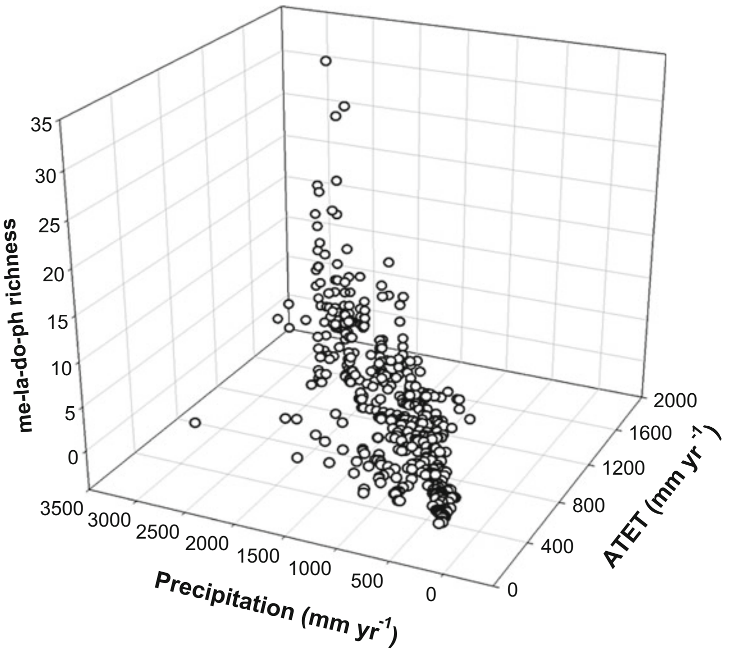


Fig. 9 Example of a *modal* PFT (me-la-do-ph) with mesophyll leaf size class, lateral leaf inclination, dorsi-vental (hypostomatous) leaf supported by phanerophyte structure, showing distribution against mean annual precipitation (mm) and mean annual actual evapotranspiration (mm). Data points (*circles*) are from 1138 (40 m × 5 m) transects recorded using the VegClass proforma and the LLR strategy

scale is illustrated in Table 4, which includes examples of the most species and PFT-rich, closed forests recorded along latitudinal and altitudinal gradients from the equator to the sub-arctic.

Functional Redundancy

Concept and Evidence

Species designated within a functional group are, by definition, ecologically equivalent and therefore it is argued that they provide some measure of system redundancy (Martinez 1996; Mooney 1997; Blondel 2003; Franks et al. 2009). The ‘functional niche’, defined as the area occupied by a species in an n-dimensional functional space, has also been put forward by Rosenfeld (2002) as a useful conceptual tool for understanding redundancy. A principle that directly supports redundant species as guarantors of reliable ecosystem functioning has been drawn

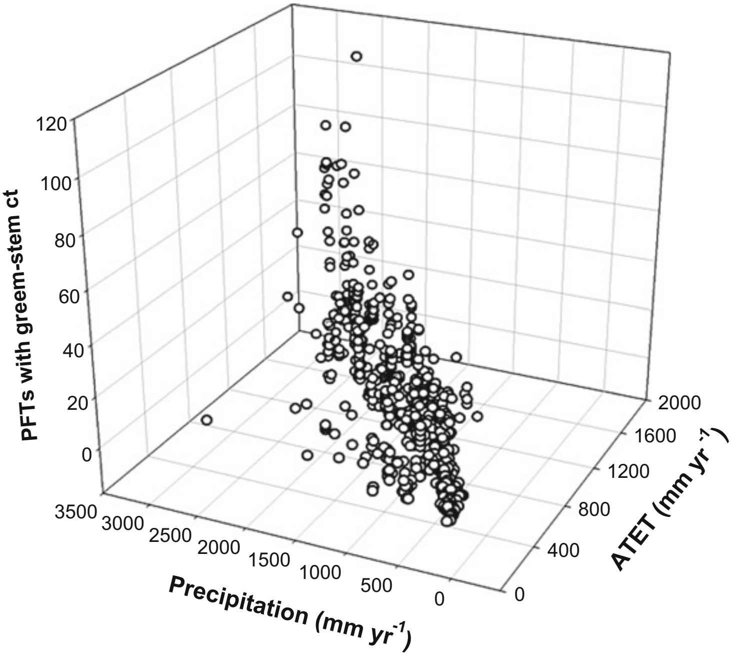


Fig. 10 Counts of *modal* PFTs containing a plant functional trait or element (PFE) 'ct' indicating green-stem or corticular photosynthesis, matched against mean annual precipitation (mm) and mean annual actual evapotranspiration (mm). Data points (*circles*) represent counts recorded within 1138 (40 m × 5 m) transects recorded using the VegClass proforma and the LLR strategy

from elementary principles of engineering that indicate reliability always increases as redundant components are added to a system (Naeem 1998). This argument has been applied widely across environmental scales in plant ecology, where it is claimed that ecosystem resilience depends on functional or 'ecological' redundancy (the number of species contributing similarly to an ecosystem function) and on response diversity (how functionally similar species respond differently to disturbance) (Laliberté et al. 2010; Mayfield et al. 2010; Messier et al. 2010). On the other hand, where there is limited understanding about the exact form of the species–ecosystem relationship under differing conditions, it is also argued that we should not ignore the 'insurance value' of maintaining all species circumstances (Lawton and Brown 1993; Walker 1992; Bolger 2001).

As a concept that is intimately connected with the interpretation and evaluation of plant functional typology, redundancy has attracted broad theoretical support among ecologists based on localised studies or computerised simulations and then often with very limited criteria (Cowling et al. 1994; Pillar and Sosinski 2003; Petchey and Gaston 2002a, b, 2006, 2007; Blondel 2003; Flynn et al. 2009; Laliberté et al. 2010; Mouchet et al. 2010). The essentially intuitive support for the concept is not supported by most empirical observations. To begin with, species

Table 4 Comparative richness in plant species, plant functional types and Plant Functional Complexity (PFC) in closed forest types across an equatorial to sub-arctic latitudinal and altitudinal range in 33 countries

No.	Country	Location	Georeference	Forest type	Species richness	PFT richness	PFC value
1	Indonesia (Sumatra)	Tesso Nilo, Riau Province	0°14′51″ S 101°58′16″ E	Complex primary forest, logged 1997	202	68	338
2	Indonesia (Sumatra)	Pancuran Gading, Jambi Province	1°10′12″ S 102°06′50″ E	Lowland forest interplanted with ‘jungle’ Rubber (*Hevea brasiliensis*)	112	47	236
3	India	Arunachal Pradesh, Tipi—Pakke Sanctuary	27°2′3″ N 92°36′58″ E	Complex lowland forest selectively logged	107	74	314
4	Indonesia (Borneo)	Gunung Banalang, Long Puak, Pujungan, E. Kalimantan	2°43′32″ N 115°39′46″ E	Disturbed complex ridge forest	104	44	232
6	Papua New Guinea	Kuludagi/West New Britain Province	5°38′46″ S 150°06′14″ E	Complex, primary lowland forest.	99	52	234
7	Bhutan	Near Chasilaka	26°57′15″ N 89°33′48″ W	Secondary forest *Alsinandra* dominant tree. Dense Acanthaceae groundlayer	98	72	358
8	Costa Rica	Braulio Carillo, Parque Nacional	10°09′42″ N 83°56′18″ W	Partially disturbed forest, palm dominated. Many epiphytes.	94	71	336
9	Cameroon	Awae Village	3°36′05″ N 11°36′15″ E	Late secondary forest. Previously logged.	94	43	232
10	Brazil	Pedro Peixoto, Acré (West Amazon basin)	10°01′13″ S 67°09′39″ W	Secondary forest (Capoeira) 3–4 years after abandonment	78	43	230
11	Brazil	Alcalinas Canamá N.W. Mato Grosso (West Amazon basin)	10°04′06″ S 58°46′00″ W	Primary lowland forest on shallow granitic soils.	75	54	298
12	Perú	Jenaro Herrera, Ucayali river (West Amazon basin)	4°58′00″ S 73°45′00″ W	‘High terrace’ lowland forest—selective logging	72	39	208

(continued)

Table 4 (continued)

No.	Country	Location	Georeference	Forest type	Species richness	PFT richness	PFC value
13	Russia	Vladivostok, forest adjacent to Botanical Institute	43°13′18″ N 131°59′40″ E	Tall broadleaf/conifer (*Pinus koraiensis*) forest with herbaceous groundlayer.	70	29	144
14	Vietnam	Cuc Phuong National Park, Ninh Binh Province	20°48′33″ N 105°42′44″ E	Lowland forest partly disturbed; on limestone	69	46	256
15	Estonia	Saaremaa	58°14′10″ N 22°26′22″ E	Oak forest (*Quercus robur*) with conspicuous forb layer.	68	34	176
16	Perú	Von Humboldt forest reserve, Pucallpa (W. Amazon basin)	8°48′01″ S 75°03′54″ W	Primary forest selectively logged, 1960	63	31	258
17	Fiji	Bua, Vanua Levu	16°47′36″ S 178°36′45″ E	Disturbed lowland forest on ridge	60	37	158
18	Thailand	Ban Huay Bong, Mae Chaem watershed	18°30′42″ N 98°24′13″ E	Humid-seasonal, deciduous dipterocarp forest fallow system	58	44	200
19	Kenya	Shimba Hills near Mombasa	4°11′33″ S 39°2534″ E	Semi-deciduous forest in game park area. Disturbed (logged).	56	33	214
20	Malaysia (Borneo)	Danum Valley, Sabah	4°53′03″ N 117°57′48″ E	Primary forest subject to reduced impact logging, Nov 1993.	54	39	208
21	Guyana	Iwokrama forest reserve	4°35′02″ N 58°44′51″ W	Primary swamp forest in blackwater system.	52	34	192
22	Georgia	Gezgeti, Mt Kazbegi Central Caucasus Mts	42°40′01″ N 44°36′27″ E	*Betula litwinowii* Krummholz	47	35	198
23	Bolivia	Las Trancas (Santa Cruz)	16°31′40″ N 61°50′48″ W	Semi-evergreen, lowland vine forest, Logged 1996	46	33	302
24	Australia	Atherton tableland, North Queensland	17°18′28″ S 145°25′20″ E	Upland humid forest managed for sustainable timber extraction	46	25	187

25	Panama	Barro Colorado island	9°09′43″ N 79°50′46″ W	Semi-evergreen vine forest, ground layer grazed by native animals	43	30	238
26	Brazil	Reserva Biologica da Campiña Km 50 near Manaus (East Amazon basin)	2°35′21″ S 60°01′55″ W	Moderately disturbed, microphyll, evergreen vine forest on siliceous sands	42	27	276
27	Philippines	Mt Makiling, Luzon	14°08′46″ N 131°13′50″ E	Regen. forest planted in 1968 with *Swietenia*, *Parashorea*, *Pterocarpus*	42	26	194
28	Outer Mongolia	Bear Cub Pass, Khentii Mountains	48°58′35″ N 107°09′18″ E	Mixed Larch and Birch forest	40	25	188
29	Norway	Near Tromsø University and Botanical garden	69°40′41″ N 18°58′13″ E	*Betula tortuosa* forest with dense forb layer.	38	28	150
30	Vanuatu	Yamet, near Umetch, Aneityum Island	20°12′32″ S 169°52′33″ E	Coastal primary forest, logged, with *Agathis macrophylla* (Kauri) overstorey	38	22	217
31	Mexico	Zona Maya, Yucatan peninsula	19°02′26″ N 88°03′20″ E	Logged secondary lowland forest.	37	26	288
32	Indonesia (Borneo)	Batu Ampar, Central Kalimantan	0°47′48″ N 117°06′23″ E	Primary forest, heavily logged 1991/1992	35	23	286
33	Russia	Kamchatka, Upper Tupikin Stream	55°54′36″ N 158°45′46″ E	Stone Birch (*Betula ermanii*) forest with herbaceous ground layer	35	22	138
34	West Indies (France)	Near Mont Pelée, Martinique	0°47′48″ N 117°06′23″ E	Humid, lowland forest on volcanic slopes, heavily disturbed.	32	24	279
35	Mozambique	Supita, near Mopeia	17°56′20.6″ S 35°43′33.8″ E	Semi-deciduous microphyll vine forest. Community reserve	31	24	144

(continued)

Table 4 (continued)

No.	Country	Location	Georeference	Forest type	Species richness	PFT richness	PFC value
36	Argentina	Iguazú Parque Nacional de las Cataratas	25°39′00″ S 54°35′00″ W	Lowland vine forest, disturbed	28	24	302
37	French Guyana	B.E.C. 16 km from Kourou	14°49′23″ N 61°7′37″ W	*Tierra firme* simple evergreen forest on white sand	28	18	146
38	Indonesia (Borneo)	Mandor Nature Reserve, North of Pontianak	0°17′12″ N 109°33′00″ E	Low microphyll evergreen forest in blackwater system on siliceous sand	25	21	228
39	Austria	Heilligenkreutz	48°03′19″ N 16°7′48″ E	Disturbed riparian forest	23	16	116
40	England	Newbridge, River Dart NP Devon	50°31′23″ N 03°50′7.5″ W	Deciduous oak forest	20	19	160
41	Norway	Near Kongsfjord	70°39′36″ N 29°11′53″ E	*Betula tortuosa* partially closed forest with herbaceous understorey dominated by *Cornus suecica*.	13	9	70
42	Spain	Pedro Alvarez Reserve, Tenerife	28°32′4″ N 16°19′0″ W	'Laurisilva' upland forest	12	9	46

Data summary from 1138 (40 m × 5 m) transects with richest vascular plant species and *modal* Plant Functional Type (PFT) and Plant Functional Complexity (PFC) values in each country listed in descending order, extracted from a series of global, ecoregional surveys and restricted to closed forests. All data collected using a standard 'VegClass' sampling protocol and LLR strategy (Gillison 2002, 2013). Forest conditions range from relatively intact to highly disturbed

Sources: International Centre for Agroforestry Research, Alternatives to Slash and Burn Programme (ICRAF/ASB); Center for International Forestry Research (CIFOR); WWF AREAS project; The World Bank, and CBM (Center for Biodiversity Management) are evolutionarily and ecologically unique, and grouping into any functional classification will inevitably ignore some biologically relevant information (Fonseca and Ganade 2001), in addition to which, where indications of redundancy appear in trait overlaps, further study usually reveals that each species occupies fairly separate functional space (Sandquist and Cordell 2007). At finer ecological scales, studies of biological soil crust organisms (Bowker et al. 2011) reveal considerable functional singularity between taxa (notably lichens) that may be expressed through both visible and non-visible attributes thus raising the question of phenotypic limitations in functional typology. The general level of imprecision in assessing functional redundancy is well illustrated by an Australian rangeland study (Walker 1992; Walker et al. 1999) in which "functionally equivalent" species were classified mainly according to height, specific leaf area and longevity while excluding potentially critical features in grazing land systems such as life-history traits, rooting system, water use efficiency, fire and drought tolerance and herbivore resistance. In that study functional equivalence was identified through ordination procedures that by themselves are open to significant information loss and a highly arbitrary characterisation of functional differences between species (Fonseca and Ganade 2001; Villéger et al. 2008; Mouchet et al. 2010). Elsewhere, Gitay et al. (1996) and Gillison (2013) argue that the level of knowledge required to implement the method described by Walker et al. (1999) would be very difficult to achieve in practice and, if applied, would run the risk of generating misleading outcomes about ecosystem performance.

Tests for Redundancy

Hard evidence for redundancy and the functional consequences of species loss among terrestrial vascular plant species is singularly lacking, and adequate experimental designs for in situ testing of functional redundancy are yet to be determined. Rather than assuming functional redundancy, Sullivan and Zedler (1999) recommend testing for similarity of group members under varied conditions, e.g. alone and with their common neighbours and under benign and stressful conditions. It is also argued (Rosenfeld 2002) that experiments designed to assess redundancy based on a single functional attribute will be biased towards finding redundancy, because species are more likely to have non-overlapping functional niches in a multi-dimensional functional space. In this respect Gamfeldt et al. (2008) showed that due to multi-functional complementarity among species, overall functioning is more susceptible to effects of species loss than are single functions. The most comprehensive testing for functional redundancy appears to be among soil organisms and related bacterial and fungal microcosms (Yin et al. 2000; Wohl et al. 2004; Bowker et al. 2011), where the high degree of environmental control suggests that similar experimental rigour in studies of vascular plant assemblages would be impractical. Cyclic patterns in highly dynamic community types present clear limitations to redundancy testing if conducted solely at one specific stage of succession or in vegetation types such as arctic tundra where, because the age of some tundra tussock grasses may exceed 100 years (Bret-Harte et al. 2008), any experimental manipulation to test for redundancy would take a very long time.

Redundancy and Functional Scale

Measures of functional redundancy are closely coupled to varying scales of functional typology from molecule to ecosystem and, by aggregation, to biome. Whereas partitioning functional diversity within and among communities indicates that both trait convergence and divergence co-operate in the formation of assemblages from the local species pool, in spite of changes in species composition, considerable trait convergence at the regional scale implies ecological redundancy among communities at that scale (de Bello et al. 2009). According to Pillar and Sosinski (2003), redundancy at the population level, as indicated by the degree of association between traits based on a matrix of populations by traits, differs from that at the community level, which is the result of redundancy at the population level plus its manifestation in terms of different plant types and quantities in the matrix of populations by communities. The removal of assumed 'functionally redundant' species can also influence community dynamics and processes, indicating that there are important functional differences not captured by broad groupings (Cadotte et al. 2009).

The performance of functional traits and syndromes is inevitably influenced by their position along a hierarchy of environmental filters ranging from global climate to local factors such as soil type and land-use history. These filters, in turn, determine the level of functional typology and thus the criteria used to assess redundancy, including differing measures of functional diversity and niche complementarity (Petchey and Gaston 2002b; Mouchet et al. 2010). As illustrated by Laliberté et al. (2010) in a meta-analysis of traits known to influence ecosystem processes, regional land-use intensification can reduce both functional redundancy and response diversity significantly, although specific relationships may vary considerably among the different land-use gradients. In such cases, environmental context can be critical in evaluating niche complementarity and thereby functional redundancy. Similar studies of vegetation response along a land-use intensity gradient in Sumatra, Indonesia (Gillison et al. 2013), revealed a rise in the number of PFTs relative to species at levels of intermediate disturbance that was significantly higher than that recorded in a more species-diverse mature forest. This response pattern is consistent with the intermediate-disturbance hypothesis as well as cyclic patterns of natural disturbance in forest mosaics (e.g. tree-fall gaps), where functional traits and syndromes cycle in situ. In such conditions, where one successional phase may facilitate another in a tropical lowland forest, or where facilitation can be antagonistic between species in alpine herbfields

(Schöb et al. 2013a, b), protocols by which criteria are selected to assess functional redundancy require careful analysis within the context of ecosystem dynamics.

Redundancy and Conservation

Complementarity between functional groups, while playing clearly into links with redundancy, is rarely tested in complex vegetation types and yet may have important consequences for conservation planning at landscape scale. It is frequently argued that, because of the uncertainties surrounding the concept of species redundancy, it is unproductive to apply the concept in conservation where species may be lost needlessly (Lawton and Brown 1993; Collins and Benning 1996; Gitay et al. 1996). It is also axiomatic that, where clear evidence indicates that the number of different functional groups increases with the number of species (Gillison 2013), conserving a large proportion of the functional traits of species will also require conserving a large proportion of all species (Petchey and Gaston 2002a). Based on these principles, conservation planning and management therefore need to employ a conservative approach that maximizes and maintains species diversity at every stage.

Stoichiometric and Metabolic Scaling of Functional Types

Biological stoichiometry theory considers the balance of multiple chemical elements in living systems. Ecological stoichiometry, on the other hand, recognizes that organisms themselves are outcomes of chemical reactions and thus their growth and reproduction can be constrained by supplies of key chemical elements, especially C, N and P (Chapin et al. 1986; Niinemets and Kull 1998; Sterner and Elser 2002; Elser and Hamilton 2007; Ågren 2008; Danger et al. 2008; Elser et al. 2010). In ecology, stoichiometric units are most commonly used as molar ratios in physiological research and in aquatic systems because they reflect the actual stoichiometric relationships, but most literature in terrestrial ecology reports mass ratios (Sterner and Elser 2002; Güsewell 2004). Across environmental scales, natural selection has shaped the form and function of plants so that leaves exhibit a net positive return on resource investment, by which the total mass of carbon assimilated by a leaf over its life span will be greater than the total mass of carbon invested in the leaf (Chabot and Hicks 1982; Williams et al. 1989; Westoby et al. 2002; Blonder et al. 2011)—a relationship consistent with the LHS and LES strategic models. Within this selective process and across multiple scales, the species-specific, stoichiometric constants controlling trait covariation in regulating metabolic processes appear to be largely independent of biome or leaf type (Kikuzawa and Lechowicz 2006; Minden 2010; Blonder et al. 2011). This suggests that, while genetically pre-determined morphological and physiological characteristics of leaf and other functional traits in terrestrial vascular plants find expression within a realized resource niche (cf. Vasseur et al. 2012), overall ecological performance and fitness will be subject to stoichiometric control, typically operating in a C:N:P type environment. Such control of size-dependent scaling of leaf support investments may also be mediated by life form and climate (Niinemets et al. 2007).

Plant traits related to size and growth rate are particularly important because they determine the productive capacity of vegetation and the rates of decomposition and nitrogen mineralization (Chapin 2003). Metabolic scaling theory considers how size affects metabolic properties from cells to ecosystems. In this context plant stoichiometry exhibits size scaling, as foliar nutrient concentration decreases with increasing plant size, especially for phosphorus. Thus, in line with the LES strategy, small plants, frequently with small leaves, have lower N:P ratios. Foliar nutrient concentration is also reflected in other tissues (root, reproductive, support), permitting the development of empirical models of production that scale from tissue to whole-plant levels (Gordon and Jackson 2000; Elser et al. 2010; Minden 2010). Global trends (see also Reich and Oleksyn 2004; Ballantyne et al. 2008) couple latitude as well as environmental phosphorus concentration with plant stoichiometry. Research thus far suggests that an improved knowledge of the stoichiometric role in the plant size-nutrient-environment nexus can lead to a better understanding of factors such as carbon dioxide, temperature and nitrogen deposition along gradients of environmental change at global scale (Elser et al. 2010; Reich and Oleksyn 2004; cf. Laughlin 2011). At within-community scale, however, stoichiometric control of leaf N may be mediated significantly by a variety of local filters such as photon flux density (PPFD) as observed by Posada et al. (2009), who found tree leaves in a tropical forest canopy optimized photosynthetic use of PPFD rather than N per se. As with biome-invariant scaling exhibited in the LES strategy, response patterns demonstrated at global level in stoichiometric and metabolic scaling may not necessarily hold at ecosystem or community level.

Scale-Related Trait Performance Within and Between Species

The search for traits that reflect plant performance adequately along biophysical gradients has generated a series of scale-invariant models at global dimensions that reveal typically robust linear correlates between functional traits and key physical environmental variables, as illustrated in the LES and LHS strategies. In the majority of these cases species are typically described by functional trait measurements collected from a few individuals from one or few populations and averaged at the population or species level, disregarding the intra-specific functional variability (Albert et al. 2010a). As currently described, plant strategies centred around economic parsimony assume that infra-specific variation in functional traits is of negligible significance compared to individual species or community-weighted means of inter-specific functional traits. Yet the potential ecological significance of within-species variation in functional traits is rarely subjected to empirical or experimental analysis. Despite the widespread focus on inter-specific variation in trait-based ecology, recent studies across widely differing ecosystems provide increasing evidence that intra-specific trait variability can play a fundamental role in plant community responses to environmental change and community assembly (Gillison 2013; Kichenin et al. 2013). New evidence is also emerging that, using a single trait value to describe a given species can hide large functional variation for this species along environmental gradients and that intra-specific as well as inter-specific functional variability can have significant effects on community dynamics and ecosystem functioning. Such information can be critical to understanding ecological patterns in changing environments (Albert et al. 2010a, b; Gillison 2013).

The detection and analysis of intra-specific trait variation are, to a large extent, context-dependent, with localized observations unlikely to reveal as much within-species variation as in those made along wide-ranging biophysical gradients. Recent recognition of the role of intra-specific traits in ecosystem performance is evident from studies of genotypic variation and phenetic plasticity across a range of spatio-temporal scales. This is apparent at latitudinal scale (de Frenne et al. 2013), in arctic tundra (Soininen et al. 2013), along elevational gradients in alpine and subalpine vegetation (Jung et al. 2013; Kichenin et al. 2013), in temperate herbaceous vegetation (Siefert 2012), in temperate forests (Grady et al. 2013; Jackson et al. 2013) and in tropical forests (Martínez-Garza et al. 2005; Hulshof and Swenson 2010).

The studies referred to above are based on values obtained from differing groups of single functional traits rather than whole-plant (combinatorial) syndromes. The *modal* PFT combinations embodied in the LLR strategy provide a basis for analysing both inter-specific and intra-specific variation in whole-plant variation along environmental gradients as well as unique PFTs (not linked with species) and their component PFEs for individual plants. The latent information embodied in this flexible approach is illustrated in Table 5, in which intra-specific variation in the genus *Betula* is expressed in leaf size class, leaf inclination and presence of green stem photosynthesis in phanerophytes (woody plants > 2 m tall). Numerical analysis of this formalized intra-specific variability is facilitated through quantitative values attached to each PFT and PFE in the LLR system and via the VegClass computer program (Gillison and Carpenter 1997; Gillison 2002).

Functional Types and Traits as Bioindicators Across Multiple Scales

Bioindicators are widely used in assessing and monitoring biophysical environmental conditions, such as acid rain, pollutants, landscape rehabilitation, contamination and environmental impacts on biota. For biodiversity assessment and monitoring at a range of environmental scales, surrogate measures include a wide range of

Table 5 Circumboreal intraspecific variation in the genus *Betula*

Species	*modal* PFT	Location	Country
B. daurica	mi-co-do-de-ph	Shkotovo	Russia
B. daurica	no-co-do-de-ph	Vladivostok	Russia
B. daurica	no-la-do-de-ch	Vladivostok	Russia
B. ermanii	mi-pe-do-de-ph	Gothenburg (cult.)	Sweden
B. ermanii	no-co-do-de-ph	P. Kiyevka Pass	Russia
B. ermanii	no-la-do-de-ch	Kamchatka	Russia
B. ermanii	no-la-do-de-ct-ph	Kamchatka	Russia
B. ermanii	no-pe-do-de-ct-ph	Kamchatka	Russia
B. ermanii	no-pe-do-de-ph	Kamchatka	Russia
B. litwinowii	mi-la-do-de-ph	Mt Kazbegi	Georgia
B. litwinowii	mi-pe-do-de-ct-ph	Mt Kazbegi	Georgia
B. litwinowii	mi-pe-do-de-ph	Mt Kazbegi	Georgia
B. nana	na-pe-do-de-ph-ad	Abisko	Sweden
B. nana	na-ve-do-de-ch-ad	Båtsfjord	Norway
B. nana	no-ve-do-de-ch	Saaremaa	Estonia
B. pendula	mi-pe-do-de-ph	Ascona	Switzerland
B. pendula	mi-ve-do-de-ch	Tromsø	Norway
B. pendula	mi-pe-do-de-ph	Kuresoo bog	Estonia
B. pendula	mi-pe-do-de-ch	Saaremaa	Estonia
B. pendula	me-la-do-de-ch	Saaremaa	Estonia
B. pendula	mi-la-do-de-ch	L. Peipsi area	Estonia
B. pendula	no-pe-do-de-ph	Raplamaa	Estonia
B. platyphylla	mi-co-do-de-ph	Shkotovo	Russia
B. platyphylla	mi-co-do-de-ph	Khentii Mts	Mongolia
B. platyphylla	mi-pe-do-de-ct-ph	Khentii Mts	Mongolia
B. platyphylla	no-co-do-de-ph	Kamchatka	Russia
B. platyphylla	no-ve-do-de-ph	Kamchatka	Russia
B. playphylla	mi-pe-do-de-ct-ph	Kamchatka	Russia
B. tortuosa	mi-pe-do-de-ph	Abisko	Sweden
B. tortuosa	mi-co-do-de-ct-ph	Kongsfjord	Norway
B. tortuosa	mi-co-do-de-ch	Helligskogen	Norway
B. tortuosa	mi-la-do-de-ct-ph	Helligskogen	Norway
B. tortuosa	mi-co-do-de-ph	Tromsø	Norway

All data collected using the VegClass recording protocol and the LLR methodology. Variation in PFT combinations reflect differences in regional thermal regimes and in local physiographic (especially aspect and hydrology) and soil property gradients. For PFT coding see Table 2

environmental units or arbitrary ecosystem 'types' or combinations of both (Oliver et al. 2004; Carmel and Stroller-Cavari 2006; Grantham et al. 2010; Gillison 2013). There is no apparent consensus on how to use bioindicators (Büchs 2003) as they tend to be geared to widely varying scale and purpose. While few examples of generic indicators exist beyond the ecosystem level, for national forest inventories Newton and Kapos (2002) argue that biodiversity indicators should be appropriate across local and broader scales. For biodiversity at least, plant species are the most widely used of all surrogates, but considerable debate surrounds their efficacy in predicting the distribution of other taxa (Lawton et al. 1998; Lewandowski et al. 2010; Lindenmayer and Likens 2011; Sætersdal and Gjerde 2011). Vandewalle et al. (2010) suggest that the development of indicators using functional traits could complement, rather than replace, existent biodiversity monitoring procedures. In this way, comparison of the effect of land-use changes on biodiversity is facilitated and can be expected to influence conservation management practices positively. While the potential utility of this approach shows promise, field validation is sparse at local and landscape scales (Gillison and Liswanti 2004; Bardgett 2005; Liira et al. 2008; Lavorel et al. 2011) and, with some exceptions in remote sensing (e.g. Kooistra et al. 2007), is seemingly non-existent at broader regional and biome scales.

Data recorded using the LLR strategy along biophysical gradients can exhibit predictable changes in plant species and *modal* PFT combinations as well as vegetation structure. As indicated by Vandewalle et al. (2010), complementary functional traits can be used to characterize biological habitat and thus facilitate predictive modelling of the distribution of taxa. One fundamental measure of habitat characterization namely niche complementarity, is typically expressed for conservation and management purposes through species assemblages and species turnover. When used independently, vascular plant species and PFTs can provide a limited measure of niche complementarity that is subsequently improved when both are expressed as a species:PFT ratio. Across multiple scales the ratio can be shown to vary predictably along resource-availability and disturbance gradients, reflecting quick-slow response strategies contained in LES, LHS and CSR. This is illustrated, for example, in a regional gradient of land-use intensity along which the species: PFT ratio is initially high in an old-growth forest and becomes progressively reduced with increasing disturbance as more ecological niches become available with fewer species available per niche, until the ratio may approximate unity at a disturbance extreme (Gillison et al. 2013). While evident across localized environmental gradients, the pattern can be repeated across biomes; for example, a lowland tropical rain forest in Indomalesia has a species:PFT ratio of 2.97 compared to an exposed Icelandic lava field with a ratio of 0.88.

Apart from serving as an alternative measure of niche complementarity, the species:PFT ratio can be used as a bioindicator for conservation management purposes. Changes in termite species richness along a Sumatran land-use intensity gradient were correlated significantly with plant species richness and modal PFT richness; a correlation that was greatly improved when termite species richness was regressed against the species:PFT ratio (Gillison et al. 2003; Bardgett 2005). The high correlation between relative abundance of termite species and the species:PFT ratio in Sumatra is also repeated in Brazil (Gillison et al. 2013) along a similar land-use intensity gradient. When combined, the data also reveal a constant relationship using the same ratio (Fig. 11), despite there being significant differences in the evolution of biota in these two biogeographically separate regions (cf. Heberling and Fridley 2012).

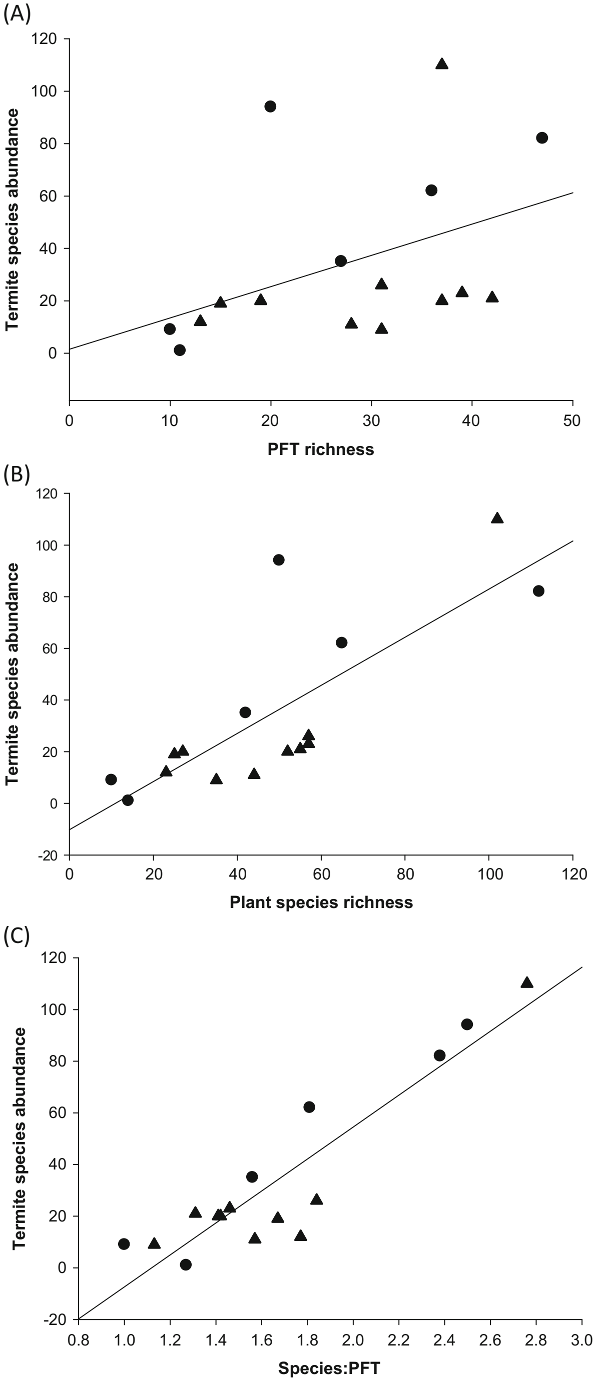


Fig. 11 Plant functional types as indicators of relative termite abundance across two biogeographic regions. *Solid triangles* are samples from Mato Grosso, Brazil; *Solid circles* are samples from Sumatra, Indonesia: (**a**) *modal* PFT richness, (**b**) plant species richness, (**c**) species:PFT ratio

Discussion

In the past few decades there has been incremental, albeit rapid progress across three phases of investigation in plant functional ecology. The first of these reflected a change from models based on ‘adaptive’ Raunkiær life forms to broader, more prescriptive groupings of functional traits within and between communities as well as individual species (Grime 1977; Box 1981, 1996; Gillison 1981; Keddy 1992). This paved the way to a more tightly focused approach leading from ‘noisy’ sets of highly co-varying functional traits towards acquisitive-economic models which sought to identify parsimonious sets of traits that were, on the one hand, recognizably independent in terms of function but, would at the same time, elucidate relationships better between environment and species investment in resource acquisition and return (Westoby 1998; Westoby et al. 2002; Wright et al. 2004). While the spectrum of traits embodied in these biome-invariant models has improved theoretical insights with respect to plant functional and environmental relationships, in practice the methodology is constrained by the need for laboratory-based measurements, thereby limiting field observations. The methodology also excludes, by default, much of the world’s vegetation cover in arid lands, which support extensive areas of succulent or highly seasonal vegetation types with corticular photosynthesis and metabolic pathways that differ from most other vascular plant species.

There is an emerging awareness that the ecological signals generated by parsimonious sets of functional traits may be less clear than previously thought. Current evidence suggests there could be significant information loss where parsimonious, functional criteria exclude co-varying traits that include additional key functional characteristics related to water-use efficiency, photosynthesis and growth. Mechanisms controlling trait convergence and divergence reflected in habitat filtering and niche differentiation may be interacting in tandem within certain trait syndromes, for example along aridity gradients, raising further questions about whole-plant interactive relationships. A realization that whole-plant functional syndromes rather than dispersed functional traits may provide better insights into plant functional response across multiple scales is evident in holistic shoot-root models that scale from tissue to whole-plant levels (Gordon and Jackson 2000; Craine et al. 2005; Elser et al. 2010) to regional scale (Liu et al. 2010; Kang et al. 2013) and above (Fortunel et al. 2012). Evidence for the decoupling of leaf and wood traits as separate functional axes (Kang et al. 2013) supports further the possibility that measures of niche dimensionality across environmental scales will increase as our understanding of whole-plant function improves.

In the majority of cases the successful application of different strategies has much to do with environmental context as well as spatial scale. It is here that new findings about intra-specific variation will be enhanced by studies along extended biophysical gradients, thereby feeding back into models otherwise based on measures of inter-specific response and community-weighted means. The move towards global trait datasets (e.g. Kattge et al. 2011) will facilitate a more comprehensive synthesis of information and data than exists at present and is a welcome initiative that should lead to improved models of plant-environmental relations across multiple scales. A pervasive problem nonetheless concerns widespread inconsistencies in methods of data recording, storage and access that, if not managed properly, have the potential to generate misleading outcomes in plant ecological research. To this extent and as presented in this chapter, the global data underlying the VegClass LLR system have the advantage of a uniform protocol of field collection, collation and meta-analysis consistent with international standards of data management. Uniformity of this kind greatly enhances the investigation of trait performance across multiple scales and suggests that similar advantages are to be gained through the standardization of methods of data collection and analysis.

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Part II
Regional Vegetation Analysis and Synthesis

Evergreen Broad-Leaved Forest of East Asia

Song Yong-Chang and Da Liang-Jun

Abstract Under the influence of alternating subtropical high atmospheric pressure and tropical cyclonic influence, large regions within 23–35° N latitude have desert or semi-desert, especially on continental wet sides. Only the Mediterranean region, eastern North America and East Asia have evergreen broad-leaved forest (EBLF), a special vegetation type. Especially in southeastern China, central and southern Japan, as well as southernmost Korea, all under the influence of a monsoon climate, this vegetation type appears to be typical and luxuriant. Based on ecologically conditioned physiognomy and floristic composition, the EBLF of East Asia are classified into: (1) typical summer-rain EBLF, (2) subtropical seasonal EBLF, and (3) subtropical ombrophilous EBLF. The consistencies and differences of these types are compared and discussed.

Introduction

As we look at a vegetation map of the world, at once we might notice that a large part of the mid-latitude region of the Northern Hemisphere, between 23° and 35° N latitude is covered by desert or semi-desert. The exceptions are in eastern North America, East Asia, and the coastal Mediterranean region, where a unique form of forest vegetation occurs, the so-called "evergreen broad-leaved forest" (EBLF). The EBLF in East Asia is so well developed and its area is so large, that it comprises a major portion of the warm-temperate/subtropical forest area of the whole world. For a relatively long period, this unique vegetation type did not draw enough attention from scientists or other people. Academic discussions on EBLF were

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We have modified the classification system for evergreen broad-leaved forest of China. The new classification system was shown in a new book Song Y-C (2014) Evergreen broad-leaved forest in China. Classification-Ecology-Conservation. Science Press, Beijing, 801 . The readers who interet on it, please check the new book for more detail.

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concerned mostly about the Laurusilvae of the Mediterranean area and adjacent east-Atlantic islands, referring only in rare cases to the Asian EBLF, and then only very briefly (Ovington 1983). Since the 1970s, through the work of Japanese scholars (e.g. Suzuki 1975; Miyawaki 1981; Fujiwara 1981–1986; Kira 1991), the Japanese EBLF has become well known to vegetation scientists around the world. In the 1980s, research results on the EBLF of China (e.g. Wu 1980; Song 1983, 1988a, b; Zhong 1992), accompanying the increased communication between China and the world, brought these forests to the attention of the world academy (e.g. Klötzli 1988; Hübl 1988; Box et al. 1991). This paper will summarize the evergreen broad-leaved forest of East Asia, based on comparison with other EBLF areas in the Northern Hemisphere.

Characteristics of EBLF of East Asia

There are different meanings for the term EBLF. Generally speaking, these can be divided into two categories. One is the narrow sense, which regards the EBLF only as the typical EBLF created by the monsoon climate (Klötzli 1988); the other is the broad sense, in which EBLF is the type of forest composed of evergreen broad-leaved trees occurring in extra-tropical areas. This includes not only the winter-rain and summer-rain evergreen broad-leaved forests, but also temperate rainforest (Ovington 1983, etc.), even subtropical rainforest. Here we discuss the EBLFs at global scale, so the broad sense is adopted.

EBLF around the world share many common features, such as forest canopies composed of evergreen trees, limited extent in extra-tropical regions, and inability to tolerate long-term low temperature and drought. These forests do not show the typical characteristics of tropical rainforests, however, and show big differences in climate conditions, ecological characteristics and floristic composition (Table 1).

Evergreen broad-leaved forest in the Canary Islands and Mediterranean region grows under a mediterranean climate, with precipitation relatively low and concentrated in the winter (or at least not in summer); the summer is very dry, the annual temperature range is small, and the major restrictive factor for the distribution of EBLF is the water supply. This type of EBLF is a topographic climax, which only exists at a certain elevation on the Canary Islands, where there is a cloud belt and misty weather. The communities appear to show some xerophilization. The floristic composition mostly involves Mediterranean elements, plusa large number of Macaronesian elements. The forest storeys are composed mainly of Lauraceae, Theaceae, and Ericaceae (Hübl 1988; Nakamura et al. 1999; Arco Del and Wildpret de la Torre 1999), with apparently no species at all from the evergreen Fagaceae.

The EBLF of southeastern North America occurs in a moist warm-temperate climate (subtropical in south Florida), with precipitation distributed more evenly over the year and a rather small annual temperature range (Olson 1983). The communities appear to be mesophytic, with floristic composition involving mainly East Asia-North American disjunct elements. The dominant species are Fagaceae

Table 1 Climatic conditions, eco-physiognomy and floristics of EBLFs of the Northern Hemisphere

	East Asia	Eastern North America	Canary Islands plus Mediterranean region
Climatic Condition	Subtropical to warm-temperate monsoon climate, with hot moist summer and fairly cold winter	Subtropical to warm-temperate moist climate with precipitation distributed more evenly over the year	Mediterranean climate, with precipitation concentrated in winter (or at least not in summer)
AAT (°C)	13–20 (22)	18–21	13–15
CMT (°C)	0.9–10 (16)	9–13 (10–19)	9–11
ATR (°C)	10–26	15–18 (8.5–17)	7–9
WI (°C)	85–180 (210)	165–225	100–145
CI (°C)	−10 to 0	0	0
Pa (mm)	>1000	1000–1500 (1200–1600)	400–600
Ps (%)	33–63	25–39	0.3
Pw (%)	2–14	14–31	60
Ecological features	Mesophytism; trunks straight, communities tall; scaled-buds abundant (at least in typical EBLFs)	Mesophytism; trunks straight, communities tall, leaves of main trees have no serration.	Light xerophilization; communities generally lower; many trees with hypsophyllary buds
Floristic composition	Dominated by Sino-Japanese elements; many endemic elements	Dominated by East Asia-North American disjunct elements; Caribbean elements present	Dominated by Mediterranean elements, with many endemic Macaronesian elements
Lauraceae	*Machilus* (*Persea*) spp. *Beilschmiedia* spp. *Neolitsea* spp. *Cinnamomum* spp.	*Persea borbonia* *Persea palustris* *Nectandra coriacea*	*Persea indica* *Laurus azorica* *Ocotea foetens* *Apollonias barbujana*
Theaceae	*Gordonia* spp. (China) *Camellia* spp. *Eurya* spp. *Cleyera* spp.	*Gordonia lasianthus*	*Visnea mocanera*
Oleaceae	*Ligustrum* spp. *Osmanthus* spp.	*Osmanthus americanus*	*Picconia excelsa*
Rosaceae	*Prunus* spp. *Rhaphiolepis* spp. *Photinia* spp.	*Prunus caroliniana* *Prunus myrtifolia*	*Prunus lusitanica* *Bencomia caudate*
Myricaceae	*Myrica rubra*	*Myrica cerifera*, etc.	*Myrica faya*
Ericaceae	*Vaccinium* spp. *Rhododendron* spp.	*Vaccinium arboreum* *Lyonia ferruginea*, etc.	*Erica arborea*
Fagaceae	*Cyclobalanopsis* spp. *Castanopsis* spp. *Lithocarpus* spp.	*Quercus virginiana* *Q.hemisphaerica* *Q. myrtifolia*, etc.	–
Magnoliaceae	*Magnolia* spp. *Michelia* spp. *Manglietia* spp.	*Magnolia grandiflora* *Magnolia virginiana*	–

(continued)

Table 1 (continued)

	East Asia	Eastern North America	Canary Islands plus Mediterranean region
Sapotaceae	*Sinosideroxylon* (China)	–	*Sideroxylon marmulano*
Hamamelidaceae	*Distylium* spp.	–	–
Daphniphyllaceae	*Daphniphyllum* spp.	–	–
Elaeocarpaceae	*Elaeocarpus* spp.	–	–
Sabiaceae	*Meliosma* spp.	–	–

AAT annual average temperature, *CMT* coldest-month temperature, *ATR* annual temperature range, *WI* Warmth Index, *CI* Coldness Index, *Pa* annual precipitation, *Ps* precipitation in summer (Jun, Jul, Aug) as percentage of annual precipitation, *Pw* precipitation in winter (Dec, Jan, Feb) as percentage of annual precipitation

and Magnoliaceae, but the genus *Castanopsis* are entirely absent? (Box and Fujiwara 1988; Fujiwara and Box 1994).

The EBLF of East Asia occurs under a monsoon climate, with hot, moist summers and fairly cold winters; the annual temperature range is drastic. These communities also appear to be mesophytic, with floristic composition involving mainly Sino-Japanese elements. The dominant species are Fagaceae, Lauraceae, Theaceae, Magnoliaceae, and Hamamelidaceae, sometimes mixed with a few coniferous or deciduous trees. These species cannot tolerate conditions that are too wet or too dry, and are hurt by freezing temperatures. The major limiting factor for their distribution is low temperature in winter.

Classification of EBLF in East Asia

The EBLF of East Asia extends from 39 to 23° N and from 141 to 97° E (see Fig. 1). Because of the different geographic locations and climatic conditions, the EBLF in different places are distinct not only in eco-physiognomic features but also in floristic composition. These forests can be divided into three main types (Table 2).

Typical Summer-Rain EBLF of East Asia

The basic characteristics of typical summer-rain EBLF are shown above and have been summarized in earlier papers (Song 1994, 1995). This type occurs in central and southern Japan, southernmost Korea, and the eastern and western parts of China, as well as on mountains of Taiwan (Hsieh 1997). Based on the habitat and floristic components, the typical summer-rain EBLF can be divided into four regional subtypes. Their differences are shown in Tables 3 and 4.

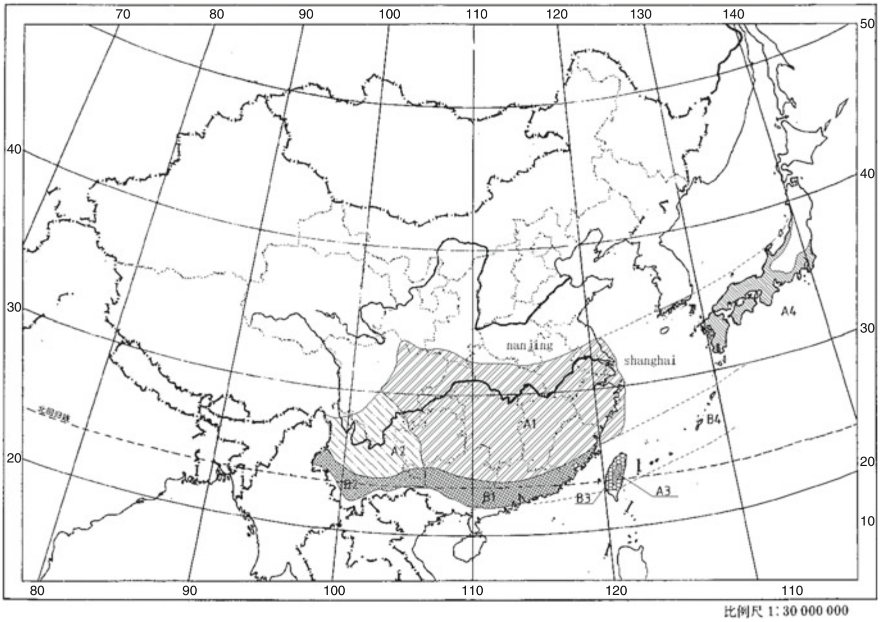

Fig. 1 The distribution of EBLF in East Asia. A1. Typical EBLFs of eastern China; A2. Typical EBLFs of western China; A3. Typical Montane EBLFs of Taiwan; A4. Typical EBLFs of Japan and Korea; B1. Subtropical seasonal EBLFs of eastern China; B2. Subtropical seasonal EBLFs of western China. B3. Subtropical seasonal EBLFs of Taiwan; B4. Subtropical seasonal EBLFs of Japan

Typical EBLFs of Eastern China

The dominant species composing the tree layer belong to the genera *Castanopsis, Cyclobalanopsis, Lithocarpus, Machilus, Cinnamomn, Schima,* and *Altingia*, etc. Some warmth and humidity-loving conifers and deciduous trees also appear in this community. The herbaceous undergrowth is predominated by Pteridophytes, including tree ferns. The flora is composed of Sino-Japanese elements. Diagnostic species are *Cyclobalanopsis glauca*, *Camellia freterna, C. cuspidata*, and *C. oleosa*. This community can be called the *Camellio-Cyclobalanosietea glaucae*, and divided into three collective groups[1] (Song 2004). The distribution of each type is shown in Fig. 2 and the distribution of the main species in Fig. 3.

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[1] In China people always use the term “formation group” for such units; in order to avoid misunderstanding with the term “formation”, here we use the term “collective group”, similar to the “collective type” of Whittaker (1980).

Table 2 Characteristic of main types of EBLF in East Asia

Type	Typical summer-rain EBLF	Subtropical seasonal EBLF	Subtropical ombrophilous EBLF
Climatic conditions	Warm-temperate to subtropical monsoon climate, with hot moist summer and fairly cold winter; large annual temperature range	Subtropical monsoon climate, with hot moist summer and warm winter; smaller annual temperature range	Subtropical monsoon climate, with hot moist summer and warm winter; very moist habitats
Ecological feature	Mesophytization; stratification quite distinct with hemispherical crowns and more regular canopy; leaves smooth leathery; microphylls–mesophylls; trunks straight, with rough thick, dark brown bark; buds are scale-covered; lianas and epiphyte occur, but thick lianas and epiphytic spermatophytes very rare or absent.	Mesophytization; stratification distinct; canopy regular; leaves mesophyll and medium; trunks straight with thin thick brown bark; lianas and epiphytic plants less abundant than in subtropical rainforests; buttressing and cauliflory uncommon.	Meso-hydrophytization; mainly mesophylls; trunks straight with thinner bark; plank-buttresses common; thick lianas, epiphytic ferns and phanerogams; means of protection against transpiration weakly developed. Much more complex structure.
Characteristic of floristic elements	Dominated by Sino-Japanese elements, many relict and endemic species.	Dominated by Sino-Japanese elements, Indo-Malaysia elements frequently present, more tropical elements.	Dominated by Sino-Japanese elements, Indo-Malaysia elements frequently present, more tropical elements.

I. *Lithocarpus*-*Cyclobalanopsis* Collective Group

The ecological amplitude this collective group is wide, since it is more cold-tolerant and occurs mainly in the northern part of the EBLF zone. Cold and drought-tolerant species of *Lithocarpus* and *Cyclobalanopsis*, such as *Lithocarpus glaber, L. harlandii, L. hancei; Cyclobalanopsis glauca, C. myrsinaefolia, C. sessilifolia, C. gracilis*, and *C. stewardiana*, are the dominant and diagnostic species of this group. It includes six dominance types (Do-Ty).[2] These are: *Cyclobalanopsis glauca*, *Castanopsis sclerophylla*, *Lithocarpus glaber* Do-Ty*; Cyclobalanopsis myrsinaefolia, C. gilva, C. sessilifolia* Do-Ty; *Cyclobalanopsis stewardiana, C. gracilis* Do-Ty; *Litsea coreana* var. *sinensis-Lithocarpus harlandii* Do-Ty; *Cyclobalanopsis oxyodon, C. multinervis* Do-Ty; and *Quercus engleriana-Lithocarpus cleistocarpus* Do-Ty.

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[2] In China people always use the term of “formation” for this unit, here we use “dominance type” (Do-Ty) instead of the corresponding term “alliance” used by the Braun-Blanquet school.

Table 3 Distribution and ecological feature of four subtypes of the typical EBLF in East Asia

	Eastern China	Western China	Montane Taiwan	Japan and Korea
Subtype	*Camellio-Cyclobalanopsetea glaucae*	*Camellio-Cyclobalanopsetea glaucoidis*	*Castanopsio-Cyclobalanopsetea longinuxi*	*Camellietea japonicae*
Distribution	23°–33° N 100–1500 (2800) m a.s.l.	23°–30° N 1500–2500 (2800) m a.s.l.	22°–25° N 800–2300 m a.s.l.	26°30′–40°35′ N <850 m
AAT (°C)	15–18	10–17	10–19	13–18
CMT (°C)	2–10	4–10	5–14	0.9–10
ATR (°C)	18–26	10–14	9–9.5	13–21
WI (°C)	125–180	91–170	67–170	85–180
CI (°C)	−10 to −2 (0)	0	0	−10 to 0
Pa (mm)	1000–2000	800–1500	2355–3962	1200–2500
Ecological features	Mesophytic; leaves smaller to medium, trunks straight, with thicker brown bark.	Some xeromorphization; leaves smaller, slightly sclerophyllous; trunks crooked, with thick bark.	Mesophytization; leaves smaller to medium; trunks straight, with thicker brown bark	Mesophytic; leaves smaller to medium; trunks straight, bark brown and thicker
Characteristic floristic elements	Dominated by Sino-Japanese elements, rich in relict and endemic species.	Mainly Sino-Himalayan elements, rich in endemic species.	Dominated by Sino-Japanese elements, rich in endemic species.	Dominated by Sino-Japanese elements.

AAT annual average temperature, *CMT* coldest-month temperature, *ATR* annual temperature range, *WI* Warmth Index, *CI* Coldness Index, *Pa* annual precipitation

Table 4 Dominant and diagnostic species of the subtypes of typical EBLF in East Asia

Subtypes	East China	West China	Montane Taiwan	Japan and Korea
Cyclobalanopsis glauca	do/di	+	+	do/di
Cyclobalanopsis myrsinaefolia	do/di	+	+	do/di
Machilus thunbergii	do/di	–	+	do/di
Castanopsis eyrei	do/di	–	+	–
Castanopsis carlesii	do/di	–	do/di	–
Castanopsis sclerophylla	do/di	–	–	–
Lithocarpus glabra	do/di	–	–	–
Schima superba	do/di	–	–	–
Cinnamomum subavenium	do/di	–	–	–
Camellia oleosa	di	–	–	–
Camellia fraterna	di	–	–	–
Castanopsis platycantha	do/di	+	–	–
Castanopsis carlesii var. spinulosa	do/di	do/di	–	–
Cyclobalanopsis glaucoides	–	do/di	–	–
Cyclobalanopsis delavayi	–	do/di	–	–
Castanopsis delavayi	–	do/di	–	–
Castanopsis orthacantha	–	do/di	–	–
Lithocarpus dealbatus	–	do/di	–	–
Schima noronhae	–	di	–	–
Camellia pitardii var. *yunnanensis*	–	di	–	–
Camellia forrestii	–	di	–	–
Lithocarpus amygdalifolis	–	–	do/di	–
Cyclobalanopsis longinux	–	–	do/di	–
Cyclobalanopsis mori	–	–	do/di	–
Neolitsea acuminatissima	–	–	di	–
Symplocos arisanensis	–	–	di	–
Michelia formosana	–	–	di	–
Trochodendron aralioides	–	–	di	+
Cyclobalanopsis acuta	–	–	–	do/di
Castanopsis cuspidata	–	–	–	do/di
Castanopsis sieboldii	–	–	–	do/di
Camellia japonica	+	–	+	di
Camellia sasanqua	–	–	–	di
Camellia lutchuensis	–	–	–	di

do = dominant species, di = diagnostic species, + = species present as companion

II. *Schima-Castanopsis* Collective Group

This group is the representative type of the EBLF of eastern China, occurring widely in the mid-subtropical region (sensu *sinico*). *Schima superba, S. argenta*

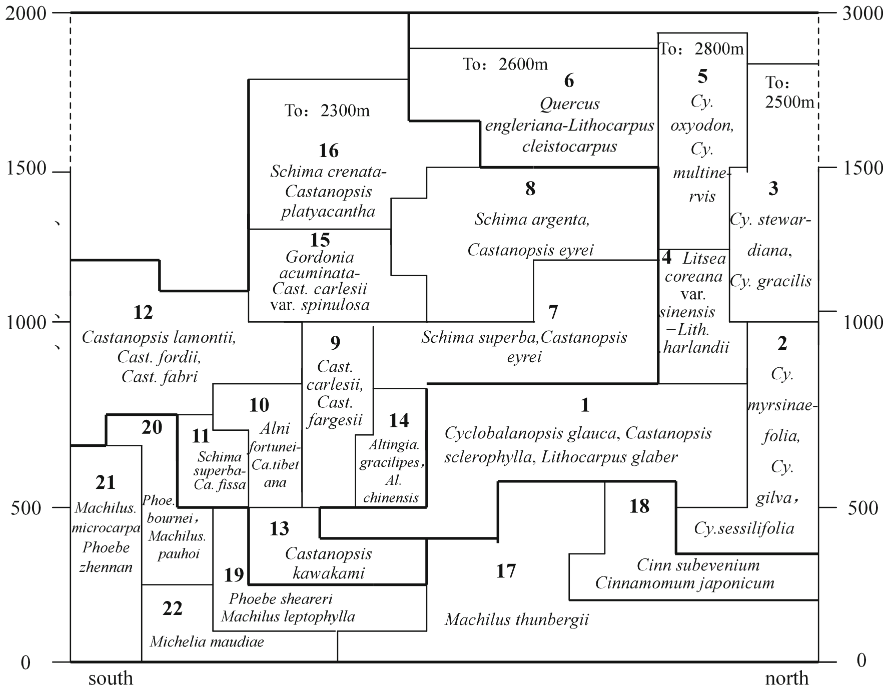
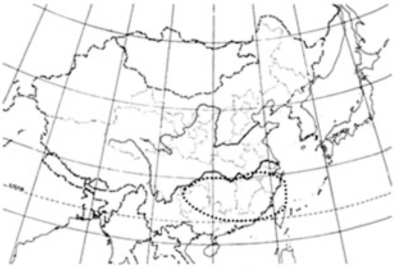


Fig. 2 Distribution of evergreen broad-leaved forests in Eastern China. 1. *Cyclobalanopsis glauca*, *Castanopsis sclerophylla*, *Lithocarpus glaber* Do-Ty; 2. *Cyclobalanopsis myrsinaefolia, Cyclobalanopsis gilva*, *Cyclobalanopsis sessilifolia* Do-Ty; 3. *Cyclobalanopsis stewardiana*, *Cyclobalanopsis gracilis* Do-Ty; 4. *Litsea coreana* var. *sinensis-Lithocarpus harlandii* Do-Ty; 5. *Cyclobalanopsis oxyodon, Cyclobalanopsis multinervis* Do-Ty; 6. *Quercus engleriana*, *Lithocarpus cleistocarpus* Do-Ty; 7. *Schima superba*, *Castanopsis eyrei* Do-Ty; 8. *Schima argenta, Castanopsis eyrei* Do-Ty; 9. *Castanopsis carlesii*, *Castanopsis fargesii* Do-Ty; 10. *Alniphyllum fortunei, Castanopsis tibetana* Do-Ty; 11. *Schima superba, Castanopsis fissa* Do-Ty; 12. *Castanopsis lamontii, Castanopsis fordii, Castanopsis fabri* Do-Ty; 13. *Castanopsis kawakami* Do-Ty; 14. *Altingia gracilipes*, *Altingia chinensis* Do-Ty; 15. *Gordonia acuminata*, *Castanopsis carlesii* var. *spinulosa* Do-Ty; 16. *Schima crenata*, *Castanopsis platyacantha* Do-Ty; 17. *Machilus thunbergii* Do-Ty; 18. *Cinnamomum subevenium*, *Cinnamomum japonicum* Do-Ty; 19. *Phoebe sheareri*, *Machilus leptophylla* Do-Ty; 20. *Phoebe bournei*, *Machilus pauhoi* Do-Ty; 21. *Machilus microcarpsa*, *Phoebe zhennan* Do-Ty; 22. *Michelia maudiae* Do-Ty. The vertical scale is elevation, in meters

and species of *Castanopsis* are diagnostic and dominant species. This group contains ten dominance types: *Schima superba, Castanopsis eyrei* Do-Ty; *Schima argenta, Castanopsis eyrei* Do-Ty; *Castanopsis carlesii, Castanopsis fargesii* Do-Ty; *Alniphyllum fortunei-Castanopsis tibetana* Do-Ty; *Schima superba-Castanopsis fissa* Do-Ty; *Castanopsis lamontii, Castanopsis fordii, Castanopsis fabri* Do-Ty; *Castanopsis kawakamii* Do-Ty; *Altingia gracilipes,Altingia chinensis* Do-Ty; *Gordenia acuminata-Castanopsis carlesii* var. *spinulosa* Do-Ty; *Schima crenata-Castanopsis platyacantha* Do-Ty.

Lithocarpus glaber

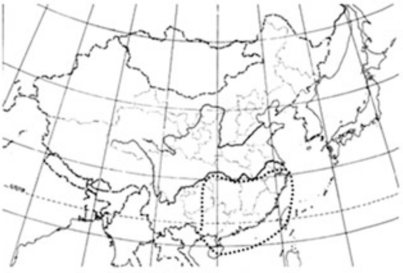
Castanopsis carlesii



Castanopsis eyrei

Castanopsis fargasii

Castanopsis sclerophylla



Schima superba

Fig. 3 Distribution of the main species of typical evergreen broad-leaved forest in Eastern China. *Lithocarpus glaber, Castanopsis sclerophylla, Castanopsis eyrei, Castanopsis fargesii, Castanopsis carlesii, Schima superba*

III. *Cinnamomum-Machilus* Collective Group

This is a hydrophilous type of EBLF in eastern China and is often seen in moist valleys. The main component taxa are *Cinnamomum, Machilus, Phoebe* and *Michelia*. It contains six dominance types: *Machilus thunbergii* Do-Ty; *Cinnamomum subevenium*, *Cinnamomum japonicum* Do-Ty; *Phoebe sheareri*, *Machilus leptophylla* Do-Ty; *Phoebe bournei*, *Machilus pauhoi* Do-Ty; *Machilus microcarpa, Phoebe zhennan* Do-Ty; and *Michelia maudiae* Do-Ty.

Typical EBLF of Western China

This type of EBLF arises under the impact of the southwest monsoon from the Indian Ocean. It is a drought-adapted semi-moist type of EBLF, occurring mostly at altitudes of 1600–2500 m, mainly over the plateau region of northern and central Yunnan and Guizhou provinces and also the mountainous area of southwestern Sichuan. Under the Indian Ocean monsoon, there are many rainy days from summer until autumn, with much precipitation and warm, moist weather. From winter until spring, because of dominance by continental high pressure and its dry air mass, precipitation is low and the weather is warm and dry. The annual temperature variation is relatively small. The trees of the upper layer bear rigid, relatively small leaves, with hairy dorsal surfaces; the tree trunks are slightly crooked and have coarse, thick bark (Jin 1979; Song 1988a). The upper tree layer is predominated by species of *Castanopsis*, *Cyclobalanopsis* and *Lithocarpus*. Species such as *Cyclobalanopsis glaucoides, Cyclobalanopsis delavayii, Castanopsis orthacansa, Castanopsis delavayii, and Lithocarpus dealbatus* are both dominant species and diagnostic species. The forests sometimes also contain a few deciduous trees, such as *Prunus conradinae* and *Celtis yunnanensis*, and some coniferous trees, such as *Pinus yunnanensis*, *Keteleeria evelyniana, and Cypressus duclouxiana*. In addition, there are many unique species. The flora of this type is composed primarily of Chinese-Himalayan elements. This type of EBLF can be called *Camellio-Cyclobalanopsetea glaucoidis* and divided into two collective groups. Their distributions are shown in Fig. 4 and the distribution of their main species in Fig. 5.

I. *Castanopsis-Cyclobalanopsis* Collective Group

This is a semi-moist typical EBLF, widely distributed in western China, and the zonal vegetation type of central and northern parts of the Yunnan Plateau. Xeromophy in this type is obvious. The diagnostic and dominant species are: *Cyclobalanopsis glaucoides, Cy. delavayi, Castanopsis orthacantha*, and *Ca. delavayi*. It contains four dominance types: *Cyclobalanopsis glaucoides* Do-Ty; *Cyclobalanopsis delavayii* Do-Ty; *Castanopsis orthacantha* Do-Ty; and *Castanopsis delavayii* Do-Ty.

II. *Montane Lithocarpus* Collective Group

This is the montane EBLF of the Yunnan Plateau, occurring in the cloud belt of mountains at altitudes of 2000–2900 m. The habitats are warm and moist. The dominant and diagnostic species are *Lithocarpus* spp., *Manglietia* spp., *Schima noronhae*, and *Chimonobambusa* spp. This group contains six dominance types: *Lithocarpus craibianus* Do-Ty; *Lithocarpus echinophorus* Do-Ty; *Lithocarpus*

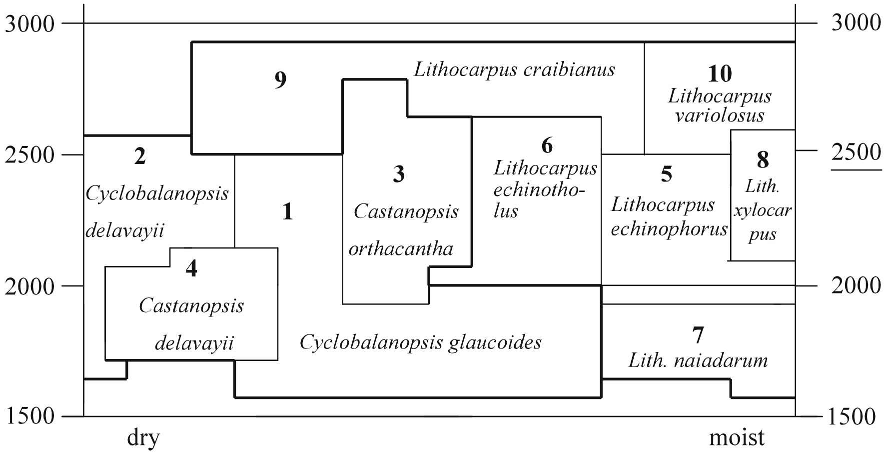
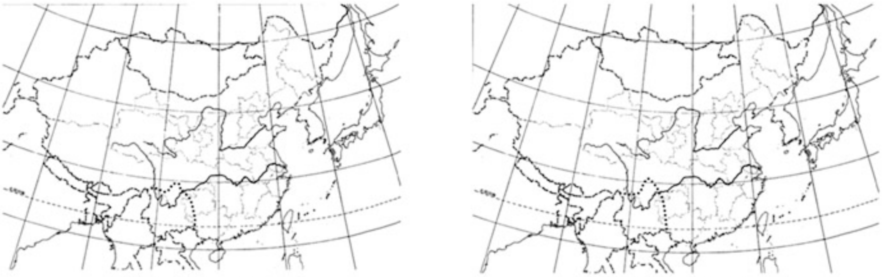
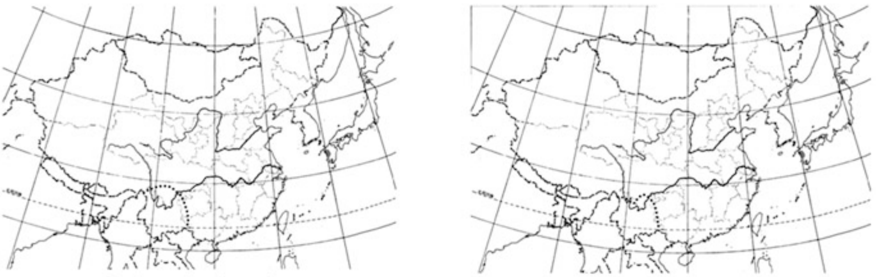


Fig. 4 Distribution of typical evergreen broad-leaved forests in Western China. 1. *Cyclobalanopsis glaucoides* Do-Ty; 2. *Cyclobalanopsis delavayi* Do-Ty; 3. *Castanopsis orthacantha* Do-Ty; 4. *Castanopsis delavayi* Do-Ty; 5. *Lithocarpus echinophorus* Do-Ty; 6. *Lithocarpus echinotholus* Do-Ty; 7. *Lithocarpus naiadarum* Do-Ty; 8. *Lithocarpus xylocarpus* Do-Ty; 9. *Lithocarpus craibianus* Do-Ty; 10. *Lithocarpus variolosa* Do-Ty. The vertical scale is elevation, in meters


Cyclobalanopsis delavayii

Cyclobalanopsis glaucoides


Castanopsis orthacantha

Lithocarpus dealbatus

Fig. 5 Distribution of the four main species of typical evergreen broad-leaved forest in Western China *echinotholus* Do-Ty; *Lithocarpus xylocarpus* Do-Ty; *Lithocarpus naiadarum* Do-Ty; and *Lithocarpus variolosus* Do-Ty.

Typical Summer-Rain EBLF of Japan and Korea

The typical EBLF of Japan occurs mainly in Kyūshū, Shikoku, Chūgoku, and the center of Honshū. The southern limit is at 26°30′ N and the northern limit at 37°30′ N (along the coast) (Satoo 1983). Some authors, however, have argued that the northern limit reaches 39° N (Pacific side) and 40°35′ N (Japan Sea side) (e.g. Fujiwara 1981). The upper limit of distribution is at 850 m on Kyūshū, 750 m on Shikoku, and 600 m on Honshū (Satoo 1983). The climate is a typical monsoon climate, but compared to eastern China, the winter is a little warmer and the summer a little cooler. That means that the annual temperature variation is not very drastic, as it is in eastern China. The precipitation is higher, so the weather is moister. The Warmth Index (WI) of EBLF is in the range 85–180 °C (Kira 1954), while the Coldness Index (CI) at the northern limit is −10 °C (Hattori and Nakanishi 1985). Mean annual temperature is 13–21 °C (Shidei 1974).

The typical EBLF in Japan is very similar to its counterpart in eastern China. The tree layers are also constituted by *Castanopsis, Cyclobanopsis* and *Machilus*, especially *Castanopsis cuspidata*, *Ca. sieboldii*, *Cyclobalanopsis glauca, Cy. myrsinaefolia*, and *Machilus thunbergii*. Shrub species are members of the Theaceae, Cornaceae and Araliaceae, such as *Camellia japonica, Aucuba japonica, Fatsia japonica, Dendropanax trifidus*, *Ilex integra*, and *Neolitsea sericea*. The herbaceous layers are provided by species of the Liliaceae and Myrsinaceae and by Pteridophytes. The major liana species are *Trachelospermum asiaticum* var. *intermedium*, *Hedera rhombea*, and *Kadsura japonica*. *Camellia japonica* is designated as the character species, and the class was named *Camellietea japonicae* (Miyawaki 1981). The distribution and main species are shown in Fig. 6.

The typical EBLF in Korea is restricted to the southmost part of the peninsula plus offshore islands, with a northern limit at 35°30′ N. The Warmth Index is 85–180 °C, and the Coldness Index at the northern limit is −7 to −10 °C (Yim 1977). The floristic composition of EBLF in Korea is essentially the same as in Japan.

The EBLFs of Japan and Korea were classified into three groups based on the dominant species and spatial distribution (Numata et al. 1972; Miyawaki 1990). According to the Braun-Blanquet system, they are classified into 1 class, 3 orders, 8 formations and 56 associations (Miyawaki 1981; Fujiwara 1981). In order to compare with the EBLF throughout East Asia, these two systems are synthesized. The typical EBLF of Japan and Korea is divided into two collective groups based on eco-physiognomic features and dominant species (Table 5).

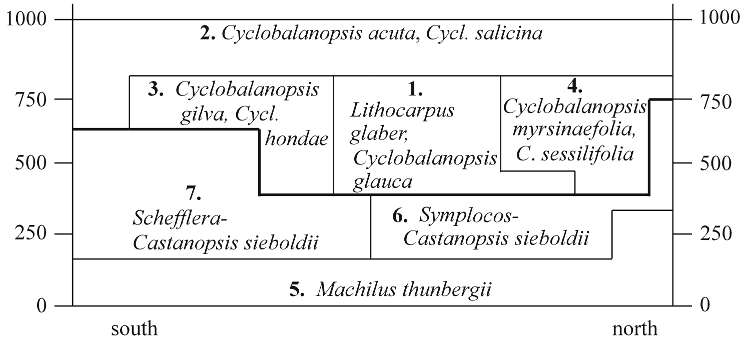


Fig. 6 Distribution of typical evergreen broad-leaved forests in Japan. 1. *Lithocarpus glaber, Cyclobalanopsis glauca* Do-Ty; 2. *Cyclobalanopsis acuta*, *C. salicina* Do-Ty; 3. *Cyclobalanopsis gilva, C. hondae* Do-Ty; 4. *Cyclobalanopsis myrsinaefolia, C. sessilifolia* Do-Ty; 5. *Machilus thunbergii* Do-Ty; 6. *Symplocos, Castanopsis sieboldii* Do-Ty; 7. *Schefflera, Castanopsis sieboldii* Do-Ty

I. *Lithocarpus-Cyclobalanopsis* Collective Group

This was called "evergreen oak forest" by Numata et al. (1972) and is dominated by species of *Cyclobalanopsis* (Quercus), in some cases also by species of *Lithocarpus*. It has a broad ecological amplitude, being more cold-tolerant, and occurs in inland and mountainous regions at higher elevation. The collective group can be compared with the order Illicio-Quercetalia acutae, according to characteristic classification. It includes four dominance types: *Lithocarpus glaber, Cyclobalanopsis glauca* Do-Ty; *Cyclobalanopsis acuta*, *C. salicina* Do-Ty; *Cyclobalanopsis gilva, C. hondae* Do-Ty; and *Cyclobalanopsis myrsinaefolia, C. sessilifolia* Do-Ty (Table 5).

II. *Machilus thunbergii-Castanopsis* Collective Group

This is the "*Machilus thunbergii* and *Castanopsis sieboldii* forest" of Numata et al. (1972). The dominant species of the tree layer are *Castanopsis sieboldii* and *C. cuspidata*, accompanied by *Machilus thunbergii*, which can also dominate sometimes. This collective group occurs mainly on terraces and mountains with gentle slopes near the coast. The habitats are thus moist, and the soil is generally deep. This collective group can be compared with the *Myrsino-Castanopsietalia sieboldii*. It includes three dominance types: *Machilus thunbergii* Do-Ty; *Symplocos-Castanopsis sieboldii* Do-Ty; and *Schefflera-Castanopsis sieboldii* Do-Ty (Table 5).

Table 5 The main types of evergreen broad-leaved forest in Japan

EBLF of Japan (in this paper)	EBLF of Japan (Numata et al. 1972)	EBLF of Japan (K. Fujiwara 1981)
Typical (summer-rain) EBLF of Japan	EBLF of Japan	*Camellietea japonicae*
I. *Lithocarpus-Cyclobalanopsis* collective group	I. Evergreen oak forests	A. *Illicio-Quercetalia acutae*
(1) *Lithocarpus glaber, Cyclobalanopsis glauca* Do-Ty	*Cyclobalanopsis glauca* forest	(a) *Quercion acuto-myrsinaefoliae*
(2) *Cyclobalanopsis acuta*, *Cy. salicina* Do-Ty	*Cyclobalanopsis salicina* forest	
	Cyclobalanopsis acuta forest	
(3) *Cyclobalanopsis gilva*, *Cy. hondae* Do-Ty	*Cyclobalanopsis gilva* forest	
(4) *Cyclobalanopsis myrsinaefolia,* *Cy. sessilifolia* Do-Ty	*Cyclobalanopsis myrsinaefolia* forest	
II. *Machilus thunbergii-Castanopsis* collective group	II. Forests of *Machilus thunbergii* and of *Castanopsis sieboldii*	B. *Myrsino-Castanopsietalia sieboldii*
(5) *Machilus thunbergii* Do-Ty	*Machilus thunbergii* forest	(b) *Maeso japonicae-Castanopsion sieboldii*
(6) *Symplocos-Castanopsis sieboldii* Do-Ty	*Castanopsis sieboldii* forest, with *Machilus thunbergii*	
(7) *Schefflera-Castanopsis sieboldii* Do-Ty	*Castanopsis sieboldii* forest mixed with *Schefflera octophylla*, etc.	(c) *Psychotrio-Castanopsion sieboldii*
	Quercus phillyraeoides scrub	(d) *Rhaphiolepido-Quercion phillyraeoidis*
Subtropical seasonal EBLF of Japan	III. Subtropical EBLFs	C. *Diospyro maritimae-Mallotetalia philippensis*
III. *Ficus-Bischofia* collective group	Forests of *Machilus kobu*, *Livistonia boninensis, Freycinetia formosa* var. *boninensis*	(e) *Psychotrio manilensis-Acerion oblongi*
(8) *Turpinia ternata-Bischoffia javanica* Do-Ty		
(9) *Ficus-Beilschmiedia erythrophloia* Do-Ty		

Typical EBLF of Mountains on Taiwan

EBLFs can be seen over the entire island, but the typical, natural evergreen broad-leaved forests can only be found in the mountainous area at elevations of 800–2300 m. The upper tree layer is composed mainly of species of *Cyclobalanopsis,* *Castanopsis*, and *Machilus*, such as: *Cyclobalanopsis longinux, Cy. morii, Cy. stenophylloides*, *Castanopsis carlesi, Lithocarpus kawakamii*, and *Machilus thunbergii*. The herbaceous layer is provided mainly by herbaceous ferns. Some thermophilous conifers and deciduous broad-leaved trees are found too. *Cyclobalanopsis longinux, Cy. morii, Cy. stenophylloides*, *Trochodendron aralioides, Neolitsea acuminatissima* and *Symplocos arisanensis* can be recognized as diagnostic species. This type of EBLF can be called *Castanopsio-Cyclobalanopsetea longinuxi*. There is only one collective group (Song and Xu 2003).

I. Montane *Castanopsis-Cyclobalanopsis* Collective Group

This is the montane EBLF of Taiwan, distributed on mountains with warm, moist climate. The dominant and diagnostic species are as mentioned above. At present it is divided into three dominance types: *Cyclobalanopsis morii, Castanopsis carlesii* Do-Ty; *Lithocarpus kawakami*, *Cyclobalanopsis longinux* Do-Ty; and *Cyclobalanopsis stenophylloides, Cyclobalanopsis sessilifolia* Do-Ty (Song and Xu 2003; Song et al. 2003; Song 2004).

Subtropical Seasonal EBLF of East Asia

The subtropical seasonal evergreen broad-leaved forest was named “subtropical evergreen seasonal forest” by Ellenberg and Mueller-Dombois (1967). In China people have different names for these forests; for example, the book “The Vegetation of China” (1980) referred to them as part of the “monsoon evergreen broad-leaved forest”. It is a transitional type from the tropical seasonal rainforests or semi-deciduous monsoon forest to evergreen broad-leaved forest. It is also known as semi-moist transitional EBLF (Song 1994). The species of the upper storeys are mostly thermophilous species of Fagaceae and Lauraceae, plus many species of Myrtaceae, Meliaceae and Moraceae, even a few deciduous plants of tropical seasonal rainforest, such as *Albizia, Englhardtia* and *Bauhinia*. The understoreys include diverse tropical elements such as plants of the Rubiaceae, Myrsinaceae, Palmae, Leguminosae, Euphorbiaceae, and Rutaceae, which are observed very often. Lianas and epiphytic plants, however, are not as abundant as in rainforests, and buttress roots and cauliflory are scarcely seen.

Subtropical seasonal EBLFs occur mainly in southern China, on Taiwan and in southernmost Japan. Based on their floristic components, the seasonal EBLFs can be divided into four subtypes (Table 6). The distribution of main species is shown in Fig. 7.

Table 6 Dominant and diagnostic species of four subtypes of seasonal EBLF in East Asia

Subtypes	East China	West China	Taiwan	Southernmost Japan
Distribution	22°–24° N	22°–24° N	21°45′–25°56′ N	24°–26° N
	<500 m a.s.l.	1100–1500 m a.s.l.	<800 m a.s.l.	
Castanopsis hystrix	do	do	–	–
Castanopsis uraiana	do	–	do	–
Castanopsis chinensis	do/di	–	–	–
Castanopsis tonkinensis	do/di	+	–	–
Cryptocarya chinensis	do/di	–	di	+
Cryptocarya concinna	do/di	–	di	–
Diospyros morrisiana	di	–	do	–
Elaeocarpus nitentifolius	di	–	–	–
Beilschmiedia tsangii + *B. fordii*	do	–	–	–
Machilus chinensis	do/di	–	–	–
Machilus nakao	do/di	–	–	–
Rhodoleia championi	do/di	–	–	–
Syzygium levineei	di	–	–	–
Castanopsis fleuryi	–	do	–	–
Castanopsis indica	–	do	di	–
Schima villosa + *S. wallichii*	–	do	–	–
Lithocarpu truncatus	–	di	–	–
Camellia vietnamensis	–	di	–	–
Diospyros yunnanensis	–	di	–	–
Elaeocarpus braceanus	–	di	–	–
Engelhardtia acerifolia	–	di	–	–
Gauitheria yunnanensis	–	di	–	–
Machilus kurzii	–	di	–	–
Schefflera diversifolia	–	di	–	–
Castanopsis carlesii var. *sessile*	–	–	do	–
Lagerstroemia subcostata	–	–	do	–
Michelia compressa	–	–	do	–
Englhardtia colebrookiana	–	+	di	–
Syzygium euphlebium	+	–	di	–
Diospyros maritima	–	–	di	di
Helicia formosana	–	–	di	–
Lasianthus plagiophyllus	–	–	di	–
Machilis japonica var. *kusanoi*	–	–	di	–
Turpinia formosana	–	–	di	–
Pithecellobium lucidum	–	–	di	–

(continued)

Table 6 (continued)

Subtypes	East China	West China	Taiwan	Southernmost Japan
Castanopsis cuspidata var. *sieboldii*	–	–	–	do
Beilschmiedia erythrophloia	–	–	+	di
Bischoffia javanica	–	–	+	di
Michelia formosana	–	–	+	di
Macaranga tanarius	–	–	+	di
Lasianthus cyanocarpus	–	–	+	di
Adinandra ryukyuensis	–	–	–	di
Bredilia balansae	–	–	–	di
Schima wallichii spp. *liukiuensis*	–	–	–	di
Tarenna gyokushinkwa	–	–	–	di

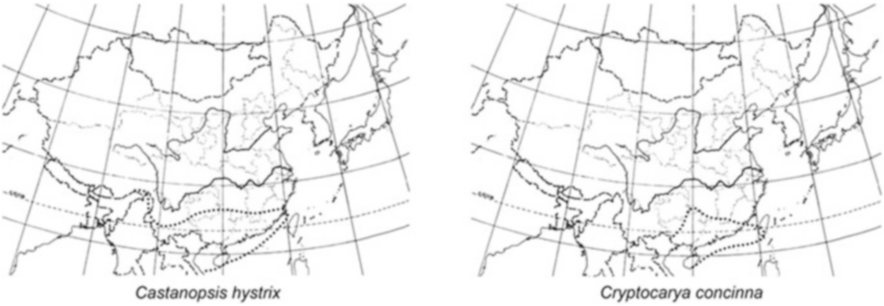


Fig. 7 Distribution of the main species of subtropical seasonal EBLFs in East Asia

Subtropical Seasonal EBLF of Eastern China

Subtropical seasonal EBLFs of southeastern China are predominated by thermophilous species of *Castanopsis* and *Cryptocarya*, such as *Castanopsis hystrix, Ca. chinensis, Ca. tonkinensis, Ca. uraiana, Cryptocarya chinensis* and *Cr. concinna*; plus *Beischmiedia* spp. *Machilus* spp., *and Syzygium* spp. Trees of the Moraceae and Elaeocarpaceae are also important companion in the upper layer. The lower tree layer and shrub layer are filled with complicated tropical elements. Lianas and epiphytes are not as abundant as in rainforest. The diagnostic species are *Cryptocarya* and warmth-loving *Castanopsis* species. This type can be called *Cryptocaryo-Castanopsietea* and divided into two collective groups (Song 2004).

I. *Cryptocarya-Castanopsis* Collective Group

This is the warmth-loving EBLF of eastern China, occurring on hills and lower mountains of southern Guangdong, Guangxi, and Fujian. The dominant and diagnostic species are: *Cryptocarya chinensis, Cr. concinna,* and *Castanopsis hystrix, Ca. uraiana* and *Ca. tonkinensis*. The group contains two dominance types: *Cryptocarya chinensis-Castanopsis hystrix, Cryptocarya chinensis* Do-Ty; and *Cryptocarya concinna-Castanopsis tonkinensi*s Do-Ty.

II. *Cinamomum-Machilus-Beilschmiedia* Collective Group

This is the warmth and moisture-loving type of seasonal EBLF of eastern China, distributed on lower mountains at elevations of 400–800 m in Guangxi. The diagnostic species are species of *Beischmiedia* and *Machilus*. This group contains two dominance types: *Machilus chinensis, Machilus nakao* Do-Ty; and *Beilschmiedia tsangii, Beilschmiedia fordii* Do-Ty.

Subtropical Seasonal EBLF of West Mainland of China

This kind of forest is a zonal vegetation of the southern, subtropical region of the Yunnan Plateau, occurring at altitudes of 1100–1500 m. The forests are predominated by thermophilous species of C*astanopsis*, such as *Castanopsis hystrix* and *Castanopsis indica*, plus *Schima villosa*, *Schima wallichii*, *Machilus kurzii*, etc. Intermingling deciduous species are *Engelhardtia colebrookiana, Albizia chinensis, Kydia calycena*, and others. Some conifers occur there too, such as *Pimus kesiya* var. *langbianensis, Podocarpus imbricatus* and *P. neriifolia*. The flora is composed mainly of Indo-Malaysian elements, with many species from tropical rainforests and monsoon forests. The diagnostic species are warmth-loving species of *Machilus* and *Castanopsis*. This type can be called *Lithocarpo-Castanopsietea* and contains two collective groups.

I. *Lithocarpus-Castanopsis* Collective Group

The species composition of this group is very complex. The dominant and diagnostic species are warmth-loving species of *Lithocarpus* and *Castanopsis*, plus *Schima wallichii* and *S. villosa*. The group contains two dominance types: *Castanopsis hystrix, Castanopsis indica* Do-Ty; *Lithocarpus truncatus-Castanopsis fleuryi, Castanopsis fabrii* Do-Ty.

II. *Machilus* Collective Group

This group occurs mainly on limstone substrates. The dominant and diagnostic species are *Machilus kurzii, Castanopsis hystrix* and *Schefflera diversifolia*. At present only one dominance type is recognized: *Machilus kurzii, Castanopsis fargesii* Do-Ty.

Subtropical Seasonal EBLF of Taiwan

Seasonal EBLF is the zonal vegetation type of subtropical areas of Taiwan. The composition of the upper tree layer includes mainly some thermophilous species of Fagaceae and Lauraceae, such as *Castanopsis carlesii* var. *sessile*, *Cryptocarya chinensi, Machilus japonica* var. *kusanoi*, *Phoebe formosana* and *Machilus zuihoensis*. In addition, some species of Elaeocapaceae, Magnoliaceae, Proteaceae, Ebenaceae are observed too, including *Sloanea formosana, Michelia compress, Helicia formosan* and *Diospyros morrisiana*. Frequently seen species in the shrub layer are *Schefflera octophylla, Tricalycia dubia, Psychotria cochinchinensis, Myrsine seguinii, Blastus cochinchinensis*, etc. Large woody lianas are found very often, mostly *Bauhinia championii, Mussaeda parviflora, Stauntonia hexaphylla, Hiptage bengalensis, Pileastagia viburnoides, Mucuna macrocarpa* and *Fissistigma oldhamii* (Song et al. 2003, Song 2004). This type of forest is named *Machilus-Castanopsis* forest, as suggested by Su (1984), and can be called *Machilo–Castanopsietea*.

I. *Machilus-Castanopsis* Collective Group

This type occurs widely on hills and mountains below 800 m. The diagnostic species are *Pithecellobium lucidum, Diospyros morrisiana, Schefflera octophylla, Ardisia quinquegona,* etc. It contains four dominance types: *Lithocarpus amygdalifolius, Cyclobalanopsis longinux* var. *koui* Do-Ty; *Cryptocarya chinensis, Castanopsis uraiana* Do-Ty; *Machilus japonica, Castanopsis carlesii* var. *sessile* Do-Ty; and *Tupinia ternata, Machilus japonica* Do-Ty (Song et al. 2003; Song 2004).

Subtropical Seasonal EBLF of Japan

The seasonal EBLF of Japan occurs mainly on the Ryukyu islands of southernmost Japan. The southern limit is at 24° N and the northern limit at 26° N. Because the islands are small, and much of their area is constituted by limestone substrates and old raised coral reefs, the soil layer is very thin. The heavy influence of human activities has also hindered the development of the seasonal EBLF. The floristic composition in genera, though, is largely similar to that of the seasonal EBLF of

Taiwan and continental China. The main genera are *Beilschmiedia, Schefflera, Ficus, Macaranga, Tarenna, Lasianthus, Pithecellobium, Bredilia, Mallotus, Murraya, Diospyros Psychotria, Bischoffia, Michelia, Myrsine, Turpinia, Lagerstroemia, Cyathea, Psychotria* and *Livistona* (Miyawaki and Okuda 1990). At present this type contains only one collective group; it was named *Diospyro-Mallotetalia philippensis* by Fujiwara (1981).

I. *Ficus-Bischofia* Collective Group

This occurs mainly on the Ryukyu Islands. Based on the dominant and character species, it can be divided into two dominance types: *Turpinia ternata-Bischoffia javanica* Do-Ty and *Ficus-Beilschmiedia erythrophloia* Do-Ty.

Subtropical Ombrophilous EBLFs of East Asia

Subtropical ombrophilous evergreen broad-leaved forest, also called "subtropical rainforest", is the transitional form between tropical rainforest and evergreen broad-leaved forest, occurring mainly in the very moist habitats of valleys. The main differences between subtropical ombrophilous EBLF and subtropical seasonal EBLF, as well as the typical EBLF referred here, is that the structure of the former is much more complex. These usually have plank buttresses, thick lianas, and epiphytic ferns and phanerogams. The physiognomy of tropical rainforest is more obvious, with hydrophilous species with macrophylls as the main component. The means of protecting against transpiration losses is weakly developed in subtropical ombrophilous EBLFs.

Subtropical ombrophilous EBLFs occur mainly in Taiwan and southernmost China, including Hong Kong. The herbaceous layer is studded with big-leaved plants and tropical ferns. There are abundant lianas and epiphytes, including some quite large woody lianas and epiphytic vascular plants. Buttresses, cauliflory, and stranglers are quite remarkable. Based on their floristic components, the ombrophilous EBLF can be divided into two subtypes (Table 7).

Subtropical Ombrophilous EBLF of Eastern China

This occurs in the southernmost part of Fujian, Guangdong, Guangxi, and in Hong Kong. Species frequently seen in the tree layer are species of *Ficus*, *Machilus*, *Syzygium* and *Castanopsis*. The tropical species of *Ficus* and *Machilus* are recognized as diagnostic species, so it can be called *Fico-Syzygietea,* and divided into two collective groups.

Table 7 Diagnostic species of subtypes of ombrophilous EBLF in East Asia

Eastern China		Taiwan	
Distribution	22°–24° N	Distribution	21°45′–25°56′ N
	<500 m a.s.l.		<800 m a.s.l.
Cleistocalyx operulata	do/di	*Machilus japonica* var. *kusanoi*	do/di
Ficus chlorocarpus	do/di	*Castanopsis stellato-spina*	do
Ficus fistulosa + *Ficus variolosa*	do/di	*Ficus fistulosa* + *Ficus nervosa*	do/di
Syzygium jambos	do/di	*Ficus septica* + *Ficus ampelas*	do/di
Syzygium hancei	do/di	*Ficus irisana*	di
Endospermum chinense	do/di	*Cyathea spinulosa* + *C* . *polycarpa*	do/di
Aquilaria sinensis	do/di	*Cyathea lepifera*	di
Sterculia lanceolata	di	*Arenga engleri*	di
Sarcosperma laurinum	di	*Lagerstroemia subcostata*	di
Pithecellobium lucidum + *P. clyperia*	di	*Acer albopurpurascens*	di
Canarium album	di	*Dendrocnide meyeniana*	di
Pygeum toperigii	di	*Astonia ferruginea*	di
Acronychia pedunculata	di	*Wendlandia formosana*	di
Ecdysanthera utilis + *E.rosea* (L)	di	*Syzygium euphlebium*	di
Spatholobus suberectus (L)	di	*Calamus formosana* (L)	di
Rourea microphylla (L)	di	*Daemonrops mararitae* (L)	di
Gnetum montanum (L)	di	*Pseudodrynaria coronans* (E)	di
Bowringia callicarpa (L)	di	*Erycibe henryi* (E)	di
*Tetrastigma planicau*le (L)	di	*Hiptage benghalensi*	di
Ventilago leiocarpa (L)	di	*Pothos chinensis* (E)	di
Bowringia callicarpa (L)	di	*Epipremnum pinnatum* (E)	di
Embelia rudis (L)	di	*Alocasia macrorrhiza* (H)	di
Calamus rhabdocladus (L)	di	*Alpinia speciosa* (H)	di

L liana, *E* epiphyte, *H* herbaceous

I. *Syzygium-Castanopsis* Collective Group

This occurs in southern Fujian. The dominant and diagnostic species are *Castanopsis uraiana*, *C. hystrix* and *Syzygium hancei*. There is only one dominance type: *Castanopsis hystrix, Castanopsis uraiana* Do-Ty.

II. *Ficus-Cleistocalyx* Collective Group

This occurs in southern Guangdong, Guangxi, and in Hong Kong. The dominant and diagnostic species are *Ficus* spp. *Syzygium* spp. *Cleistocalyx operculatus, Endospermum chinense, Pithecellobium clyperia, Sterculia lanceolata*, *Aqularia sinensis*, etc. This group contains three dominance types: *Syzygium jambos-Cleistocalyx operculatus* Do-Ty; *Ficus* spp.*, Endospermum chinense* Do-Ty; and *Syzygium levinei, Aquilaria sinensis* Do-Ty.

Subtropical Ombrophilous EBLFs of Taiwan

This kind of forest occurs over lower areas of Taiwan that have high precipitation (3500–4000 mm) and high temperatures (annual average temperature 18–20 °C), i.e. in moist ravine habitats. The community is rather tall, with complicated stratification, and the canopy looks uneven. Frequent tree-layer species are *Ficus* spp., *Dysoxylum buskusense, Lagerstroemia subcostata, Bischofia javaneia, Machilus japonica* var. *kusanoi,* and *Terpinia ternata.* The shrub layer, however, shows a more complicated pattern of species. It is composed mainly of *Dendrocnida meyeniana, Lasianthus chinensis, Leea guineensis* and *Cyathea* spp. Large woody lianas and epiphytic angiosperms grow luxuriously, among which the main species are: *Derris laxiflora, Hiptage benghalensis, Pothos chinensis, Erycibe henryi, Mucuna macrocarpa, Ficus sarmentosa* var. *nipponica,* and *Asplenium nidus*. Buttressing and cauliflory are observed. Tree ferns and large herbaceous plants are rather abundant (Song and Xu 2003). This type of forest might be similar to the so-called *Ficus-Machilus* forest, suggested by Su (1984). The diagnostic species are species of *Ficus, Machilus, Cyathea* and *Alocasia*. This can also be called *Fico Machiletea.* It has only one collective group:

I. *Ficus-Machilus* Collective Group

The tree layer is composed mainly by species of *Ficus* and warmth-loving species of *Castanopsis* and *Machilus*. Diagnostic species are: *Arenga engleri, Cyathea podophylla, Calamus formosana, Daemonrops mararitae* and *Alocasia macrorrhiza.* There are three dominance types: *Ficus septica-Ficus irisana* Do-Ty; *Ficus fistulosa-Machilus japonica* var. *kusanoi* Do-Ty; and *Beilschimiedia tsangii-Castanopsis stellato-spina* Do-Ty (Song and Xu 2003; Song 2004).

Summary and Discussion

EBLF in East Asia is a unique vegetation type, because it depends on the monsoon climate. These forests are not only distinctly different from the EBLF of the Southern Hemisphere, but also different from EBLF elsewhere in the Northern Hemisphere. The southern part of East Asia was affected less by Quaternary glaciations, so the EBLF over this area has preserved many more ancient species than its counterparts of North America and Europe, and shows more remarkable biodiversity. All of them, though, are direct descendents of Tertiary evergreen forests.

The EBLFs in East Asia occur over extensive areas, from northern limits at 39° N to southern limits around the Tropic of Capricorn (and from 141° E westward to 98° E). Such a vast area of EBLF varies greatly due to different climatic conditions and different floristic compositions and ecological characteristics. The EBLF can be divided into three main types (zones) latitudinally: (1) typical summer-rain EBLF, (2) subtropical seasonal EBLF, and (3) subtropical ombrophilous EBLF. The typical EBLF corresponds to warm-temperate and some subtopical evergreen broad-leaved forest in the narrow sense (Klötzli 1988; Song 1983, 1988a, b). The northern limit of typical summer-rain EBLF in China coincides with the 0 °C isotherm of mean minimum January temperature and the limit of subtropical seasonal EBLF coincides with the 15 °C isotherm (Fig. 8).

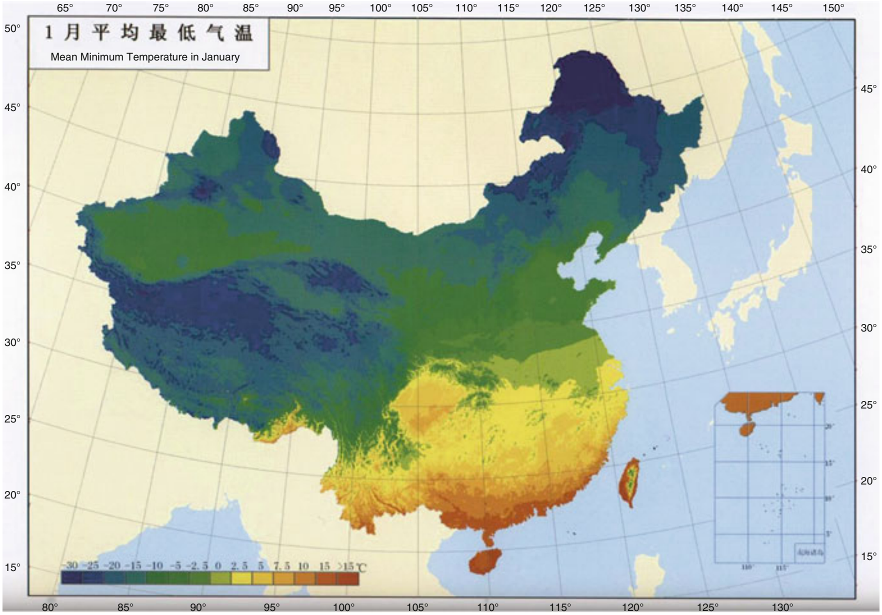


Fig. 8 Mean minimum temperature of January in China (from Yu et al. 2005)

There are many terms for the subtropical seasonal and the subtropical ombrophilous EBLF, such as subtropical rainforest (He 1955; Lin 1961), subtropical evergreen monsoon forest (Inst. Botany Guangdong 1976), subtropical monsoon evergreen broad-leaved forest (Wu 1980; Editorial Group of Vegetation of Yunnan 1987), south subtropical evergreen broad-leaved forest (Zhang et al. 1989), and others. All of these terms indicate the transitional characteristics of these types, from tropical to subtropical. They both have features of monsoon forest and rainforest, as well as a component of tropical elements. The differences between subtropical seasonal EBLF and subtropical ombrophilous EBLF are the rainforest features, such as the woody lianes, epiphytic plants, buttressing and cauliflory, which are more obvious in the ombrophilous EBLF; the ombrophilous type also occurs where there is higher precipitation and where habitats are very moist.

The EBLFs of East Asia can be divided longitudinally into an oceanic subtype (Japan and Korea), a moist continental subtype (eastern China), a semi-moist continental subtype (western China), and a moist island subtype (Taiwan).

The EBLFs in Japan and Korea are influenced strongly by the oceanic climate, and the species component has many more oceanic characteristics. The Japanese archipelago and Korean peninsula are also located further north, and thus have simpler species compositions. In the tree layer there are only two species of *Castanopsis*, four species of *Cyclobalanopsis* and one species of *Machilus* that can become dominant species. Additionlly, the southernmost islands of Japan are largely raised coral reefs, so the development of subtropical seasonal EBLF and ombrophious EBLF there is restricted. Even so, the main component genera and some species constituting EBLF are present. The Japanese islands were connected with the Asian continent until the Pliocene epoch, and even in the Quaternary they were connected and separated several times. This relationship enabled an interchange of flora, so the EBLF of Japan is quite similar to that of eastern China (Song 1988b). The EBLFs of these two regions have some identical species, but they also have their own diagnostic species.

The EBLF on the Asian mainland strides broadly from east to west, covering a bigger area and divided into two parts. The eastern EBLF arose under influences of the southeast Pacific monsoon and the cold current of Siberia; the western EBLF was under influence of the southwestern, Indian Ocean monsoon and of dry air coming from the tropical continent. Therefore, the EBLFs of the two regions differ not only in ecological features but also in floristic composition (Song 1988a). The boundary between the eastern and western EBLF forests of China is located on the east side of the Yunnan Plateau and in the mountain region of southwestern Sichuan. It is determined by water supply in spring (3–5 months), coinciding with the 106 mm isohyet and 55–75 mm isoline for evapotranspiration of this season (see Fig. 9). Moreover, the topography of the Asian mainland is complicated, so the southern part of China is an ideal shelter for ancient plants and favorable for the formation of new species. Consequently, the biodiversity of EBLF in China is the highest of the East Asian EBLF regions.

Taiwan has been connected with and separated from mainland Asia several times, due to fluctuations in sea level. The last separation occurred 10,000–

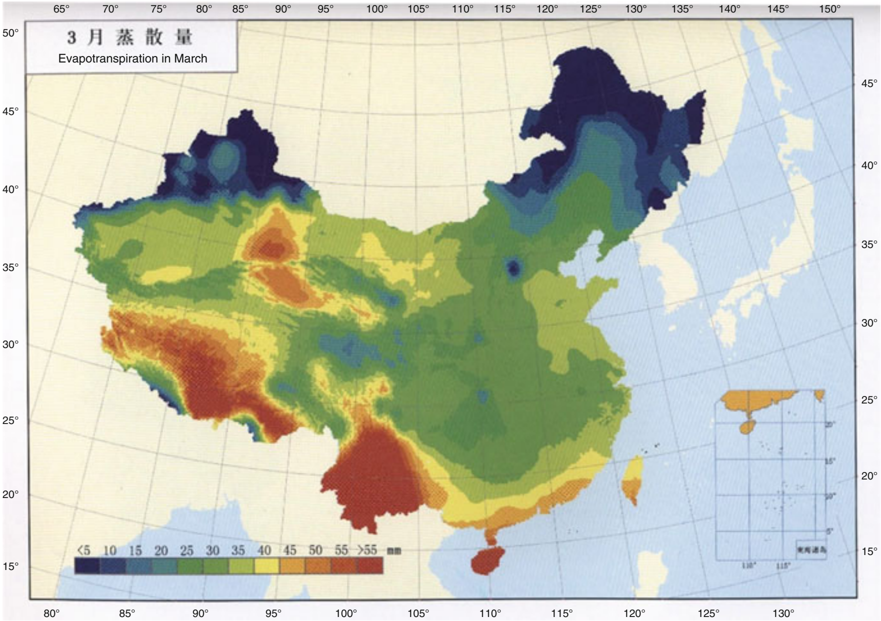


Fig. 9 Precipitation isohyet of March to May in China (from Yu et al. 2005)

15,000 years ago. Taiwain is located at the tropical margin and has warm, moist oceanic climatic conditions. Though small, Taiwan has an abundance of high mountains and complicated topography, which produce different vertical climatic belts. Plants have moved up and down repeatedly with the temperature variations, favoring species differentiation and natural selection. The EBLF in Taiwan shares many common species with its mainland counterpart, but it also possesses many endemic species and has its own characteristics.

In complexity, the EBLF is second only to tropical rainforests. The habitats of EBLF are enormously diversified, additionally due to human interference over long periods of time. The EBLF is complicated and full of secondary characteristics and transitional communities, so its classification is difficult. Up until now there have been two main approaches of vegetation classification, eco-physiognomic and floristic. The later can be divided further into classification based on character species and classification by dominance types. Beard (1980) pointed out that “It would seem that a desirable goal for the future should be the marrying of the two approaches into a single system of classification wherein floristic units are combined by their structure into physiognomic units”. We have accepted this idea and set up such a classification scheme for EBLF; the units of higher rank are based on eco-physiognomy, while the intermediate and lower units are based on species composition. At the same time, the role of dominant species and diagnostic species is also considered (Song 2004). This approach is adopted in this paper in order to facilitate the comparison of EBLF over different areas.

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Evergreen-Deciduous Broad-Leaved Forest Ecotone in Eastern China: Retrospect and New Perspectives

Song Kun and Da Liang-Jun

Abstract As a transition, the evergreen-deciduous broad-leaved forest ecotone (EDF ecotone) in eastern China occurs between the Yellow River (Huang He) and Yangtze River (Chang Jiang). Due to its wide extent, the EDF ecotone was usually treated as an independent vegetation zone in China. In this chapter, we summarize historical debates about its zonal vegetation and boundaries, and present new perspectives based on a case study that considers effects of topography on the vegetation transition pattern across the EDF ecotone. The case study showed that topographic differentiation in the forest transition pattern from evergreen to deciduous forest occurred in both latitudinal and altitudinal gradients, causing a hierarchical transition process in three dimensions. Based on these results, a mosaic transition pattern across the EDF ecotone is proposed, with more and larger evergreen patches toward the south and more and larger deciduous patches toward the north. This could result in stable mixed evergreen-deciduous broad-leaved forests in the transition areas between evergreen and deciduous patches. Finally, by comparing climate-vegetation relationships in China and Japan, we discuss the formation mechanism of the EDF ecotone and offer a new proposal for its boundary determination, based on these new perspectives.

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EDF Ecotone: Location, Zonal Vegetation and Debates

Location and Boundary

The evergreen-deciduous broad-leaved forest ecotone (EDF ecotone) in eastern China is the transition area between evergreen and deciduous broad-leaved forests in eastern China, which occurs between the Yellow River (Huang He) and Yangtze River (Chang Jiang). Due to its wide extent, the EDF ecotone was usually treated as an independent vegetation zone in China (Fig. 1). In the "Vegetation of China" (Wu 1980) and most other references (Sun 1998; China Vegetation Map Editorial Committee 2001), its southern boundary of the ecotone was assigned to around 31° N in the east and considered to reach Ta-Pa Mountain in Sichuan (southwestern China) via the south slope of Mt. Shennongjia; its northern boundary was considered consistent with a line defined by the Qinling Mountains and Huaihe River. Another viewpoint (Song 1999; Fang et al. 2002), in particular, extended the northern EDF ecotone boundary to near 35° N, making its range in the east twice as wide as in the previous scheme (Fig. 1).

Basically, the EDF ecotone is caused by the transition in broad-leaved forests from dominance by evergreen trees to dominance by deciduous trees. So the ranges of the main evergreen broad-leaved trees determine the boundary of the EDF ecotone. In East Asia, previous studies indicated that the northern and upper limits of evergreen broad-leaved trees and forests were related to low temperatures, which were usually represented by the Kira Warmth Index (WI) value of 85 °C · months (sum of monthly mean temperatures above 5 °C) and the Coldness Index (CI) value of −10 °C · months (sum of monthly mean temperatures below 5 °C). Sometimes the limit was seen as related, in subtropical and warm-temperate regions, to a value of −1 °C for the mean temperature of the coldest month (Ohsawa 1990). In China, though, the northern boundary of the evergreen broad-leaved forest zone is close to a CI value of −2 °C · months and a WI value of 135 °C · months (Song 1999); it does not reach the CI limit near −10 to −15 °C · months (Deng et al. 1985; Fang 1999). So it was suggested that moisture conditions restricted the northward distribution of evergreen broad-leaved forests in China (Fang and Yoda 1991; Fang et al. 2002). Over the past 5000 years, the boundary of the EDF ecotone varied with the shifting of the evergreen broad-leaved forest due to climatic changes. The southern boundary was near 35° N during the warmest periods and approached 29° N during the coldest periods (Liu 1992).

Zonal Vegetation

All debates about the boundaries of the EDF ecotone are related to various perceptions of zonal vegetation and zonal classification (Table 1). In most references, mixed evergreen-deciduous broad-leaved forest was used as the name of the

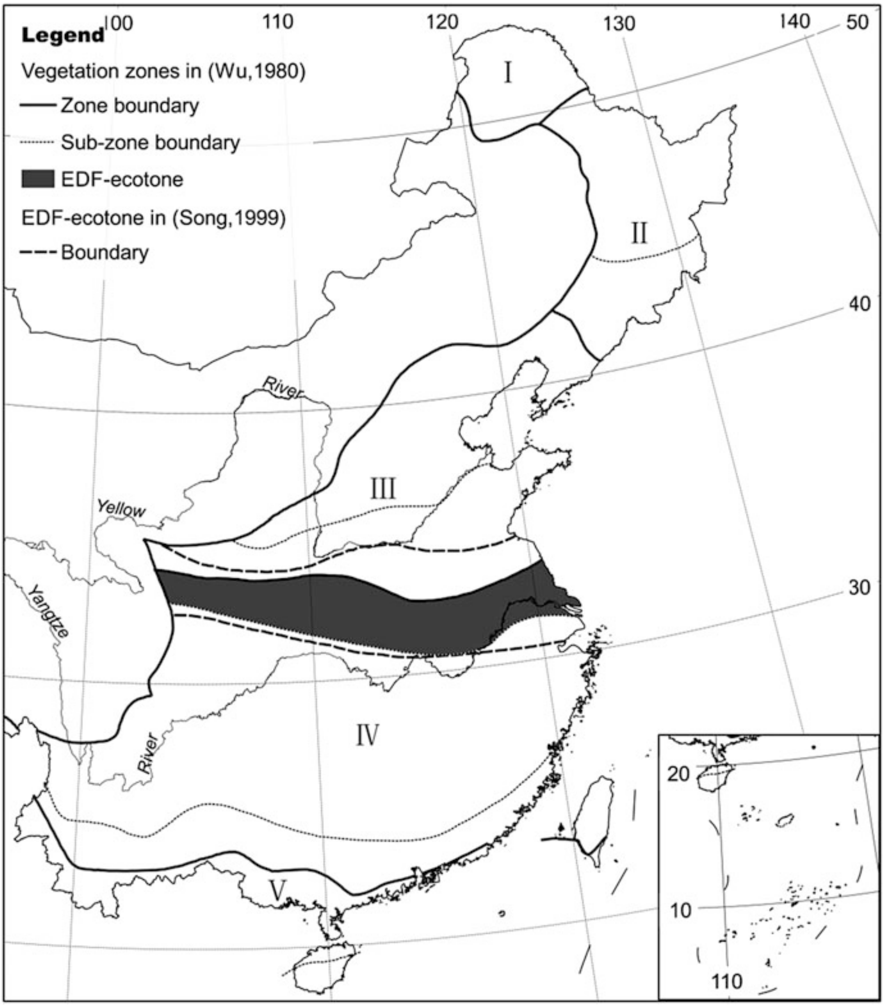

Fig. 1 Location of the EDF (evergreen-deciduous) ecotone in the vegetation zones of eastern China, according to the *Vegetation of China* (Wu 1980). I, cool-temperature coniferous forest zone; II, temperature mixed coniferous and deciduous broad-leaved forest zone; III, temperature deciduous broad-leaved forest zone; IV subtropical evergreen broad-leaved forest zone; V tropical rainforest and monsoon forest zone. Boundaries of the EDF ecotone in Song (1999) are also shown on this map

zonal vegetation in the *Vegetation of China* (Wu 1980), which emphasized the co-domination of the forests by evergreen and deciduous broad-leaved trees (DBT) (Han 1981). In this sense, the EDF ecotone was considered to be a sub-zone of the evergreen broad-leaved forest zone, which belongs to the subtropical climatic zone in the official Chinese zonation system (Wu 1980). On the contrary, a few researchers considered that, in the EDF ecotone, the canopy was dominated by

Table 1 Summary of viewpoints on vegetation and zonation of the EDF ecotone

Zonal vegetation	Vegetation zone	Climatic zone
Deciduous broad-leaved forest with evergreen broad-leaved trees in shrub and herb layers	Mixed deciduous-evergreen broad-leaved subzone in deciduous broad-leaved forest zone	Warm-temperate zone
Dominated by deciduous broad-leaved trees and evergreen elements just occurring in better hydrothermal conditions	Mixed deciduous-evergreen broad-leaved forest zone	
Forest co-dominated by evergreen and deciduous broad-leaved trees	Mixed evergreen-deciduous broad-leaved forest subzone in evergreen broad-leaved forest zone	Subtropical zone

deciduous trees and that evergreen broad-leaved woody plants occurred only in the shrub or herb layers (Qian et al. 1956). This assigned the ecotone as a sub-zone of the deciduous broad-leaved forest zone, which belongs to the ‘warm-temperate’ climatic zone in the Chinese system (Zhou 1981). In recent decades, based on regional biocoenosis assemblage and vegetation-climate relationships, some researchers (Song 1999; Fang et al. 2002) regarded the EDF ecotone as an independent vegetation zone belong to the warm-temperature zone and named it the mixed deciduous-evergreen forest, representing dominance by deciduous trees in the EDF ecotone (Fang et al. 2002).

Another issue tightly bound with the zonal vegetation of the EDF ecotone was the concept of mixed evergreen and deciduous broad-leaved forest (MEDF; cf. Eyre 1968), which was an independent vegetation type in most vegetation classification systems in China (e.g. Wu 1980) and was considered to be the climax vegetation in the EDF ecotone (Song 1999). This MEDF, however, can also occur in the evergreen broad-leaved forest region on specific topography or edaphic conditions, such as in ravines, on limestone, and in middle altitudes of mountains (Song 2011). Furthermore, the MEDF would be a disclimax vegetation type in the evergreen broad-leaved forest region under frequent, intense disturbance (Song 2011). Natural forests in the EDF ecotone region have been destroyed almost completely, and remnant natural forests are preserved only in mountain regions with extensive secondary forests. Therefore, the boundary and zonal vegetation of the EDF ecotone were distorted, and the formation mechanisms of the MEDF were misunderstood. Even now, it is still hard to distinguish which MEDF could be the climax vegetation in the EDF ecotone. Within the EDF ecotone in eastern China, a formation dominated by *Quercus variabilis* var. *brevipetiolata*, *Castanopsis sclerophylla* and *Cyclobalanopsis glauca* was commonly recorded as the climax MEDF (Liu 1992), but it can also be found in the altitude gradient of typical subtropical mountains. Meanwhile, in last two decades, patches of evergreen broad-leaved forest were recorded in some regions that were considered to be dominated by MEDF, causing a discussion about the local zonal vegetation and leading to various new schemes about the boundaries of the EDF ecotone, such as the Dabie-Shan Mountains in Anhui (Shan and Liu 1964; Han 1981; Deng et al. 1985; Han 1990; Shen 1989).

In conclusion, all debates about the EDF ecotone originated from little knowledge about how evergreen broad-leaved forests are replaced by deciduous forests with increasing latitude and how evergreen and deciduous broad-leaved trees coexist at different spatial scales in the EDF ecotone, especially the assemblage pattern of evergreen and deciduous trees in the mixed forests (MEDF). So, to resolve these questions, we conducted a study in 2010–2011, in Anhui (eastern China), where the zonal vegetation changes from evergreen to deciduous broad-leaved forest. In this study, we evaluated the vegetation transition pattern across the EDF ecotone on different topographies, which have been documented as affecting vegetation distribution greatly at fine scale but without knowledge of effects on vegetation transitions at regional scale.

Transition Pattern Across the EDF Ecotone: A Case Study in Anhui

Study Region and Methods

Anhui Province (29°22′ N–34°40′ N, 114°53′ E–119°30′ E) was a hotspot in debates on the EDF ecotone. Conditions change from a subtropical monsoon climate in the south to a warm-temperate monsoon climate in the north, with mean annual temperature from 14 to 16 °C and average annual precipitation from 750 to 1700 mm. The species composition and community structure of natural forests were compared in three mountain regions, namely the Guniujiang Mountains, Dabie-Shan Mountains, and Huang Cangyu Mountains. These mountain areas belong to the evergreen broad-leaved forest zone, the EDF ecotone, and the deciduous broad-leaved forest zone, respectively (Editorial Committee for Vegetation of Anhui 1981).

We set up 18 plots, 17 plots and 12 plots, respectively, in the basal belt (below 600 m elevation) in the Guniujiang, Dabie-Shan and Huang Cangyu mountains. Each plot was 20 m × 20 m and divided into four subplots. All trees taller than 1.5 m were identified and recorded, and the diameter at breast height (DBH, 1.5 m above ground) and height were measured. Individuals shorter than 1.5 m were also identified, measured by height, and counted for further analyses. All plots were grouped into three topographies: upper slope, lower slope and river valley, according to the topography classification of Nagamatsu and Miura (1997).

A relative importance value (IV) was used to evaluate dominance and was calculated as the mean of relative density, relative frequency and relative basal area at 1.5 m height. To analyze plant trait-environment relationships, rare species were excluded in two ways: (1) species with maximum IV less than 5 % were excluded; and (2) species with frequency less than 5 % were excluded. In total, 7 functional traits and 16 environmental variables were collected in this analysis (see details in Table 2). Functional traits were measured by following Cornelissen

Table 2 Pearson correlations between environmental variables and plant traits on different topographies, using the fourth-corner statistic (combination of models 2 and 4, after (Dray and Legendre 2008)) at community level, weighted by species abundance

		Temperature variables								Precipitation variables					Soil variables		
		MTCQ	CI	PET_{min}	ART	TSN	MAT	WI	PET	PDQ	MAP	Im	AWD	PSN	SoilN	SoilP	SOMC
Upper hillslope	WD	**−0.58**	**−0.57**	**−0.59**	**0.36**	**0.35**	**−0.40**	**−0.33**	**−0.24**	**−0.52**	**−0.50**	**−0.46**	**−0.47**	**0.47**	**0.23**	0.19	−0.06
	N_{mass}	**−0.59**	**−0.58**	**−0.59**	**0.35**	0.33	**−0.43**	**−0.35**	**−0.26**	**−0.52**	**−0.49**	−0.46	−0.45	0.46	0.18	0.21	−0.08
	P_{mass}	**−0.61**	**−0.60**	**−0.61**	**0.39**	**0.36**	**−0.42**	**−0.33**	**−0.24**	**−0.55**	**−0.52**	**−0.50**	−0.49	0.49	0.19	0.23	−0.12
	LL	**0.51**	**0.50**	**0.49**	**−0.31**	−0.28	**0.37**	**0.30**	**0.22**	**0.44**	0.40	0.39	0.39	−0.39	−0.15	−0.22	0.09
	SLA	−0.31	−0.30	−0.30	0.15	0.12	−0.27	**−0.23**	**−0.19**	−0.24	−0.22	−0.20	−0.19	0.20	0.11	0.17	−0.02
	LA	−0.25	−0.24	−0.24	0.15	0.13	−0.19	−0.16	−0.12	−0.22	−0.21	−0.20	−0.19	0.19	0.12	0.15	−0.05
	LDMC	0.38	0.37	0.37	−0.20	−0.20	**0.28**	**0.24**	**0.19**	0.31	0.29	0.27	0.30	−0.30	−0.12	−0.05	0.03
Lower hillslope	WD	**−0.43**	**−0.43**	**−0.43**	0.34	0.30	**−0.35**	**−0.26**	−0.19	−0.37	−0.36	−0.30	−0.29	0.29	0.21	0.14	0.03
	N_{mass}	**−0.62**	**−0.62**	**−0.64**	**0.64**	**0.62**	**−0.31**	−0.12	−0.01	**−0.67**	**−0.66**	**−0.63**	**−0.63**	**0.63**	0.07	−0.03	−0.30
	P_{mass}	**−0.53**	**−0.53**	**−0.54**	**0.48**	0.46	**−0.33**	−0.19	−0.10	**−0.51**	**−0.50**	−0.46	**−0.49**	**0.48**	−0.03	0.01	−0.27
	LL	**0.44**	**0.44**	**0.45**	**−0.44**	−0.39	**0.28**	0.17	0.09	**0.46**	**0.44**	0.40	0.39	−0.39	0.01	−0.19	0.16
	SLA	**−0.55**	**−0.55**	**−0.57**	**0.63**	**0.64**	−0.19	0.00	0.11	**−0.65**	**−0.65**	**−0.64**	**−0.64**	**0.64**	0.01	−0.13	**−0.37**
	LA	**0.44**	**0.44**	**0.45**	**−0.49**	**−0.53**	0.12	−0.03	−0.12	**0.51**	**0.52**	**0.51**	**0.54**	**−0.54**	−0.02	0.18	0.33
	LDMC	**0.49**	**0.50**	**0.51**	**−0.57**	**−0.60**	0.14	−0.03	−0.13	**0.59**	**0.59**	**0.59**	**0.61**	**−0.61**	0.10	0.17	**0.42**

Significant results are in boldface

MTCQ mean temperature of the coldest quarter, *CI* coldness index, PET_{min} minimum monthly potential evapotranspiration, *ART* annual range of temperature, *TSN* temperature seasonality, *MAT* mean annual temperature, *WI* warmth index, *PET* potential evapotranspiration, *PDQ* precipitation of the driest quarter, *MAP* mean annual precipitation, *Im* moisture index, *AWD* annual water deficit, *PSN* precipitation seasonality, *SoilN* total soil nitrogen, *SoilP* total soil phosphorus, *SOMC* soil organic matter content, *WD* woody density, N_{mass}/P_{mass} leaf nitrogen/phosphorus content per dry mass, *LL* leaf life span, *SLA* specific leaf area, *LA* leaf area, *LDMC* leaf dry matter content

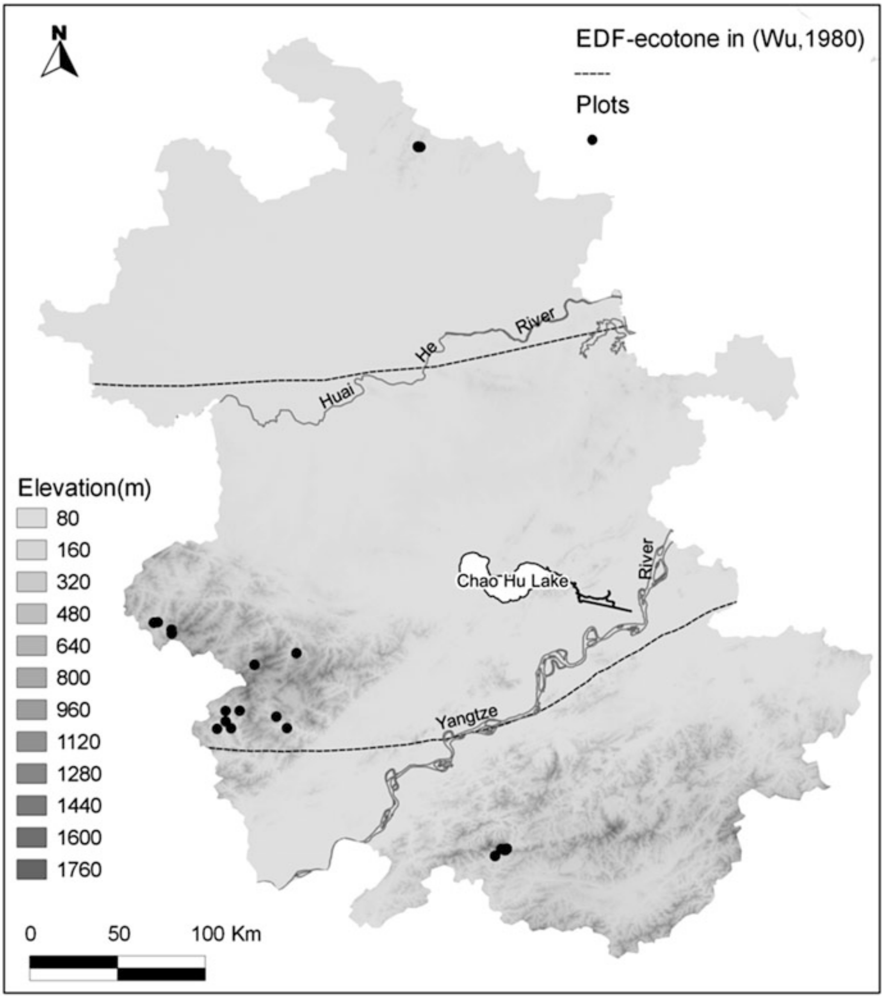

Fig. 2 Location of study sites (*solid circles*) and the boundary of the EDF ecotone (*dashed line*) in Anhui Province, eastern China, adapted from the *Vegetation of China* (Wu 1980)

et al. (2003). Climate variables were calculated based on the WorldClim database, a global climate database with a spatial resolution of 30 arc sec (Hijmans et al. 2005). To quantify the relationship of plant traits and environmental variables, we used the fourth-corner statistic. The significance of correlations was tested with 999 permutations using two different permutation models (Dray and Legendre 2008), with the 'ade4' library (Dray and Dufour 2007) in open-source R (R Core Team 2012) (Fig. 2).

Topographic Differentiation of Forest Transition Pattern Across the EDF Ecotone

In all, 195 woody plant species in 113 genera and 55 families were identified. Most species were broad-leaved trees, except for three evergreen conifer species: *Pinus massoniana*, *Cunninghamia lanceolata* and *Cephalotaxus fortunei*. There were distinctly different transition patterns between upper and lower hillslopes across the EDF ecotone. From south to north, dominance by evergreen trees decreased faster on upper slopes than on lower slopes, while dominance by deciduous trees increased faster on upper slopes than on lower slopes (Fig. 3). In the EDF ecotone, evergreen trees could dominate on the whole slope in the southern Dabie-Shan but just barely on lower slopes in the northern Dabie-Shan. This asynchronous transition pattern on different topographies produced a broad mosaic EDF ecotone filled by both evergreen and deciduous broad-leaved trees.

The turnover of the dominant species was also different on different topographies. On upper slopes, dominance shifted from *Castanopsis eyrei* and *Castanopsis sclerophylla* to *Castanopsis sclerophylla* and *Lithocarpus glaber*, which were replaced finally by deciduous *Quercus* species, such as *Q. variabilis*, *Q. aliena* and *Q. serrata*. On lower slopes, dominance shifted from *Castanopsis eyrei*, *Machilus thunbergii*, *Lithocarpus henryi* and *Cyclobalanopsis glauca* to *Cyclobalanopsis glauca* and *Castanopsis sclerophylla*, which were replaced finally by *Pteroceltis tatarinowii* and *Tilia miqueliana*. This can be summarized briefly as follows: *Castanopsis* and *Cyclobalanopsis* are replaced by deciduous trees on upper and lower slopes, respectively. *Cyclobalanopsis* species were more tolerant to cold than *Castanopsis* species. In eastern China, the coldness limit of *Castanopsis sclerophylla* is near a CI value of $-8\ ^\circ\mathrm{C} \cdot \mathrm{month}$, which makes it weaker than *Cyclobalanopsis gracilis*, with CI limit at $-15\ ^\circ\mathrm{C} \cdot \mathrm{month}$ (Deng et al. 1985). In Japan, the northern limit of *Castanopsis* trees is close to the 2 °C isotherm for the mean of the coldest month (Ohsawa et al. 1985), which is higher than the -1 °C northern limit of evergreen broad-leaved forest (Ohsawa 1990). Thus, *Castanopsis* species are replaced by deciduous trees further south than are *Cyclobalanopsis* species, which was the reason for the asynchronous transition patterns on different topographies.

Differentiation in forest transition patterns is caused by different vegetation-climate relationships on different topographies. Previous study suggested that temperature was the major driving factor on upper slopes, especially those aspects related to minimum temperatures, while precipitation seemed to be the main driving factor on lower slopes (Song et al. 2014). This was supported by the plant trait-environment relationships apparent at community level (Table 2). As temperature variables, indices for cold stress, such as mean temperature of the coldest quarter, CI and minimum monthly potential evapotranspiration ($\mathrm{PET_{min}}$), were related more to plant traits than were indices of annual temperature conditions. It was shown also that leaf traits had higher correlation with temperature variables than with precipitation on upper slopes, but the relationship was reversed on lower

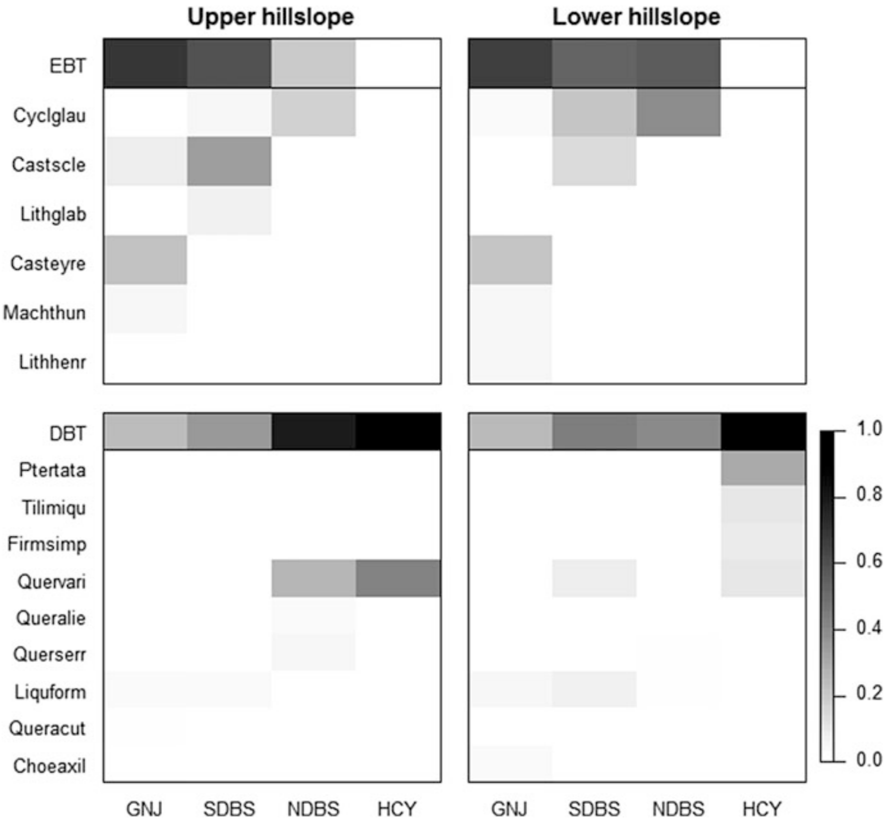

Fig. 3 Variation of importance values (IV) from south to north for evergreen broad-leaved trees (EBT) and deciduous broad-leaved trees (DBT) on upper and lower hillslopes, in Anhui Province. GNJ = Guniujiang Mountain, SDBS = south slope of Dabie-shan Mountains, NDBS = north slope of Dabie-shan, HCY = Huang Cangyu Mountain. Bigger IV values are shown by *darker gray* levels. Upper hillslopes included upper side slopes (USS), and lower hillslopes, including lower side slopes (LSS) and river beds (RB) (Nagamatsu and Miura 1997). Species abbreviations: Cyclglau = *Cyclobalanopsis glauca*, Castscle = *Castanopsis sclerophylla*, Lithglab = *Lithocarpus glaber*, Casteyre = *Castanopsis eyrei*, Machthun = *Machilus thunbergii*, Lithhenr = *Lithocarpus henryi*. Ptertata = *Pteroceltis tatarinowii*, Tilimiqu = *Tilia miqueliana*, Firmsimp = *Firmiana simplex*, Quervari = *Quercus variabilis*, Queralie = *Quercus aliena*, Querserr = *Quercus serrata*, Liquform = *Liquidambar formosana*, Queracut = *Quercus acutissima*, Choeaxil = *Choerospondias axillaris*

slopes (Table 2). On the other hand, on lower slopes, climate was correlated significantly with specific leaf area, leaf area, and leaf dry matter content. This reflects resource allocation in leaves and is closely related to available water, as has been documented many times (e.g. Cornelissen et al. 2003; Markesteijn et al. 2011). On lower slopes, woody plants showed shorter leaf life spans and allocated less of their resources to leaves with decreasing temperature and precipitation, but only shorter leaf lifespans were apparent on upper slopes. This could be because upper slopes are drier and more infertile than lower slopes (Enoki et al. 1996; Hara et al. 1996), and woody plants are prone to have more conservative strategies, such as thicker, smaller leaves with higher dry-matter content. So, woody plants may preserve similar resource allocation strategies in leaves on upper slopes across the EDF ecotone.

Mountain Mixed Forests Caused by Two-Dimensional Transition in the EDF Ecotone

Forests showed the same transition pattern from evergreen to deciduous broad-leaved forest with increasing altitude. The break points in the transition were different, however, on different topographies (Fig. 4). On upper slopes below 350 m, evergreen broad-leaved trees dominated in each vegetation layer, except that the conifer *Pinus massoniana* occurred in the emergent layer in a few plots. Above 350 m, the forest was dominated by deciduous trees, with evergreens under the canopy. A similar shift in forest structure was evident on lower slopes, but the break point was near 500 m. In river valleys the break point could be above 600 m. So it appeared that the altitude of the transitions increased from low upper slopes to high river valleys, which was related to the distribution of three dominant species, *Cyclobalanopsis glauca*, *Castanopsis sclerophylla* and *Quercus variabilis*, on the different topographies and latitudes (Fig. 5). *Castanopsis sclerophylla* occurred mostly below 350 m, and its density and height increased from river valleys to upper slopes. *Cyclobalanopsis glauca* occurred widely in the EDF ecotone but had higher density and larger individuals on lower slopes. *Quercus variabilis* occurred mostly above 350 m and had higher density and more large individuals on upper slopes. Therefore, the break point was near 350 m on upper slopes, where *Cyclobalanopsis glauca* replaced *Castanopsis sclerophylla* as the dominant evergreen tree, but most individuals were small, growing under the canopy constituted by *Quercus variabilis*. Due to the preference of *Cyclobalanopsis glauca* for lower slopes, the break points occurred at higher altitude on lower slopes and highest in river valleys.

With increasing elevation, the dominance of evergreen trees in the canopy decreased gradually and that of deciduous trees increased, beyond the range of *Castanopsis sclerophylla*. This was also caused by different habitat preferences by *Quercus variabilis* and *Cyclobalanopsis glauca* (see above descriptions). *Quercus variabilis* had a low germination rate in stands with wet soil and thick litter layer, and the growth rate of its seedlings showed a negative relationship with soil moisture (Ma et al. 2010). Lower slopes have higher soil moisture and accumulate more litter, which limits the establishment of *Quercus variabilis*. On the other hand, despite having a low germination rate and high mortality among seedlings, *Cyclobalanopsis glauca* showed great sprouting ability in all size classes (Song 2012), which could maintain its population on lower slopes through continuous recruitment.

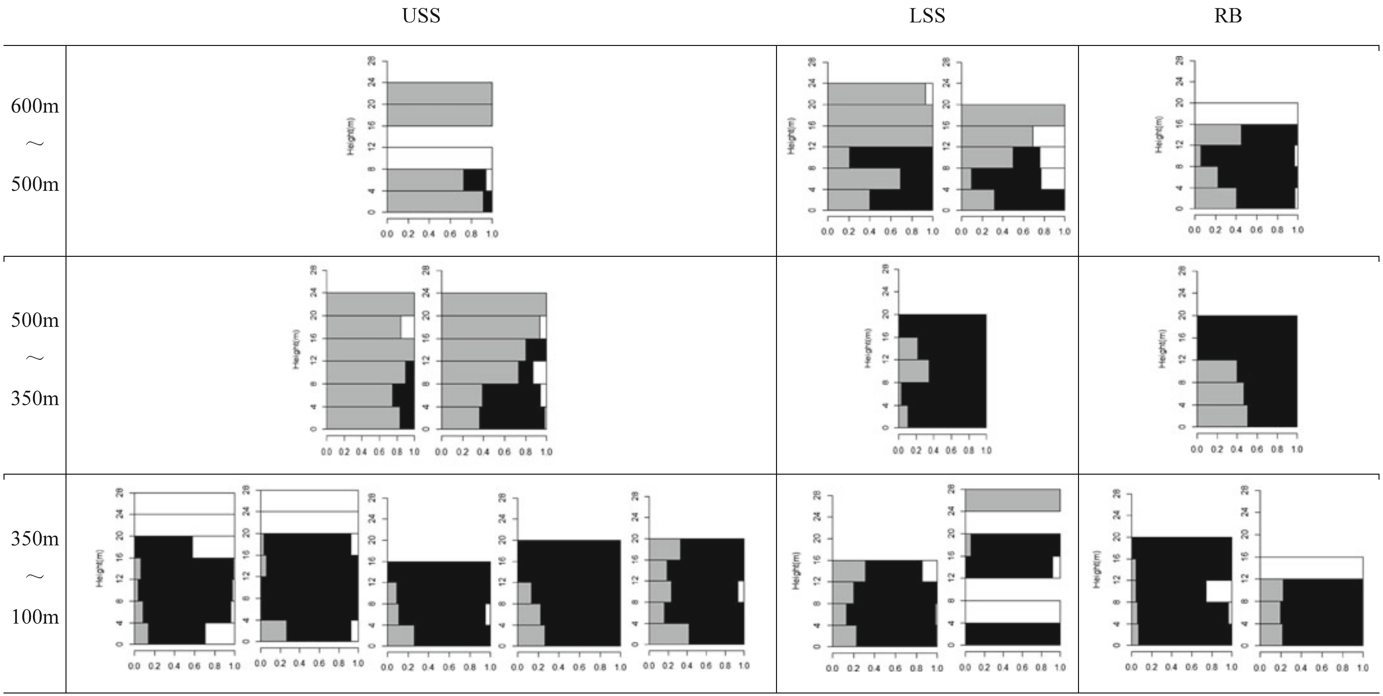

Fig. 4 Height distribution of relative basal area (RBA) for forests on different topographies in the EDF ecotone. Evergreen broad-leaved trees (EBT) are shown in *black*, deciduous broad-leaved trees (DBT) are in *gray*, and evergreen conifer trees are in *white*. *UUS* upper side slopes, *LSS* lower side slopes, and *RB* river beds

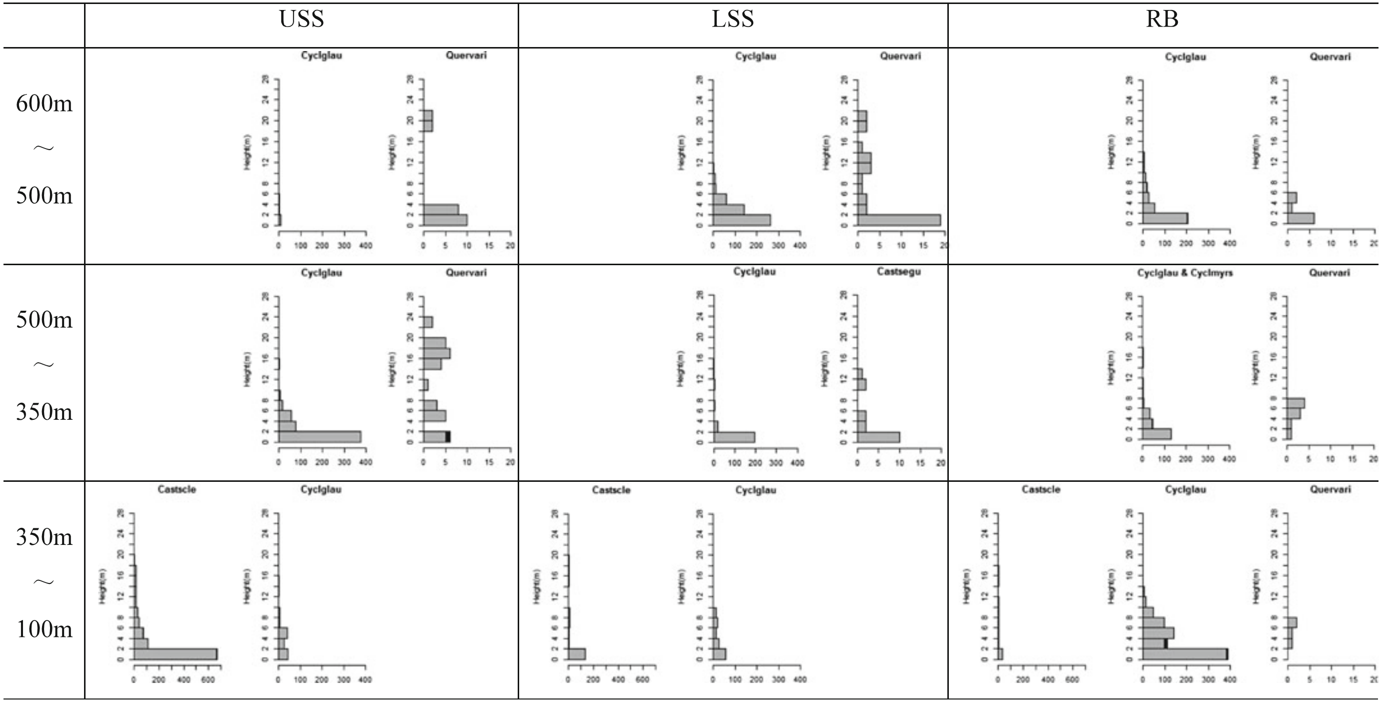

Fig. 5 Height frequency distribution of *Cyclobalanopsis glauca* (Cyclglau), *Castanopsis sclerophylla* (Castscle) and *Quercus variabilis* (Quervari) on different topographies in the EDF ecotone. Living individuals are in *gray*, dead individuals are in *black*. The horizontal axis is the individual number per 0.04 ha. *USS* upper side slopes, *LSS* lower side slopes, and *RB* river bed. Cyclmyrs: *Cyclobalanopsis myrsinifolia*, Castsegu: *Castanea seguinii*

It appears from these observations that evergreen and deciduous broad-leaved trees would probably mix and co-dominate the forests of the transition area along altitudinal and topographic gradients. These forests could be the typical ‘mixed evergreen-deciduous forest’ (MEDF, or the ‘semi-evergreen broad-leaved forest’ of other authors, e.g. Eyre 1968) in the EDF ecotone. According to the above results, the co-dominant species of this semi-evergreen forest would be *Quercus variabilis* and *Cyclobalanopsis glauca*. Based on these criteria, two plots on lower slopes at 500–600 m and one plot on an upper slope at 350–500 m were considered to be the typical ‘mixed evergreen-deciduous forest’. Each showed a structure in which deciduous trees dominated the canopy and evergreen trees dominated the understory (Fig. 4). By using the mean DBH of the five biggest individuals in each plot, we divided the plots into three stand stages (Fig. 6). Based on the DBH-age relationship established by Zhang et al. (2003) for *Quercus variabilis*, it appears that the youngest stage was about 60 years old, the middle stage about 100 years old, and the oldest stage could be more than 250 years old. With increasing forest age, the two dominant species *Quercus variabilis* and *Cyclobalanopsis glauca* had more large individuals, with continuous recruitment in the 0–20 cm DBH class. Another deciduous tree species, *Platycarya strobilacea*, showed a similar growth pattern. Conversely, two other deciduous tree species, *Quercus serrata* and *Dalbergia hupeana*, had fewer large individuals, and the conifer *Pinus massoniana* had only a few large individuals, without recruitment. All three of these species were inferred to be pioneer species of the evergreen-deciduous forest, as also in the subtropical evergreen broad-leaved forests. We suppose that this would still be a vertically mixed evergreen-deciduous (broad-leaved) forest even if the canopy individuals died, because the pioneer deciduous trees grow faster than does *Cyclobalanopsis glauca* (dashed line in Fig. 6) and the forest would return to the above-described forest dynamics.

Formation Mechanism of the EDF Ecotone and Its Characteristics and Boundaries

Interaction of Climate and Topography Causes the EDF Ecotone

As mentioned in the first section, the values of the coldness index (CI) and warmth index (WI) at the northern boundary of evergreen broad-leaved forest zone in eastern China do not reach the limit for evergreen broad-leaved trees, which were considered to be CI = −10 °C · month and WI = 85 °C · month in subtropical and warm-temperate regions. This means that there is a wide gap between the northern boundary and the temperature limit for evergreen broad-leaved forest in eastern China (Fig. 7a). Theoretically, this gap would be the potential region of the EDF ecotone. By using the WorldClim raster data (Hijmans et al. 2005), we found that

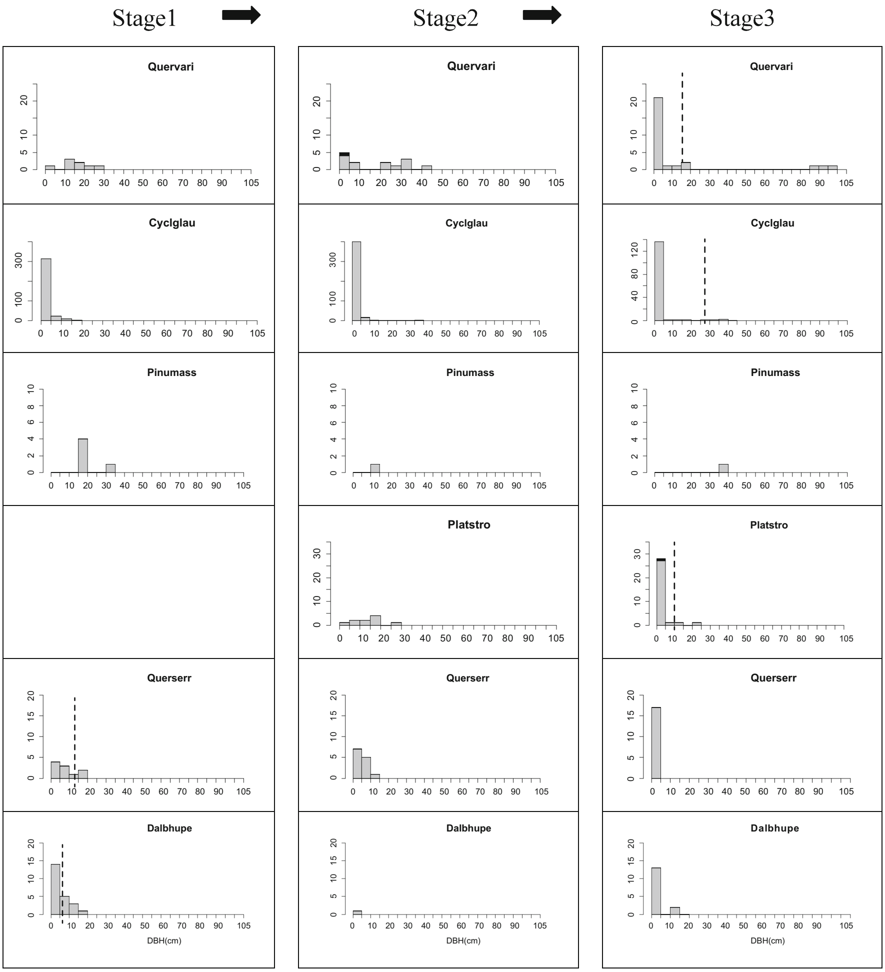

Fig. 6 Frequency distribution of diameter at breast height (DBH) for the main species in forests dominated by *Quercus variabilis* (Quervari) and *Cyclobalanopsis glauca* (Cyclglau), at three stand stages. Living individuals are in *gray*, dead individuals are in *black*. The vertical axis is the individual number per 0.04 ha. The locations of *dashed lines* on the horizontal axis indicate the DBH at which the height was 10 m for each species. Pinumass = *Pinus massoniana*, Platstro = *Platycarya strobilacea*, Querserr = *Quercus serrata*, Dalbhupe = *Dalbergia hupeana*

this gap was almost identical with that of the EDF ecotone in the scheme of Song (1999), after excluding mountain sites in the evergreen broad-leaved forest zone. On the other hand, because the distribution of evergreen broad-leaved forest coincides with its temperature limit in Japan, we presumed limitation of the evergreen broad-leaved forest by precipitation, using the 1 % quantile of the annual precipitation (ca. 1200 mm) of evergreen broad-leaved forest in Japan, wherever CI is higher than −10 °C · month. Excluding mountain sites in the evergreen broad-

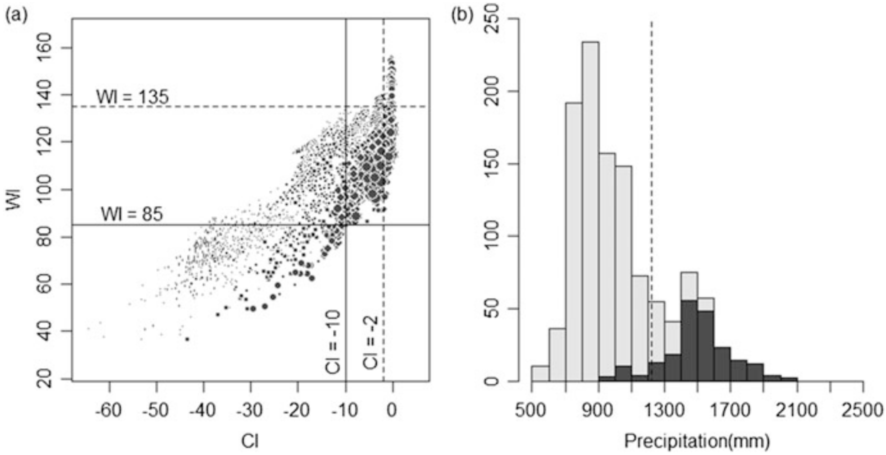

Fig. 7 Warmth Index (WI) and Coldness Index (CI) of the southern part of Eastern China (18–38° N, 105–125° E), based on WorldClim data at 2.5 min resolution (Hijmans et al. 2005). (**a**) Sites located in the *square* surrounded by the four lines of CI = −10, CI = −2, WI = 85, and WI = 135 were considered to be the potential area of the EDF ecotone; its annual precipitation distribution is shown in (**b**). Mountain sites in the evergreen broad-leaved forest zone are in *black* and the others in *gray*. The *dotted line* in (**b**) indicates the 1 % quantile of annual precipitation in the evergreen broad-leaved forest region in Japan, where CI is higher than −10

leaved forest zone showed that more than 90 % of the sites in the potential region of the EDF ecotone have annual precipitation less than the presumed limiting value (Fig. 7b). This supports the idea of a precipitation limit for the northward distribution of evergreen broad-leaved forest (Fang 1999), and so climate appears to be the mechanism for the formation of the EDF ecotone in eastern China.

If only limitation by precipitation were considered, there would be a clear boundary between the evergreen and deciduous broad-leaved forest and the EDF ecotone would be narrow, because precipitation tends to decrease monotonically northward in eastern China. As shown in our study, evergreen broad-leaved forest can occur in the EDF ecotone, and almost all records showed it occurring widely in mountain areas with habitat descriptions such as *located in valley*, *near a stream or river*, or *on humid soil*. Many studies indicated that soil water content was the most distinguishing habitat factor on different topographies, with lower slopes tending to be wetter than upper slopes (Enoki et al. 1996; Hara et al. 1996). These authors pointed out that different soil water availability caused by topography made it possible for evergreen broad-leaved forest to occur in the EDF ecotone and would be another formation mechanism for the EDF ecotone. The effect of topography on soil water content, though, is not unlimited. With decreasing precipitation and lower mountains, there could be a threshold beyond which no topography can provide the soil water needed for evergreen broad-leaved forest. That could be the reason why few evergreen broad-leaved forests were found in hilly regions of the EDF ecotone and why its northern boundary in the *Vegetation of China* (Wu 1980) did not reach the CI = −10 °C · month isotherm.

Characteristics of the EDF Ecotone and Application to Boundary Determination

Based on the study in Anhui and the formation mechanisms of the EDF ecotone, we propose that the basic characteristic of the EDF ecotone is a hierarchical transition from evergreen to deciduous broad-leaved forest along three dimensions: latitude, altitude and topography. For latitude and altitude, the climatic gradient triggers the transition. For topography, redistribution of the fallen precipitation on different topographies results in heterogeneous availability of soil water and nutrients, and seems to be a reasonable explanation for the transition. By this hierarchical transition process, the EDF ecotone would produce a mosaic landscape of evergreen broad-leaved forests and deciduous broad-leaved forests, with more and larger evergreen patches toward the south and more, larger deciduous patches toward the north (see mosaic model below). Stable evergreen-deciduous forests are more likely to occur in the transition areas between evergreen patches and deciduous patches. Because of their greater maximum height and faster growth rate, deciduous trees dominate the canopy and evergreen trees occupy the understory in these evergreen-deciduous forests, which are called vertically mixed evergreen-deciduous forests (MEDF) in this study.

By this mosaic model of the EDF ecotone, the southern boundary should be the threshold where deciduous broad-leaved forest patches occur and the northern boundary should be the threshold where evergreen broad-leaved forest patches disappear completely (Fig. 8). According to our study in Anhui, the shift of dominance from evergreen to deciduous trees with increasing latitude occurred, at lower latitude, on upper slopes more than on lower slopes, which was caused by the replacement of the dominant evergreen species *Castanopsis eyrei* and *Castanopsis sclerophylla* by deciduous species. Therefore, the northern limits of these two species could be considered to be the southern boundary of the EDF ecotone in Anhui. On the other hand, evergreen trees were finally replaced by deciduous trees on lower slopes in the north, due to the replacement of *Cyclobalanopsis glauca* by deciduous species. In the same way, the northern limit of *Cyclobalanopsis glauca* could be considered to be the northern boundary of the EDF ecotone in Anhui.

Application of this boundary determination method can be extended to the whole EDF ecotone. *Castanopsis* species and *Cyclobalanopsis* species can be chosen to determine the southern and northern boundaries, respectively, of the EDF ecotone. As we know, in *Castanopsis*, species with smaller leaves can dominate further north than can other species and can cover almost all the slopes. Their northern limits are suitable markers for the southern boundary of the EDF ecotone. Such species would be *Castanopsis eyrei*, *C. carlesii* and *C. carlesii* var. *spinulosa*. *Cyclobalanopsis* species have the greatest cold tolerance among the evergreen broad-leaved trees, and their northern limits are suitable markers for the northern boundary of the EDF ecotone. In particular, the species involved would be *Cyclobalanopsis glauca* and *C. oxyodon*.

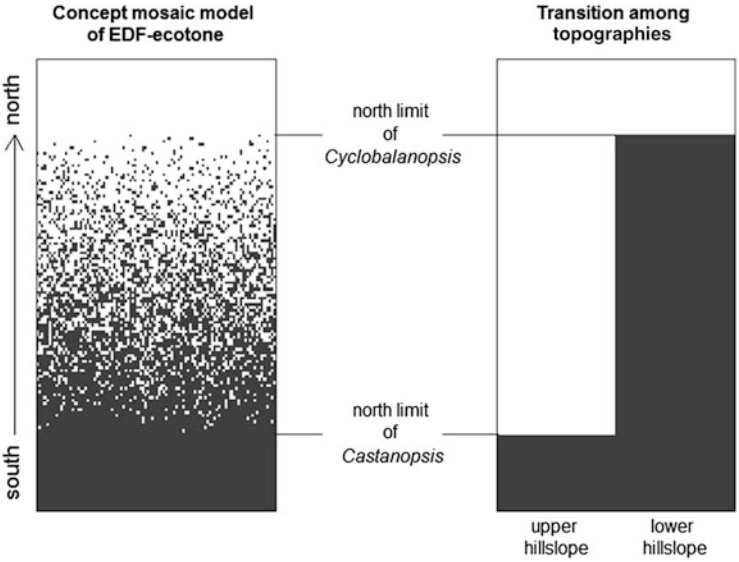

Fig. 8 In the mosaic concept of the EDF ecotone, the southern boundary is consistent with the northern limit of *Castanopsis*, whose dominance is replaced by deciduous broad-leaved trees on upper hillslopes; the northern boundary is consistent with the northern limit of *Cyclobalanopsis*, whose dominance is replaced by deciduous broad-leaved trees on lower hillslopes. The regions dominated by evergreen broad-leaved trees are in *black*, and those dominated by deciduous broad-leaved trees are in *white*

We consider that our method, based on the mosaic concept, is more reasonable than previous boundary determination methods used for the EDF ecotone. The prevalent method using the climate-vegetation relationship ignores the effect of topography on plant distribution, which has been documented in many vegetation zones; it also ignores the clearly different vegetation transition patterns on upper versus lower slopes across the EDF ecotone, as shown in our study. Another prevalent method using relevé records has limited application in eastern China because this region has been exploited intensively and is dominated by secondary forests, most of which are deciduous or evergreen-deciduous forests that can confuse the determination of the EDF ecotone boundaries. Moreover, there are fewer relevé records than floristic records in China. Actually, even for floristic records, most of the distribution data for woody plants were at the county level, across whole provinces and across the whole country (Fang et al. 2011), which seems to be too coarse for checking the boundaries of the EDF ecotone. Even so, we anticipate that this method could determine the boundaries of the EDF ecotone quantitatively and accurately, if there were enough site-based distribution data for the relevant species.

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Ecology of Relict Tertiary Deciduous Trees in Subtropical China

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Abstract How relict Tertiary deciduous trees survive and persist under current climate and frequent human activity becomes an important topic for conservation of rare and endangered species. The southeastern China-Himalaya region is one of the most important refugia for Tertiary relict flora in East Asia and harbors extraordinarily abundant relict Tertiary deciduous trees. This is also a moist subtropical region covered by evergreen broad-leaved forests in mountainous and hilly areas. The geographic distributions of these relict trees are isolated and disjunct. They occur always on unstable terrain such as valleys, ravines, steep slopes, and stream banks and form a topographic climax forest. These species are dispersed by minute wind-dispersed seeds and also reproduce vegetatively. The floristic composition of the relict-dominated communities is complex and ancient. The communities occupy particular landforms and form a mosaic pattern with the zonal vegetation. Hence, as pioneer species, relict deciduous trees can be regarded not only as 'filler species' for habitat space where zonal vegetation failed to colonize, but also as 'gap-repairing species' on gentle habitats.

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Introduction: Significance of Relict Tertiary Deciduous Trees in China

Relict floras contain survivors from plant communities that occurred throughout a large part of the Northern Hemisphere during much of the Tertiary or earlier periods (Fryxell 1962; Denk et al. 2001; Calleja et al. 2009). As the world cooled over the last 15 million years, members of relict floras were restricted to limited regions of equable climate during the early to mid-Tertiary (65–15 million years ago) and became extinct elsewhere (Wolfe 1975; Tzedakis et al. 2002; Calleja et al. 2009). Relict floras can be classified as pre-Tertiary, Tertiary, glacial, interglacial, or postglacial, according to their history and origin. Tertiary deciduous trees are common in modern relict floras and are restricted mainly to warm humid areas (refugia) in southeastern and western North America, East Asia, and southwestern Eurasia (Milne and Abbott 2002).

During the Quaternary glaciations, Tertiary deciduous trees experienced severely reduced regeneration and survived as biological refugees after extinction of their relatives elsewhere (Fryxell 1962; Denk et al. 2001; Tzedakis et al. 2002; Calleja et al. 2009). Of the well-known relict Tertiary deciduous trees, most are monotypic or oligotypic and retain traits of their ancient origins. The majority are critically threatened with extinction in the wild, as judged by IUCN criteria (Pitman and Jorgensen 2002). They are restricted mainly to relatively narrow, discontinuous ranges and occur on unstable sites such as scree slopes, eroded rocky stream banks and other steep slopes (Sakai et al. 1995; Tang and Ohsawa 2002; Wei et al. 2010). The populations of these species are very small, and their ranges are becoming isolated due to habitat fragmentation associated with frequent human disturbance (Eriksson 1998; Denk et al. 2001; Hampe and Arroyo 2002).

The mountain and hills of the subtropicalevergreen broad-leaved forest regions in China have extremely high numbers of species and relatively high proportions of Tertiary vascular relicts (Milne and Abbott 2002). During the Tertiary period, the boreo-tropical flora was gradually shaped into mesic mixed forests but became fragmented with climatic cooling during the middle and late Tertiary; further cooling in the Pleistocene forced the flora southward (Wolfe 1975; Tiffney 1985). The oldest taxa of the vascular flora persisted formerly on particular habitats as small, disjunct populations under the current conditions (Tang and Ohsawa 2002; Wei et al. 2010). Many ancient deciduous broad-leaved genera, considered to be Tertiary relicts, are found today in the subtropical broad-leaved forests of southern China, including *Davidia involucrata*, *Tetracentron sinense*, *Cercidiphyllum japonicum*, *Euptelea pleiospermum*, *Cyclocarya paliurus* and *Emmenopterys henryi* (Del Tredici 2001; Lopez-Pujol et al. 2006). These contribute to the biodiversity pool and became a particular component of the vegetation in subtropical mountain areas (Wu 1980; Shen et al. 2000). Their regeneration may be poor and, under present conditions, they are presumably highly sensitive to human alterations of their habitats (Da et al. 2009; Wei et al. 2010). How these relict Tertiary deciduous trees survive and persist under current climate conditions and frequent human activity becomes an important topic for the conservation of rare and endangered species.

Geographical Distributions of Relict Tertiary Deciduous Trees in Subtropical China

Recent molecular phylogenetic studies show that the East Asian relict Tertiary flora is best divided into two distinct refugial groups, with geographical distributions centered on Japan/Korea/northeast China and on the southeast China-Himalaya regions (Milne and Abbott 2002). The southeast China-Himalaya region includes mainly eastern China (Shandong, Jiangsu, Anhui, Shanghai, Zhejiang and Fujian provinces), central China (Hubei, Hunan, Henan and Jiangxi), southern China (Guangdong, Guangxi and Hainan), and southwestern China (Sichuan, Yunnan, Guizhou and Chongqing) and Tibet. The vegetation type dominant on mountainous and hilly areas is evergreen broad-leaved forest. The dominant trees are evergreen species belonging to the families Fagaceae (*Castanopsis*, *Cyclobalanopsis Lithocarpus*), Lauraceae (*Beilschmiedia*, *Cinnamomum*, *Lindera*, *Machilus* and *Phoebe*) and Theaceae (*Camellia* and *Eurya*) (Song 1988).

These regions have at least 28 relict Tertiary deciduous trees, the geographic distributions of which trees are discontinuous (see Table 1, cf. Fig. 1). The genus *Liquidambar*, belonging to the family Hamamelidaceae, occurs over a wide geographical range extending from North America to East Asia and the Mediterranean region (Öztürk et al. 2008). *Liquidambar acalycina* and *L. formosana* are endemic to and occur widely in subtropical China (Table 1), while *L. styraciflua* occurs in eastern North American and *L. orientalis* shows a very restricted distribution in the southwestern provinces of Turkey (Öztürk et al. 2008). The genera *Nyssa* and *Liriodendron* (belonging to the families Nyssaceae and Magnoliaceae) occur disjunctively in East Asia and North America. *Nyssa sylvatica N. aquatica* and *Liriodendron tulipifera* occur in eastern North America, while *N. sinensis*, *N. yunnanensis*, and *L. chinense* are in East Asia (Qian 2002; Milne 2006). The genera *Cercidiphyllum* and *Euptelea* extend from Sichuan (southwestern China) eastward across the Yangtze valley to Japan (Tang and Ohsawa 2002). *Cercidiphyllum japonicum* occurs mainly in low to mid-elevation warm-temperate deciduous forests in south-central China and in Japan, while *C. magnificum* is restricted to cool-temperate and sub-alpine forests of central Honshu, Japan (Krassilov 2010). The genus *Euptelea* contains only two species: *Euptelea polyandra*, which occurs in temperate deciduous forests in Japan, and *E. pleiospermum,* which is found in China.

The greatest concentration of Tertiary deciduous trees is in the region extending from southeastern China to the Himalaya. This region includes *Nyssa sinensis, Bretschneidera sinensis, Liquidambar formosana, L. acalycina, Cyclocarya paliurus, Euptelea pleiosperma, Emmenopterys henryi, Cercidiphyllum japonicum,*

Table 1 Distribution areas of relict deciduous broad-leaved trees in China

Species	Family	Distribution (province)
Nyssa sinensis	Nyssaceae	Anhui, S Fujian, Guangdong, Guangxi, Guizhou, Hubei, Hunan, Jiangsu, Jiangxi, SE Sichuan, Yunnan, Zhejiang
Nyssa yunnanensis	Nyssaceae	S Yunnan
Davidia involucrata	Davidiacea	Guizhou, W Hubei, W Hunan, Sichuan, N Yunnan
Tetracentron sinense	Tetracentraceae	S Gansu, Guizhou, SW Henan, W Hubei, NW and SW Hunan, S Shaanxi, Sichuan, S and SE Tibet, Yunnan
Bretschneidera sinensis	Bretschneideraceae	Fujian, Guangdong, Guangxi, Guizhou, Hubei, Hunan, Jiangxi, Sichuan, Taiwan, Yunnan, Zhejiang
Liquidambar formosana	Hamamelidaceae	Anhui, Fujian, Guangdong, Guizhou, Hainan, Hubei, Jiangsu, Jiangxi, Sichuan, Taiwan, Zhejiang
Liquidambar acalycina	Hamamelidaceae	Anhui, Guangdong, Guangxi, Guizhou, Hubei, Jiangsu, Jiangxi, Sichuan.
Cyclocarya paliurus	Juglandaceae	Anhui, Fujian, Guangdong, Guangxi, Guizhou, Hainan, Hubei, Hunan, Jiangsu, Jiangxi, Sichuan, Taiwan, SE Yunnan, Zhejiang.
Euptelea pleiosperma	Eupteleaceae	S Anhui, S Gansu, Guizhou, SW Hebei, W Henan, Hubei, Hunan, E Jiangxi, S Shaanxi, S Shanxi, Sichuan, SE Tibet, N and E Yunnan, NW Zhejiang
Emmenopterys henryi	Rubiaceae	Anhui, Fujian, Gansu, Guangdong, Guangxi, Guizhou, Henan, Hubei, Hunan, Jiangsu, Jiangxi, Shanxi, Sichuan, Yunnan, Zhejiang.
Heptacodium miconioides	Caprifoliaceae	Anhui, Hubei, Zhejiang
Cercidiphyllum japonicum	Cercidiphyllaceae	S and W Anhui, S Gansu, NE Guizhou, SW Henan, Hubei, NW Hunan, N Jiangxi, S Shaanxi, SW Shanxi, Sichuan, NE Yunnan, NW Zhejiang
Eucommia ulmoides	Eucommiaceae	Gansu, Guizhou, Henan, Hubei, Hunan, Shaanxi, Sichuan, Yunnan, Zhejiang
Disanthus cercidifolius ssp. longipes	Hamamelidaceae	Hunan, Jiangxi, Zhejiang
Sinowilsonia henryi	Hamamelidaceae	Gansu, Henan, Hubei, Shaanxi, Shanxi, Sichuan.
Annamocarya sinensis	Juglandaceae	Guangxi, S Guizhou, SE Yunnan
Liriodendron chinense	Magnoliaceae	Anhui, Chongqing, Fujian, Guangxi, Guizhou, Hubei, Hunan, Jiangxi, Shaanxi, SE Sichuan, Yunnan, Zhejiang
Rhoiptelea chiliantha	Rhoipteleaceae	N and W Guangxi, S Guizhou, SE Yunnan
Eurycorymbus cavaleriei	Sapindaceae	Fujian, Guangdong, Guangxi, Guizhou, Hunan, Jiangxi, Sichuan, Taiwan, Yunnan.

(continued)

Table 1 (continued)

Species	Family	Distribution (province)
Handeliodendron bodinieri	Sapindaceae	NW Guangxi, S Guizhou
Tapiscia sinensis	Staphyleaceae	Anhui, Fujian, Guangdong, Guangxi, Guizhou, Hubei, Hunan, Jiangxi, Sichuan, Yunnan, Zhejiang.
Stewartia sinensis	Theaceae	Anhui, Fujian, N Guangxi, Guizhou, Henan, Hubei, Hunan, Jiangxi, S Shaanxi, E Sichuan, NE Yunnan, Zhejiang.
Pteroceltis tatarinowii	Ulmaceae	Anhui, Fujian, S Gansu, Guangdong, Guangxi, Guizhou, Hebei, Henan, Hubei, Hunan, Jiangsu, Jiangxi, Liaoning, SE Qinghai, Shaanxi, Shandong, Shanxi, Sichuan, Zhejiang
Camptotheca acuminata	Davidiacea	Fujian, Guangdong, Guangxi, Guizhou, Hubei, Hunan, Jiangsu, Jiangxi, Sichuan, Yunnan, Zhejiang
Shaniodendron subaequale	Hamamelidaceae	Anhui, Zhejiang, Jiangsu
Poliothyrsis sinensis	Flacourtiaceae	Anhui, Fujian, S Gansu, Guangdong, Guizhou, Henan, Hubei, Hunan, Jiangsu, Jiangxi, S Shaanxi, Sichuan, NE Yunnan, Zhejiang
Fortunearia sinensis	Hamamelidaceae	Anhui, Henan, Hubei, Jiangxi, Shaanxi, Sichuan, Zhejiang
Halesia macgregorii	Hamamelidaceae	NW Fujian, N Guangdong, N Guangxi, S Guizhou, SW Hunan, S Jiangxi, Zhejiang

Source: Flora of China, www.eFloras.org

Eucommia ulmoides, Liriodendron chinense, Eurycorymbus cavaleriei, Tapiscia sinensis, Stewartia sinensis, Pteroceltis tatarinowii, Camptotheca acuminata, Poliothyrsis sinensis, Fortunearia sinensis, and *Halesia macgregorii*, which occur relatively widely. *Nyssa yunnanensis, Davidia involucrata, Tetracentron sinense, Annamocarya sinensis, Rhoiptelea chiliantha,* and *Handeliodendron bodinieri* occur mainly in southwestern China. *Heptacodium miconioides*, *Disanthus cercidifolius* var. *longipes,* and *Shaniodendron subaequale* occur only in eastern China. *Sinowilsonia henryi* occurs in central China. Thus, southwestern China appears to be the cradle of numerous neoendemisms, in addition to paleoendemisms.

Ecological and Biological Characteristics of Relict Tertiary Deciduous Trees in Subtropical China

The modern distributions of relict deciduous trees, as ancient species, suggest that they have particular ecological and biological attributes. They occur mainly on very specific unstable habitats at mid-elevations of mountainous and hilly areas, such as

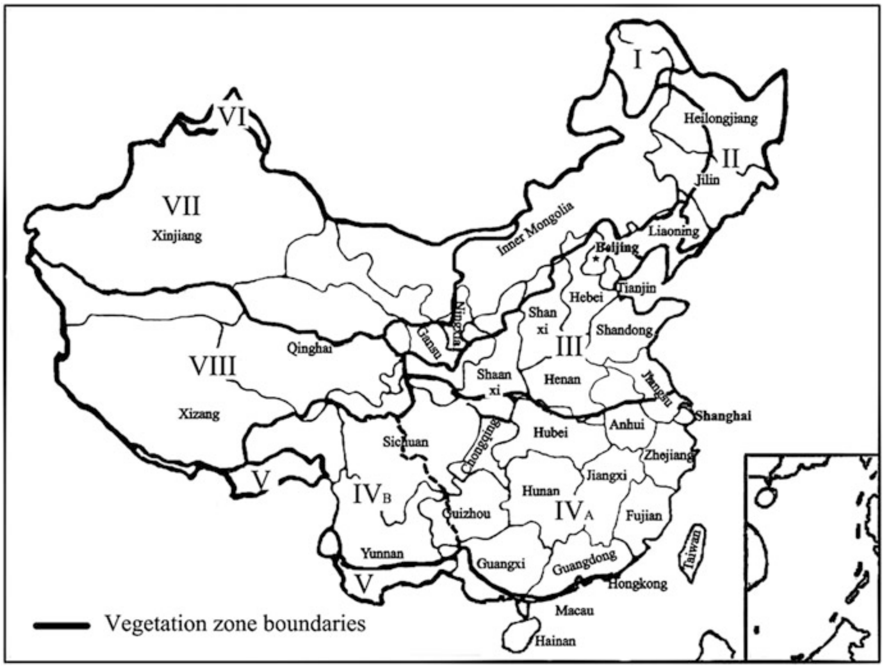

Fig. 1 Vegetation regionalization map of China (from Wu et al. 1980). I, cold-temperate coniferous forest region; II, temperate coniferous and broad-leaved forest region; III, warm-temperate deciduous broad-leaved forest region; IV, subtropical evergreen broad-leaved forest region (IV_A, eastern subregion; IV_B, Western subregion); V, tropical monsoon forest and rainforest region; VI, temperate steppe region; VII, temperate desert region; VIII, Qinghai-Tibetan plateau high cold vegetation region

in valleys and ravines, on steep slopes, and on stream banks (Table 2). All of these habitats are disturbed repeatedly by floods or landslides, and competition from other species is limited due to differences in types of landslides (Tang and Ohsawa 2002).

Apart from *D. involucrata* and *A. sinensis*, most of these trees produce abundant, wind-dispersed seeds (Table 2). The seed mass is very small, usually less than 200 g per 1000 particles. It is easy to colonize ‘safe sites’ by wind dispersal. On the other hand, these trees may produce new shoots via root suckers, coppicing and water sprouts. Root suckers originate from adventitious buds on lateral roots, while coppice shoots and water sprouts emanate from dormant buds in the stump and the base of living trees, respectively. Sprouts representing vegetative reproduction grow faster than newly established seedlings (Ky-Dembele et al. 2007), providing better resistance to stress in their first years (Deiller et al. 2003) and a stronger competitive advantage (Beaudet and Messier 2008). Thus, vegetative reproduction is considered to be a supplemental mechanism for low seed-originating recruitment, with more resources allocated to sprouts than to sexual reproduction.

Table 2 Known habitats, regeneration strategies, and dispersal agents of the main relict deciduous trees in China's subtropical forests

Species	Altitude (m)	Main habitats	Seed mass (g/1000)	Dispersal agent	Vegetative mode
Nyssa sinensis	300–1700	Valleys, streams, steep slopes	125–240	Birds	Water sprout
Nyssa yunnanensis	500–1100	Valleys	/	Birds	Water sprout
Davidia involucrata	1100–2600	Steep slopes, ravines	3400–5500	Mammals	Water sprout; coppice
Tetracentron sinense	1100–3500	Valleys, hillsides, rocky ravines	0.1–0.15	Wind	Coppice
Bretschneidera sinensis	300–1700	Humid valleys, stream banks	715–780	Wind	Coppice
Liquidambar formosana	500–800	Valleys, stream banks	4.3–6.4	Wind	Water sprout
Liquidambar acalycina	600–1000	Valleys, stream banks	4.1–4.3	Wind	Water sprout
Cyclocarya paliurus	400–2500	Steep slopes, creek valleys, forest edges	200	Wind	Water sprout
Euptelea pleiosperma	900–3600	Valleys, ravines, steep slopes	/	Wind	Water sprout; root sucker
Emmenopterys henryi	400–1600	Valleys, stream banks	0.3–0.6	Wind	Water sprout; root sucker
Heptacodium miconioides	600–1000	Stream banks, low slopes	20	Wind	Water sprout; root sucker
Cercidiphyllum japonicum	600–2700	Steep slopes, valleys, stream banks	0.75–0.9	Wind	Water sprout
Eucommia ulmoides	100–2000	Valleys, dry ravines	58–130	Wind	Root sucker; coppice
Annamocarya sinensis	200–700	Valleys, stream banks	9000–13,000	Mammals	Water sprout; coppice
Liriodendron chinense	900–1000	Valleys	22–35	Wind	Coppice
Tapiscia sinensis	500–2200	Valleys, ravines	40–55	Wind	Water sprout
Stewartia sinensis	500–2200	Gentle slopes	9–12	Wind	Coppice
Pteroceltis tatarinowii	100–1500	Foothills, forest edges, river beds	21–28	Wind	Water sprout
Camptotheca acuminata	below 1000	Stream banks, forest edges	34–45	Wind	Water sprout
Fortunearia sinensis	800–1000	Stream banks	110	Wind	Coppice
Halesia macgregorii	700–1200	Steep slope	125–220	Birds	Water sprout

'/' indicates that cannot found

Source: Flora of China, www.eFloras.org; Fu et al. (1989)

Community Structure of Tertiary Relict Deciduous Forests in Subtropical China

Only a are few types of relict-dominated or co-dominated forests in subtropical areas have been described. Books on provincial forests have summarized the main forest types, including forests of *Davidia involucrata*, *Cercidiphyllum japonicum*, *Liriodendron chinense*, *Pteroceltis tatarinowii*, and *Liquidambar formosana*, as well as mixed forests (Table 3). Recently, many articles have analyzed community characteristics of the relict-dominated forests, including the *Eurycorymbus cavaleriei* community in Jiangxi (Mao et al. 2009), the *Tetracentron sinense* community in Yunnan (Chen et al. 2008), the *Emmenopterys henryi* community in Zhejiang (Chen et al. 2007) and the *Rhoiptelea chiliantha* community in Guizhou (Yang 2003).

The floristic composition and areal types of the genera of relict-dominated communities are complex (Table 3). Many plants belong to northern temperate genera, East Asian-North American disjunct genera, tropical Asian (Indo-Malaysian) genera, East Asian genera, or genera endemic to China. The areal-types of the Tertiary deciduous trees are East Asian, Chinese endemic, and North American. Other deciduous broad-leaved trees are mainly from northern temperate genera, such as *Acer*, *Betula*, *Castanea*, *Fagus*, *Quercus*, *Padus*, *Sorbus*, *Populus* and *Ulmus*. Deciduous tree species grow in the canopy layer and even as emergents, taking the dominant place in communities on unstable habitats. Evergreen broad-leaved trees may also be common dominant or co-dominant species, especially species of *Cyclobalanopsis*, *Lithocarpus*, *Castanopsis, Machilus, Phoebe* and *Camellia*. These also appear in the canopy layer but can occur in the sub-canopy. In addition, *Pteroceltistatarinowii* forests are always distributed in limestone mountain regions, with common components including the deciduous genera *Celtis, Zelkova, Pistacia, Platycarya* and *Carpinus* and the evergreen genera *Cyclobalanopsis, Photinia, Machilus, Lindera* and *Cinnamomum.*

Relict Deciduous Forests on Micro-landforms on Tianmu-Shan Mountain of Eastern China

The Tianmu-Shan Nature Reserve (30°18′30″ to 30°21′37″ N, 119°24′11″ to 119°27′11″ E, in northwestern Zhejiang), established in 1960, is one of the most famous protected areas in China, due to its remarkable number of large trees. The reserve is also very rich in plant biodiversity, containing about 2160 species of higher plants, with 29 taxa included in the Chinese Plant Red Data Book. There are also unusual wild populations of *Ginkgo biloba*, *C. paliurus*, *L. formosana*, *L. acalycina*, *N. sinensis*, *E. henyri*, *E. pleiospermum*, *P. tatarinowii, T. sinensis, S. sinensis, C. japonicum*, *F. sinensis* and *H. miconioides*. Six of these relict Tertiary deciduous trees have been studied

Table 3 Occurrence and dominance of deciduous trees in tertiary forest types

Family	Genus range	Relict deciduous trees	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Bretschneideraceae	NTem	*Bretschneidera sinensis*							4				
Cercidiphyllaceae	EAs	*Cercidiphyllum japonicum*		1									
Juglandaceae	China	*Cyclocarya paliurus*											2
Davidiacea	China	*Davidia involucrata*	1	7				1	2				
Davidiacea	China	*Davidia involucrate* var. *vilmoriniana*		8									
Eupteleaceae	EAs	*Euptelea pleiospermum*		9									
Hamamelidaceae	EAs, NAm	*Liquidambar acalycina*	3									3	
Hamamelidaceae	EAs, NAm	*Liquidambar formosana*			1		2				2		1
Magnoliaceae	EAs, NAm	*Liriodendron chinense*					1						
Ulmaceae	China	*Pteroceltis tatarinowii*				1				3			
Theaceae	EAs, NAm	*Stewartia sinensis*		11									
Staphyleaceae	China	*Tapicia sinensis*											3
Tetracentraceae	EAs	*Tetracentron sinensis*	6	4				6					
		Other deciduous trees											
Aceraceae	NTem	*Acer flabellatum*				12			7				
Aceraceae	NTem	*Acer mono*						7		6			
Hippocastanaceae	NTem	*Aesculus wilsonii*	5										
Leguminosae	Old Wor Tr	*Albizzia macrophylla*											5
Styracaceae	TrAs	*Alniphyllum fortunei*		10									
Betulaceae	NTem	*Betula insignis*	7										
Betulaceae	NTem	*Betula luminifera*		3								4	
Betulaceae	TrAs	*Carpinus viminea*									11		
Betulaceae	TrAs	*Carpinus turczaninowii*				11							
Fagaceae	NTem	*Castanea henryi*											7
Fagaceae	NTem	*Castanea seguinii*			2								

(continued)

Table 3 (continued)

Family	Genus range	Relict deciduous trees	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Ulmaceae	PanTr	*Celtis bungeana*								7			
Ulmaceae	PanTr	*Celtis tetrandra*				3							
Rosaceae	NTem	*Cerasus serrulata*			7	9							
Leguminosae	PanTr	*Dalbergia hupeana*			3								
Cornaceae	NTem	*Cornus controversa*					7	8					
Cornaceae	NTem	*Cornus kousa* var. *chinensis*					3	12					
Ebenaceae	PanTr	*Diospyros oleifera*							8				
Ebenaceae	PanTr	*Diospyros kaki*											
Celastraceae	PanTr	*Euonymus hupehensis*							9				
Fagaceae	NTem	*Fagus longipetiolata*	9								3	1	
Fagaceae	NTem	*Fagus lucida*						9				2	
Fagaceae	NTem	*Quercus acutissima*					9			8			
Fagaceae	NTem	*Quercus aliena* var. *acutiserrata*		6									
Fagaceae	NTem	*Quercus phillyraeoides*				13					4		
Fagaceae	NTem	*Quercus fabri*			4								
Fagaceae	NTem	*Quercus variabilis*			8								
Flacourtiaceae	EAs	*Idesia polycarpa*											6
Juglandaceae	NTem	*Juglans cathayensis*	8										
Sapindaceae	EAs	*Koelreuteria paniculata*								4			
Sabiaceae	TrAs, TrAm	*Meliosma mannii*							5				
Rosaceae	NTem	*Padus obtusata*						10					
Rosaceae	NTem	*Sorbus folgneri*									6		
Rhamnaceae	Old Wor Tem	*Paliurus hemsleyanus*								2			
Simaroubaceae	TrAs, TrAm	*Picrasma quassioides*								9			
Anacardiaceae	Med WAs CAs	*Pistacia chinensis*		13		5				5			
Juglandaceae	EAs	*Platycarya strobilacea*		12	10	14				10			

Salicaceae	NTem	*Populus adenopoda*			6								
Juglandaceae	China	*Pterocarya insignis*		2									
Styracaceae	EAs	*Pterostyrax psilophyllus*	4					4					
Styracaceae	PanTr	*Styrax hypoglaucus*	2										
Tiliaceae	NTem	*Tilia tuan*		5					6				
Ulmaceae	NTem	*Ulmus bergmanniana*						5					
Ulmaceae	Old Wor Tem	*Zelkova schneideriana*								1			
Ulmaceae	Old Wor Tem	*Zelkova serrata*				10							
		Evergreen conifer trees											
Pinaceae	NTem	*Pinus massoniana*			9								4
Taxodiaceae	China	*Cunninghamia lanceolata*			5								10
		Evergreen broad-leaved trees											
Fagaceae	EAs, NAm	*Castanopsis chunii*	10										
Fagaceae	EAs, NAm	*Castanopsis fabri*										9	
Fagaceae	EAs, NAm	*Castanopsis eyrei*											8
Fagaceae	TrAs	*Cyclobalanopsis multinervis*						2	1		1		
Fagaceae	TrAs	*Cyclobalanopsis glauca*				2							
Fagaceae	TrAs	*Cyclbalanopsis gracilis*										7	
Fagaceae	TrAs	*Cyclobalanopsis myrsinaefolia*											9
Fagaceae	TrAs	*Cyclobalanopsis sessilifolia*									8		
Fagaceae	EAs, NAm	*Lithocarpus calophyllus*										6	
Fagaceae	EAs, NAm	*Lithocarpus cleistocarpus*									5		
Fagaceae	EAs, NAm	*Lithocarpus corneus*										5	
Fagaceae	EAs, NAm	*Lithocarpus hancei*										8	
Lauraceae	TrAs	*Machilus chuanchienesis*					4						
Lauraceae	TrAs	*Machilus nanmu*				4							
Lauraceae	TrAs	*Lindera communis*				6							

(continued)

Table 3 (continued)

Family	Genus range	Relict deciduous trees	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Lauraceae	TrAs, TrAu	*Cinnamomum wilsonii*				8							
Lauraceae	TrAs, TrAm	*Phoebe chinensis*							3		10		
Lauraceae	TrAs, TrAm	*Phoebe zhennan*					8						
Theaceae	TrAs	*Cammellia pitardii*						3					
Theaceae	TrAs	*Cammellia oleifera*					5						
Clethraceae	TrAs, TrAm	*Clethra faberi*					6						
Rosaceae	EAs, NAm	*Photinia davidsoniae*				7		11					
Magnoliaceae	TrAs	*Michelia platypetala*									7		
Daphniphyllaceae	TrAs	*Daphniphyllum oldhami*									9		
Symplocaceae	PanTr	*Symplocos lucida*						13	10				

Forest types—I: *Davidia involucrata* forest; II: *Cercidiphyllum japonicum* forest; III: *Liquidambar formosana* forest; IV: *Pteroceltis tatarinowii* forest; V: *Liriodendron chinense* forest; VI: *Davidia involucrata* forest; VII: *Cyclobalanopsis multinervis-Davidia involucrata* forest; VIII: *Zelkova schneideriana-Pteroceltis tatarinowii* forest; IX: *Cyclobalanopsis multinervis-Liquidambar formosana-Fagus longipetiolata* forest; X: *Fagus longipetiolata-Liquidambar acalycina-Davidia involucrata* forest; XI: *Liquidambar formosana* forest. The numbers indicate relative dominance

Sources: I, IV, V: Guangxi Forest; II, III, VII, IX: Hubei Forest; VI: Hunan Forest; X: Guangdong Forest; VII, XI: Anhui Forest

E East, *N* North, *W* West, *C* Central, *As* Asia, *Tem* Temperate, *Tr* Tropical, *Am* America, *Wor* World, *Med* Mediterranean

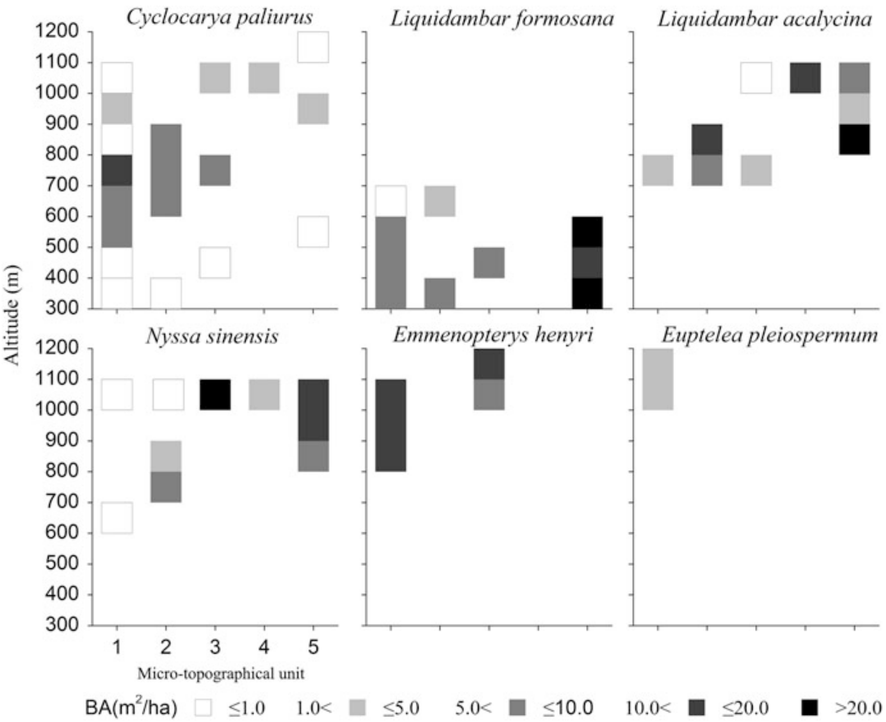

Fig. 2 Distribution patterns of relict deciduous trees on different micro-topographical units on Tianmu-Shan mountain (NW Zhejiang). Micro-topographical units: 1, river bed; 2, valley slope; 3, head hollow; 4, side slope; 5, crest slope

from 2009 to 2010. Their occurrence on different micro-landforms is suggested in Fig. 2.

Individuals of *C. paliurus* were scattered over all micro-landforms, from the lowest to highest altitudes. Their basal area (BA, in cm^2) indicated that they dominate mainly in river beds and on valley slopes between 500 and 900 m, in mixed communities of evergreen and deciduous species. Individuals of *L. formosana* and *L. acalycina* were also scattered over almost all topographies and showed greater dominance. *L. formosana* occurred at altitudes below 700 m, while *L. acalycina* was found above 700 m. The distribution of *N. sinensis* was on all micro-landforms between 600 and 1100 m, where it dominated mainly on head hollows and steep side-slope habitats, with higher basal area. *E. henyri* occurred usually in floodplains between 800 and 1100 m, with larger individuals; their BA on head hollows and side slopes, though, was more than 5.0 m^2/ha. The distribution of *E. pleiospermum* was confined strictly to floodplains between 1000 and 1200 m. Hence, relict deciduous trees on Mt. Tianmu-Shan dominated on each micro-landform in growth and survival.

Based on the potential climax vegetation and the floristic composition and community structure, three vegetation zones were identified, namely: (1) an evergreen broad-leaved forest zone (400–950 m) where the main dominant species were *Schima superba* and *Castanopsis eyrei*; (2) a zone of evergreen and deciduous broad-leaved mixed forest (950–1100 m) where the main components were *Quercus glandulifera* var. *breviptiolata* and *Quercus aliena* var. *acuteserrata*; and (3) a deciduous broad-leaved forest zone (1100–1500 m) that was composed mainly of *Castanea sequinii*, *Q. glandulifera* var. *brevipetiolata*, *Cornus kousa* ssp. *chinensis* and *Malus hupehensis* (Da et al. 2009). The vegetation physiognomy of subtropical mountain forests occurred in a mosaic pattern, with patches of relict-dominated forests due to heterogeneous landforms. Especially in mid-elevation montane forests, the forest types dominated by *N. sinensis*, *L. acalycina*, *E. henyri*, *E. pleiospermum* or *C. paliurus* occurred mainly in riparian zones or on steep slopes; these would likely develop into topographic climax communities. *L. formosana*-dominated forests occurred mainly in foothill ravines and occupied slope habitats as a pioneer species.

Discussion and Conclusion

Ancient Origins of Mountain Flora in Subtropical Evergreen Broad-Leaved Forest Areas

There are extensive ranges of evergreen broad-leaved forest in the humid subtropical zone of southern China(Wu 1980). The entire range is dominated by evergreen trees of the genera *Cyclobalanopsis*, *Castanopsis,* and *Lithocarpus*, associated with other evergreen trees from genera such as *Cinnamomum*, *Ilex*, *Sympolcos,* and *Camellia* (Song 1988). A main characteristic of the floristic community of evergreen broad-leaved forests is its ancient origin. Several phylogenetically primitive groups of vascular plants have survived until the present day due to the limited ice coverage in East Asia during the Quaternary glaciations. Many gymnosperms are monotypic or oligotypic, denoting an antiquity most likely stemming from relicts or remnants of groups occurring more widely during the Tertiary period or even earlier (Qian 2001). Some examples of ancient lineages include the Cretaceous Cercidiphyllacea, Magnoliaceae, Rhamnaceae and Eupteleaceae, and the Tertiary Bretschneideraceae, Eucommiaceae, Nyssaceae and Theaceae. Some of these paleoendemics have remained superficially unchanged for millions of years, thus earning the name ‘living fossils’ (Qian 2001).

The relict, monotypic Eucommiaceae and Davidiacea are endemic to China. In addition, nearly endemic families include the monotypic Bretschneideraceae, Rhoipteleaceae, Cercidiphyllaceae, Eupteleaceae and Tetracentraceae. Of the well known endemic genera in China, most are monotypic or oligotypic, including *Pteroceltis*, *Sinowilsonia*, *Fortunearia*, *Cyclocarya*, *Camptotheca*, *Handeliodendron*, *Eurycorymbus* and *Tapiscia* (Lopez-Pujol et al. 2006; Table 1). The endemic species *C. paliurus*, *D. involucrata*, *P. tatarinowii*, *E. henryi,* *E. ulmoides,* and *T. sinensis* illustrate the ancient origin and persistence of the flora of the subtropical region. Thus, there are so many relict Tertiary deciduous trees in subtropical China, indicting the ancient origins of the mountain flora of the subtropical evergreen broad-leaved forest.

Coexistence Mechanisms of Relict Deciduous Trees at Local Scale

In hilly or mountainous areas, landform as well as altitude is one of the most important factors affecting vegetation pattern within a climatic region (Hara et al. 1996; Nagamatsu and Miura 1997; Nagamatsu et al. 2003). Ohsawa (1987, 1992) offered the concept of topo-community to interpret the differentiation of micro-topographic communities in complex landforms in mountainous regions. These patchy communities occurring formerly in limited areas were differentiated based on their floristic composition and the age of their dominant species. Different species are adapted to topographic features by exploiting distinct niches in the complex heterogeneous environment. The communities dominated by relict species communities in a given local area could be considered topo-communities.

The biological and ecological characteristics of relict deciduous trees suggest that these species require very particular unstable habitats, where there is less competition from other trees. They survive by dispersing minute seeds, with the seedling recruitment supplemented by vegetative reproduction. Habitats including valleys, stream banks, steep slopes, creek valleys, ravines, hillsides, and rocky ravines are often sculpted by fluvial processes and mass soil movements from tributaries and adjacent hillsides. These can be classified further into many different micro-landforms. Many relict deciduous trees dominate patches at intermediate altitudes on unstable topographies. In Japan, *C. japonicum* is a deciduous riparian canopy tree species occurring throughout the cool-temperateforest region, from Hokkaido to Kyushu (Kubō et al. 2005). In contrast to evergreen species of *Cyclobalanopsis* and to other deciduous trees, *Quercus* species are found commonly on non-scree slopes. On Emei-Shan mountain in southwestern China, the relict taxa *Davidia*, *Cercidiphyllum*, *Tetracentron* and *Euptelea* survived and adapted to unstable conditions by their high sprouting ability. On gentle slopes, where relict trees are scarce, evergreen *Castanopsis* and *Machilus* and deciduous *Styrax* and *Prunus* dominate the forest and constitute the canopy layer (Tang and Ohsawa 2002). The relict plant communities investigated in the current study represent the typical vegetation in riparian zones at mid-altitudes in the Shennongjia Mountains (Wei et al. 2010). Thus, it appears consistent that these relict deciduous trees occur mainly on unstable habitats, especially riparian habitats. The distribution of relict trees is displaced in riparian zones along with altitude. Relict deciduous trees often occur on unstable habitats where zonal vegetation failed to colonize; the relicts can thus be regarded as ‘filler species’ of habitat space.

Furthermore, as a deciduous component, relict trees such as *C. japonicum*, *L. formosana* and *N. sinensis* often show typical characteristics of pioneer species (Shang 2013). These species have long life spans and status as climax species. They experience intermittent recruitment through the active production of minute wind-dispersed seeds and often constitute the canopy layer for long periods together with shade-tolerant climax trees (Shen et al. 2000). They maintain canopy size by a physiology that involves sprouting plus mass dispersal of seeds of minimal size. When pioneer species invade large disturbed sites, deciduous trees with short life spans grow faster and form even-aged cohorts. Niche partitioning occurs with the progress of the serial community. Relict deciduous trees with long life spans become canopy trees after other canopy trees die (Sakai and Ohsawa 1994). Once the relict trees grow into the canopy, they maintain that position for some time due to their long life spans and sprouting ability (Tang and Ohsawa 2002). Thus, at landscape scale, communities dominated by relict species can persist for long periods and form parts of vegetation mosaics in the zonal vegetation (Fig. 3). For example, *Liqudambar* forests grow on gentle slope habitats and occur widely in the evergreen broad-leaved forest zone, in hilly or lower mountain regions, in the

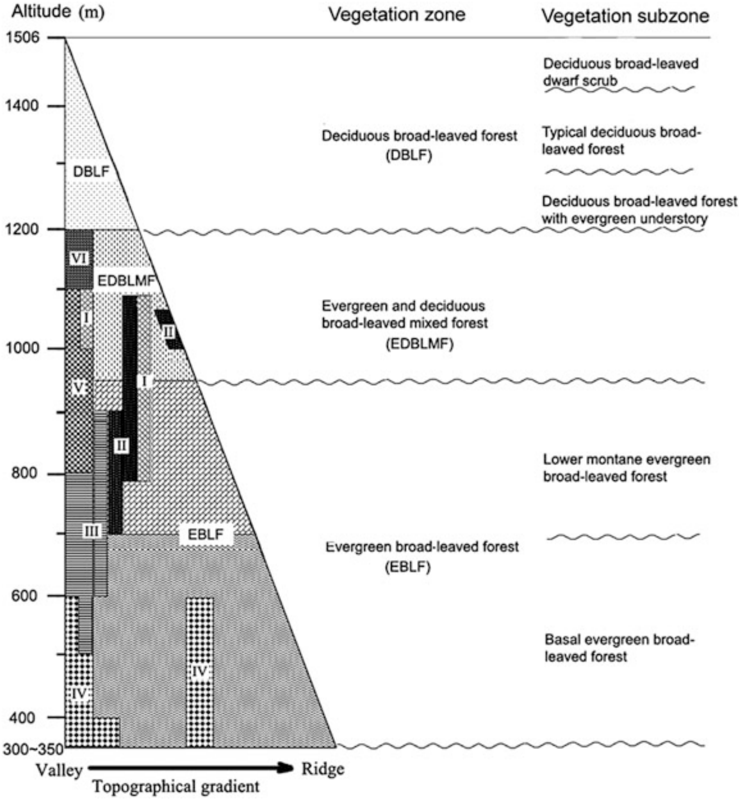

Fig. 3 Distribution pattern of vegetation on Tianmu-Shan Mountain

subtropical area (Shang et al. 2011). *Nyssa* forests and *Liqudambar* forests occur also as parts of vegetation mosaics at montane or mid-altitude sites (Fig. 3). Thus, relict deciduous trees can be regarded as 'gap-repairing species' on gentle slopes.

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Classification of Lower Montane Evergreen Forests in Southern India and Sri Lanka

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Abstract Lower Montane Evergreen Mixed Forests (MEM) in Sri Lanka and South India are composed of tropical taxa. They occur at mid-elevations, as high as 900–1400 m above sea level, in the three main mountain massifs of Sri Lanka and in several ranges of the Western Ghats in nearby southern Kerala and adjacent Tamil Nadu (India). We report on the quantitative floristic composition of stands of this altitudinal zonal formation and determine the dominant arborescent taxa. In all we recognize 12 distinct forest types, 7 in the Western Ghats and 5 in Sri Lanka.

In South India we sampled 21 stands in Kerala, of which 12 were located on Ponmudi Mountain and three in Tamil Nadu. In all, 117 species were recorded, in 98 genera and belonging to 40 families. MEM forests were classified by cluster analysis into four types on Ponmudi and three additional types in the other locations sampled in South India. The dominance of *Vateria indica* (Dipterocarpaceae) in one of the Ponmudi stands indicates a MEM stand that is transitional to the lowland tropical rainforest. The following families are represented as canopy dominants in one or more of the seven Lower Montane (MEM) types in south India: Myrtaceae, Clusiaceae, Sapindaceae, Ebenaceae, Bombacaceae, Anacardiaceae, Sapotaceae; as well as understory dominants in the families Xanthophyllaceae, Fabaceae and Euphorbiaceae.

In Sri Lanka, 120 species of flowering plants, in 80 genera and 40 families, were recorded in 10 stands. Of these, 49 species (41 %) are endemic to Sri Lanka. Our MEM stands are classified into five forest types by cluster analysis. These forests are mainly enriched by taxa common in the lowland “Wet Zone” and, to a markedly

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lesser degree, by those from the (Upper) Montane Evergreen forests. The occurrence of *Doona* (*Shorea*) spp. at certain sites represents a variation of the MEM forests, apparently influenced by specific environmental factors. MEM forests have been and still are widely exploited for the cultivation of cardamom (*Elettaria cardamomum*), which has resulted in massive disturbance to a forest type that is unusually rich in endemics. Numerous understory taxa and perhaps some canopy taxa are absent from many sampled stands. The following families are dominants in our Sri Lanka stands of Lower Montane Forest: Myrtaceae, Anacardiaceae, Clusiaceae, Elaeocarpaceae, Moraceae, Myristicaceae, Lauraceae, Euphorbiaceae, Sapotaceae, Bombacaceae, Ebenaceae. All of these 11 families can be considered characteristic dominants of Lower Montane forests in the adjacent Western Ghats. These South Indian-Sri Lankan lower-montane mixed forests have most families and many genera in common with those described for northeastern Queensland, Australia, where dipterocarps are absent.

Introduction

In southeastern Asia, striking differences have been documented in the composition of evergreen angiosperm forests with changes in elevation (e.g. Brown 1919; Kitayama 1992). Whitmore and Burnham (1975) listed the following trends in tropical forests with increasing elevation: floristic richness decreases; buttressing decreases; height generally decreases, at least from the lower montane to upper montane; structure becomes simpler; crown configurations change; and leaf size decreases. Grubb (1977) noted further that, with increasing elevation, there are also decreases in: cauliflory, the frequency of compound leaves and drip tips, and the number of climbers. He also noted an increase in leaf thickness with increasing elevation. Grubb (1977) found it "... practicable to recognize four major formation types with relatively narrow ecotones between them... on the wetter slopes of the highest tropical mountains ...". He listed the four as "lowland rainforest," "lower montane rainforest," "upper montane rainforest" and "subalpine rainforest." In Sri Lanka, Perera (1975) listed three types of altitudinal forest, described physiognomically. These are equivalent to the lowland, lower-montane and upper-montane types of Grubb. Robbins (1968) suggested that the upper elevational limit of lowland rainforest in tropical latitudes be recognized at the 1000 m (3280 ft) contour. Grubb (1971) correlated the boundary between the lowland tropical rainforest and lower montane rainforest (warm-temperate oak-laurel forest) with the 20–22 °C isotherm of mean annual temperature. Greller and Balasubramaniam (1988) discussed the zonation of mixed evergreen forests in the mountains of Sri Lanka, referring to bioclimate (following H. P. Bailey 1964), physiognomy and floristic composition. They concluded that the lower warmth level (W; Bailey 1960) is W = 19.5 °C for the lowland evergreen forest and W = 17.7 °C for the lower montane forest. Ohsawa (1991), working in Sumatra and Java, related the oak-laurel lower montane forest on Mt. Pangrango, Java (3019 m) to a warmth regime "with a monthly and annual mean temperature of ca. 12 °C."

Webb (1959) proposed the term "notophyll" (2025–4500 mm^2) to describe the small-mesophyll leaves that are characteristic of "Subtropical Rainforest" in Australia. Greller and Balasubramaniam (1988) showed that notophyllous leaf size is also characteristic of lower montane forests in Sri Lanka.

In southern India, Champion and Seth (1968) noted that the change in composition from lowland tropical evergreen to "montane temperate [evergreen] forests" is subtle. Their "montane subtropical forest" appears to reflect only a "falling off in the luxuriance of the [lowland] forest" and not the presence of a "characteristic subtropical flora," as is present in southeastern Asia. Pascal (1984, Fig. 84) illustrated the variation of evergreen forest types with elevation in the Western Ghats, recognizing the following types at 8–9° N latitude in Kerala (southwestern India): *Dipterocarpus- Anacolosa* (100–600 m), *Cullenia exarillata-Mesua ferrea-Palaquium ellipticum* (600–1400 m), forests transitional to Lauraceae (1400–1600 m), *Schefflera* sp.-*Gordonia obtusa-Meliosma arnottiana* (1600–1900 m), and montane sholas (1900–2400 m), which were described by Meher-Homji as forests that occupy sheltered sites in the "folds" of otherwise non-forested hills and small valleys. Above 1500 m, Champion and Seth recognized a "Shola Forest" series of *Schefflera-Gordonia-Meliosma*. Varghese and Balasubramanyan (1999), working in the lower montane belt of southern India (Agastyamalai region), state that "*Dimocarpus longan* dominates at low altitudes… *Cullenia exarillata* at the medium altitudes… and *Mesua* [*ferrea*] at the high altitude." In adjacent Tamil Nadu, on the eastern slopes of the Agastyamalai Range, in the lower montane belt, Ganesh et al. (1996) recognize a *Cullenia-Aglaia-Palaquium* subtype.

For Sri Lanka, Gaussen et al. (1968) summarized information on lower montane forests (900–1500 m), describing the forests as of "lower size" and without the "emergents" of the lowland forests, and as having upper-elevation species and "in particular the family Lauraceae" present in large numbers. Werner (1984) characterized forests in this elevational belt as reaching 20–35 m, with small mesophyll leaves and covered by lianas and root climbers. Gaussen et al. (1968) listed the following genera as characteristic of the best-developed of these forests: *Doona*, *Palaquium*, *Homalium*, *Calophyllum*, *Syzygium*, (*Bhesa*), *Cullenia*, *Mastixia*, *Myristica*, *Cryptocarya*, *Neolitsea* and *Celtis* in the canopy; and *Carallia*, (*Dillenia*), *Semecarpus*, *Acronychia*, *Cinnamomum*, *Litsea,* and *Meliosma* in the subcanopy. Greller and Balasubramaniam (1993) recognized two sub-zones of mid-elevational (lower montane) forests in Sri Lanka and gave floristic lists for both types. One type of sub-zonal forest is dominated by a mixture of families (Myristicaceae, Lauraceae, Euphorbiaceae, Anacardiaceae, Myrtaceae, and others)—the Mid-elevational Evergreen Mixed (MEM) type. *Doona* (Dipterocarpaceae) dominates the other type, along with a few other, mostly sub-dominant families—the Mid-elevational Evergreen Dipterocarp type (MED).

Werner (1984) distinguished a *Myristica* forest from a *Doona* forest as two of four subdivisions of rainforest.

In this study, we seek to make explicit the floristic distinction between lowland tropical evergreen forest and lower montane tropical evergreen forest, in some ranges of south India and in adjacent Sri Lanka. We present some new and some newly analyzed, quantitative data on composition of arborescent taxa in 34 stands of lower montane forests that are dominated by a mixture of families. Pure stands of *Doona gardneri* in the lower montane belt of Sri Lanka are excluded from our samples, although stands that contain *Doona* as a major dominant are included. Using cluster analysis, we seek to quantify the classification of lower montane tropical forest in Sri Lanka-South India, adding new forest types to those already recognized by Varghese and Balasubramanyan (1999), Pascal and Pelissier (1996), Meher-Homji, and others.

Study Sites: India

Physical Features

Agastyamalai Range, Kerala: Bonaccord and Athirmala

Table 1 gives a geographical and topographical description of the sites sampled in southern Kerala and adjacent Tamil Nadu, in the Western Ghats (Archaean Group of Rocks). Figure 1 is a map showing general locations. Bonaccord Tea Estate is approximately 30 km southeast of Palode, on the eastern flank of Chemunji Peak ridge at Koviltherimalai. Near our study area (855–1070 m) at Bonaccord, evergreen forests are the general vegetation of undisturbed uplands. Our study site in Athirmala Forest ranged from 1000 to 1200 m above sea level, on a steep west-facing slope (30–40 %), a flank of Agastyamalai (mountain) (8°37′ N, 77°15′ E; 1869 m).

Agastyamalai Range, Tamil Nadu: Kakkachi and Kannikatti

In the Tirunelveli District, Tamil Nadu, on the E side of Agastyamalai, we collected compositional data for two forest stands, one at Kakkachi Cardamom Plantation (on a small hilltop at ca. 1380 m) and at Kannikadi, near the village of Mundanthurai (flat site, ca. 900 m).

Nelliampathy

In the Nelliampathy Range (10°30′ N, 76°45′ E) of the Anamalai Hills, east of Thrissur (Trichur), in Thrissur (Trichur) district of Kerala, we collected

Table 1 South India: descriptions of sampled sites (line transect data)

Stand name	Location	Coordinates	Elevation	Site description	Date of sample	%Basal Area/%Density
Kannikatti (101 trees)	Tamil Nadu, Tirunelveli	8°37′ N; 77°15′ E	914 m	Flat area on eastern slope of Agastyamalai; 106 trees	30 Jul 1989	Cullenia exarillata 23.3/14.9; Palaquium ellipticum 19.6/15.8; Mesua ferrea 19.1/10.9; Gluta travancorica 10.1/1.0; Garcinia echinocarpa 6.1/5.9; Diospyros ebenum 2.6/11.9; Knema attenuata 4.3/10.9
Kakkachi (97 trees)	Tamil Nadu, Tirunelveli	8°37′ N; 77°15′ E	1280–1311 m	South-facing slope above marsh and small stream; 101 trees	31 Jul 1989	Cullenia exarillata 29.1/22.9; Myristica malabarica 15.3/2.9; Syzygium densiflorum 10.0/10.5; Dimocarpus longan 5.8/9.5; Hydnocarpus alpina 5.3/0.9; Melicope lunu-ankenda 3.4/8.6
Athirmala (103 trees)	Kerala, Trivandrum (Thiruvananthapuram) Dist.	8°37′ N; 77°15′ E	1000–1200 m	Agastyamala: West-facing slope, 30–40 %; 103 trees	1 Mar 1990	Cullenia exarillata 43.2/32.0; Humboldtia unijuga 10.3/25.2; Elaeocarpus tuberculatus 8.9/7.8; Garcinia gummi-gutta 8.6/11.7; Persea macarantha 7.2/3.9; Syzygium densiflorum 6.3/4.9; Dimocarpus longan 5.3/2.9
Nelliampathy 1 (101 trees)	Kerala, Trichur (Thrissur) Dist.	10°30′ N; 76°38′ E	1067 m	North-facing slope (max. 15 %), near ridge top; 101 trees	12 Jan 1985	Palaquium ellipticum 40.3/28.0; Cullenia exarillata 38.0/14.0; Agrostistachys borneensis 5.9/22.0
Nelliampathy 2 (66 trees)	Kerala, Trichur (Thrissur) Dist.	10°30′ N; 76°38′ E	1006 m	North facing slope to flatland (max. 5 %); 66 trees	13 Jan 1985	Persea macrantha 44.1/4.5; Cullenia exarillata 31.9/21.2; Aglaia anamalayana 4.6/28.8; Syzygium densiflorum 0.6/9.1; Mallotus resinosus 0.4/6.1

(continued)

Table 1 (continued)

Stand name	Location	Coordinates	Elevation	Site description	Date of sample	%Basal Area/%Density
B 07-1 (Bonaccord; 22 trees)	Kerala, Trivandrum (Thiruvananthapuram) Dist. (870107-1)	8°41′ N; 77° 12′ E	930 m	Valley forest, N-facing slope, betw. 2 high peaks; well-drained; red-yellow soil; litle organic matter; 5 × 50 m transect	7 Jan 1987	Palaquium ellipticum 33.8/22.7; Cullenia exarillata 20.9/4.5; Mesua ferrea 20.6/27.3; Holigarna arnottiana 17.2/13.6; Humboldtia unijuga 1.2/9.1
B 07-2 (Bonaccord; 26 trees)	Kerala, Trivandrum (Thiruvananthapuram) Dist. (870107-2)	8°41′ N; 77° 12′ E	914 m	Ridge; 5 × 50 m transect	7 Jan 1987	Gluta travancorica 32.5/3.8; Mesua ferrea 18.3/15.4; Cullenia exarillata 13.6/7.7; Artocarpus heterophyllus 8.6/3.8; Agrostistachys borneensis 7.4/26.9; Palaquium ellipticum 5.1/11.5; Humboldtia unijuga 3.7/7.7
B 07-3 (Bonaccord; 19 trees)	Kerala, Trivandrum (Thiruvananthapuram) Dist. (870107-3)	8°41′ N; 77° 12′ E	945 m	Ridge; 5 × 50 m transect	7 Jan 1987	Palaquium ellipticum 38.2/15.8; Gluta travancorica 24.5/15.8; Cullenia exarillata 9.1/5.3; Unident.(Garcinia sp.?) 6.4/15.8; Mesua ferrea 6.0/5.3
B 07-4A (Bonaccord; 36 trees)	Kerala, Trivandrum (Thiruvananthapuram) Dist. (870107-4a; 870107-4b)	8°41′ N; 77° 12′ E	945 m	Ridge; 5 × 65 m transect	7 Jan 1987	Palaquium ellipticum 26.7/22.2; Myristica dactyloides 15.8/8.3; Cullenia exarillata 12.7/5.6; Heritiera papilio 12.0/5.6; Persea macrantha 6.7/5.6; Rubiaceae 5.3/19.4

B 08-1 (Bonaccord; 38 trees)	Kerala, Trivandrum Dist. (870108-1)	8°41′ N; 77°12′ E	945 m	Ridge, 5 × 50 m transect	8 Jan 1987	Gluta travancorica 37.8/10.5; Garcinia morella 22.4/26.3; Myristica dactyloides 13.6/10.5; Albiza procera 8.1/10.5; Agrostystachys borneensis 3.2/13.2; Humboldtia unijuga 2.3/5.3
B 08-2 (Bonaccord; 35 trees)	Kerala, Trivandrum Dist (8.70108-2)	8°41′ N; 77°12′ E	1040 m	Slope 5–10 %, below ridge; 5 × 50 m transect	8 Jan 1987	Palaquium ellipticum 18.8/17.1; Mesua ferrea 13.0/8.6; Unidentified 10.7/5.7; Cullenia exarillata 8.2/2.9; Gluta travancorica 8.2/2.9; Canthium dicoccum 7.1/5.7; Garcinia morella 5.5/8.6; Syzygium densiflorum 5.3/2.9; Agrostistacys borneensis 2.6/8.6; Holigarna arnottiana 3.6/5.7; Myristica dactyloides 2.2/5.7
B 08-4 (Bonaccord; 51 trees)	Kerala, Trivandrum Dist. (87010.8-4)	8°41′ N; 77°12′ E	1050 m	Slope 48 %, ascending to summit of Chemungi Peak (1717 m); 5 × 75 m transect	8 Jan 1987	Mesua ferrea 24.1/21.6; Albizia procera 16.8/15.7; Garcinia morella 10.3/19.6; Gluta travancorica 8.8/2.0; Poeciloneuron indicum 8.6/7.8; Holigarna arnottiana 4.6/7.8

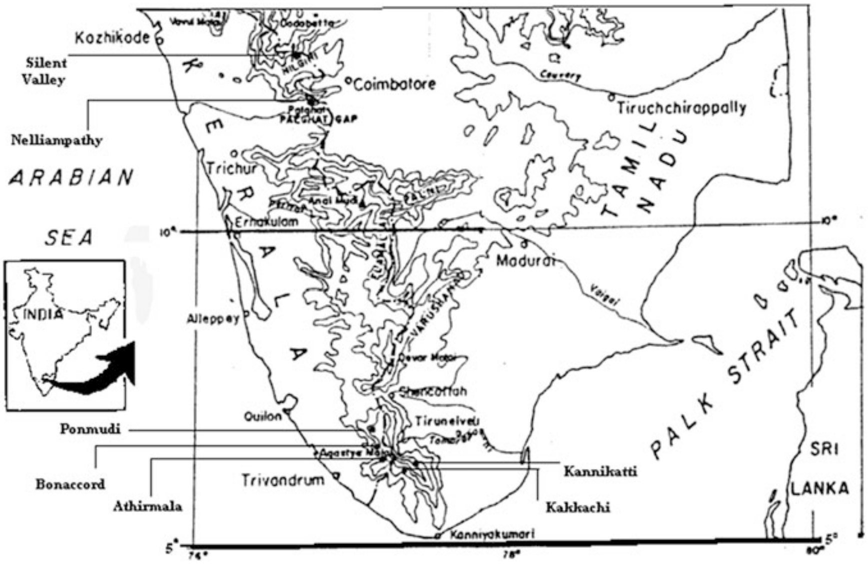

Fig. 1 Map of South India showing locations of samples; elevation ranges from 150 to 1800 m (modified from J.-P. Pascal 1993, in *Vegetatio*, 109:47–61)

compositional data for two forest stands. The first site, a north-facing 15 % slope, was located on Pothumala Estate, at 1070 m. The second site, nearly flat, was at Pantheanthode, near the Kunthi Puzha (river), at 1000 m, in Tirunelveli, Tamil Nadu.

Ponmudi

We conducted intensive sampling (Table 2) at Ponmudi Mountain (8°40′ N, 77°10′ E; 1074 m), near the summit of which are a resort hotel and bungalows. The general vegetation at the summit is a mosaic of low evergreen forests (sholas) in or near ravines, with grasslands on the convex slopes. Soils are lateritic and derived from in situ weathering of the gneissic bedrock (Nayar et al. 1986). Kallar (110 m), at the base of Ponmudi Mountain near the Kallar River, is the nearest town. At Kallar, evergreen forests are confined to the floodplains and ravines. Gradually, with increasing elevation to Ponmudi, evergreen forests occupy the deeper soils but are excluded from the rockiest sites.

Regional Climate

Lowlands At Thiruvananthapuram (Trivandrum, 63.7 m; 8°3′ N, 76°6′ E), the average annual precipitation (MAP) is 436.4 cm/year. Mean monthly temperatures

Table 2 Ponmudi Mountain, Kerala, South India (coordinates 8°40′00″ N; 77°10′00″ E): descriptions of sampled sites (census data, except where specified)

Stand name	Elevation (m)	Site description	Date of sample	Relative basal area/relative abundance
Ponmudi 114 (112 trees)	1036	Deer Park area, near ravine	Jan 14, 1987	Syzygium densiflorum 30.5/17.0; Ficus retusa 15.2/14.3; Garcinia morella 10.6/14.3; Xanthophyllum flavescens 10.3/16.1; Olea dioica 7.5/7.1; Cullenia exarillata 6.5/3.6; Schefflera racemosa 5.1/5.6
Ponmudi 116-1 (13 trees)	1036	Deer Park area, upland convex, slope <5 %; 50 × 10 m belt transect	Jan 16, 1987	Olea dioica 30.0/7.7; Dimocarpus longan 23.6/15.4; Syzygium densiflorum 18.6/15.4; Xanthophyllum flavescens 11.6/23.1; Holigarna arnottiana 8.1/7.7
Ponmudi 116-2 (22 trees)	1036	Flat; 50 × 10 m belt transect	Jan 16, 1987	Cullenia exarillata 34.1/13.6; Syzygium densiflorum 29.4/13.6; Litsea floribunda 8.9/4.5; “Chandal” 8.3/4.5; Xanthophyllum flavescens 5.3/31.8
Ponmudi 119-1 (147 trees)	975–1006	Slope 15 %, aspect ESE 120°, soil rocky; shola in ravine	Jan 19, 1987	Holigarna arnottiana 17.7/10.2; Syzygium densiflorum 11.7/8.8; Canthium dicoccum 10.5/7.5; Persea macrantha 9.5/10.2; Olea dioica 7.8/8.8; Cullenia exarillata 6.4/5.4
Ponmudi 119-2 (93 trees)	884–914	Slope 20–25 %, aspect ESE 120°; shola in ravine (continuation of Pon 119-1)	Jan 19, 1987	Gluta travancorica 12.3/17.2; Holigarna arnottiana 11.7/3.2; Elaeocarpus munronii 11.1/10.8, Schefflera racemosa 9.8/10.8; Xanthophyllum flavescens 8.2/6.5; Diospyros sp. 7.3/1.1; Syzygium densiflorum 6.9/6.5; Ficus sp. 5.8/5.4; Gordonia obtusa 5.3/6.5
Ponmudi 120-1 (107 trees)	1036–1060	Slope 45 %, small shola on the SW facing side of Ponmudi Ridge, just above Deer Park	Jan 20, 1987	Diospyros sp. 18.1/15.9, Dimocarpus longan 16.7/16.8; Syzygium densiflorum 10.8/4.7; Amygdalus(Heritiera) papilio 9.3/5.6; Cullenia exarillata 8.8/8.4; Ficus sp. 10.6/8.4; Gomphandra tetrandra 8.5/14.0; Elaeocarpus tuberculatus 6.0/0.9
Ponmudi 120-2 (61 trees)	1013–1036	Deer Park, slope 10–15 %, aspect SW 220°	Jan 20, 1987	Olea dioica 20.6/11.5; Poeciloneuron indicum 16.8/18.0; Dimocarpus longan 13.6/9.8; Ficus sp. 11.5/1.6; Gomphandra tetrandra 5.8/14.8; Palaquium ellipticum 5.1/1.6; Syzygium densiflorum 5.1/6.6

(continued)

Table 2 (continued)

Stand name	Elevation (m)	Site description	Date of sample	Relative basal area/relative abundance
Ponmudi 120-3B (106 trees)	983	Upper end of the shola sampled in Pon 120-2	Jan 20, 1987	Syzygium densiflorum 54.3/42.5; Gluta travancorica 17.8/16.0; Gordonia obtusa 15.5/16.0; Xanthophyllum flavescens 5.1/16.0
Ponmudi 121-1 (107 trees)	884–914	Slope 45 %, aspect E 90°	Jan 21, 1987	Syzygium densiflorum 32.8/22.4; Garcinia morella 10.9/8.4; Gluta travancorica 10.3/2.8; Elaeocarpus munroii 9.0/10.3; Diospyros sp. 6.5/7.5; Cullenia exarillata 6.3/2.8; Wenlandia notoniana 2.0/7.5; Xanthophyllum flavescens 2.1/6.5; Cinnamomum verum 2.8/5.6; Gordonia obtusa 1.6/5.6
Ponmudi 121-2 (74 trees)	869–899	Slope 24–44 %,aspect E 90°	Jan 21, 1987	Vateria indica 19.4/16.2; Gordonia obtusa 18.4/9.5; Gluta travancorica 16.7/8.1; Mesua ferrea 8.8/8.1; Garcinia gummi-gutta 6.8/5.4; Poeciloneuron indicum 5.6/6.8; Diospyros sp. 4.4/8.1; Gomphandra tetrandra 1.2/6.8; Syzygium densiflorum 3.6/6.8
Ponmudi 121-3 (47 trees)	914–945	Slope 60 %, aspect S 180°	Jan 21, 1987	Holigarna arnottiana 19.0/17.0; Elaeocarpus munroii 17.9/14.9; Dimocarpus longan 14.4/8.5; Schefflera racemosa 13.4/12.8; Vateria indica 5.7/2.1;Clerodendron inerme 2.9/6.4
Ponmudi 122-1 (262 trees)	853–884	Low, flat area where water collects	Jan 22, 1987	Vateria indica 22.0/9.2; Gluta travancorica 12.7/4.6; Syzygium densiflorum 10.6/10.7; Diospyros sp. 10.5/9.2; Calophyllum apetalum 7.3/2.7; Xanthophyllum flavescens 5.8/15.6; Holigarna arnottiana 5.1/7.3; Mesua ferrea 5.0/1.1; Gomphandra tetrandra 1.9/5.3; Garcinia gummi-gutta 3.7/5.0

for Thiruvananthapuram range from 26.2 °C in January (CM) to 28.8 °C in April (WM), with an average annual temperature (MAT) of 27.1 °C (Greller et al. 1997). Moisture regime can be rated as marginally "Humid" in the Bailey (1958) system. Precipitation is 300 cm/year in the town of Palode (125 m; 8°4′ N, 77°3′ E; and 39 km east of Thiruvananthapuram [Trivandrum]), Thiruvananthapuram District, Kerala (Nayar et al. 1986). Here the general vegetation is tropical deciduous forest (Greller et al. 1997). Extremes of temperature at Palode have been recorded from 19 to 34 °C (Nayar et al. 1986). The moisture regime in Palode can be rated as "Subhumid."

Lower Montane Pascal (1984) presented good records (18 years) for Silent Valley National Park in the Kundali Hills (Poochipara, 914 m; 11°05′ N, 76°79′ E). At that elevation, mean temperature of the coldest month is 17.8 °C; mean temperature of the warmest month is 23.6 °C; and mean annual temperature is 20.2 °C. Precipitation at Poochipara, Silent Valley, is 436.4 cm/year. Mahabaleshwar (1382 m) has a cold-month average temperature of 18.1 °C, warm month of 24.3 °C and a MAT of 21.2 °C; precipitation is 663.5 cm/year. Mercara (1143 m) has a cold-month average temperature of 19.1 °C, a warm month of 23.2 °C and a MAT of 21.1 °C; precipitation is 323.7 cm/year (Champion and Seth 1968). Varghese and Balasubramanyan (1999) report rainfall at Agastyamalai to be 300–500 cm/year and give a mean maximum temperature of 24 °C and mean minimum temperature of 16 °C. At all those stations the moisture regime can be rated as "Perhumid" in the system of Bailey (1958). No weather stations are present at the Ponmudi summit, but similarly high rainfall is expected to occur above 900 m on Ponmudi Mountain, because of its location on the windward western slopes of the Western Ghats. Effective precipitation is much greater in the lower montane belt than at lowland stations such as Palode. The presence of evergreen forests on the general uplands above 900 m may, therefore, be due to the high levels of effective precipitation.

Study Sites: Sri Lanka

Environmental data for all Sri Lankan study sites are presented in Table 3. The sites were located in the three general mountain massifs of the island, namely the Central Highlands, the Knuckles Range, and the Rakwana Range. Sample areas at Loolkandura (Kandy District) and Kabaragala (Nuwara Eliya District) represent the Central Highlands; Brae and Midcar (Matale District), Corbets Gap, Rangala, and Woodside (Kandy District) represent the Knuckles Range; and Hayes (Ratnapura District) represents the Rakwana Range (Fig. 2).

Metamorphic rocks of the Highland Series that date back to the middle Pre-Cambrian age (Cooray 1984) underlie all sites (Table 3). Soils on the sites are reddish brown latosols (Moorman and Panabokke 1961; Whitmore and Burnham 1975). The sites are located on gentle to moderately steep slopes at 1000–1350 m altitude.

Table 3 Sri Lanka: descriptions of sample sites (census data; ≥5 % basal area/≥5 % density by stand)

Stand name	Location	Coordinates	Elevation	Site description	Date of sample	Relative basal area/relative density
Midcar (94 trees)	Matale Dist	7°31′ N, 80°40′ E	1130 m	Steep, W-facing slope; deep soil	29 Mar 1981	Aglaia congylos (9.8/11.7), Myristica dactyloides (10.3/6.4), Cullenia (Durio) rosayroanus (9.9/6.4), Syzygium gardneri (7.9/7.7), Pseudocarapa championii (7.6/7.5), Ficus callosa (7.2/2.1), Syzygium amphoraecarpus (7.2/2.1), Fahrenheitia zeylanica (3.8/5.3), Mallotus tetracoccus (2.1/6.4), Cryptocarya wightiana (2.3/5.3)
Laggala (107 trees)	Matale Dist	7°29′ N, 80°45′ E	1005 m	N-facing slope; deep soil	19 Jan 1981	Schefflera wallichiana (20.6/3.7), Fahrenheitia zeylanica (8.7/12.1), Persea macarantha (15.2/3.7), Canthium coromandelicum (5.3/2.8), Flacourtia inermis (5.0/1.9), Dimocarpus longan (4.8/6.5), Nothopegia beddomei (3.4/8.4), Macaranga peltata (2.1/6.5), Mallotus rhamnifolius (0.5/7.5), Symplocos cochinchinensis (0.5/5.6)
Corbet’s Gap (99 trees)	Kandy Dist.	7°21′ N, 80°50′ E	1215 m	Steep S-facing slope; deep soil	15 Jan 1981	Myristica dactyloides (35.9/27.3), Bhesa ceylanica (15.9/13.1), Syzygium sp. (10.4/7.1), Elaeocarpus glandulifer (5.3/8.1), Neolitsea fuscata (4.9/5.1)
Rangala (74 trees)	Kandy Dist	7°20′ N, 80°49′ E	1220 m	Hilltop, rocky; eroded	20 Mar 1981	Elaeocarpus glandulifer (21.7/12.8), Prunus ceylanica (14.9/14.8), Gordonia ceylanica (8.1/9.4), Syzygium gardneri (9.3/4.0), Myrsine(Rapanea) sp. (9.0/8.1), Semecarpus obscura (6.6/6.7), Fagraea ceilanica (4.7/4.7), Cinnamomum sp. (5.9/4.0),
Woodside (64 trees)	Kandy Dist	7°16′ N, 80°50′ E	930 m	Moderately sloping to flat streamside; adjacent to steep N-facing hill	20 Mar 1981	Ficus fergusonii (22.6/3.1), Fahrenheitia zeylanica (9.4/10.9), Syzygium aqueum (12.0/7.8), Garcinia morella (6.1/9.4)

Kondagala (101 trees)	Kandy Dist	7°07′ N, 80°42′ E	1320 m	W-facing slope; deep soil	25 Oct 1984	Doona (Shorea) gardneri (28.0/9.9), Acronychia pedunculata (12.2/14.8), Aporosa fusiformis (12.2/8.9), Gomphandra tetrandra (6.6/4.0), Cinnamomum litsaefolium (5.6/5.0), Semecarpus nigro-viridis (3.9/7.9), Melicope lunu-ankenda (2.1/5.9)
Kabargala (101 trees)	Kandy Dist., Ela-mulla, Kabaragala Est.	7°03′ N, 80°45′ E	1035 m	Steep, SE-facing slope; deep soil	30 Oct 1984	Palaquium hinmolpedda (17.8/19.3), Nothopegia beddomei (13.9/5.6)), Semecarpus nigro-viridis (9.9/9.1), Cryptocarya wightiana (5.9/4.2), Elaeocarpus glandulifer (4.9/12.9,), Litsea gardneri (4.9/7.8), Syzygium batadamba (4.9/5.4), Fahrenheitia zeylanica (4.0/10.1)
Hayes 1 (99 trees)	Ratnapura District, Hayes Estate, Longford Div., Field no. 14	6°22′ N, 80°38′ E	1035 m	Gentle, rocky S-facing slope	14 Mar 1985	Myristica dactyloides (21.1/8.1), Fahrenheitia zeylanica (5.6/11.1), Scolopia crassipes (6.2/3.0), Nothopegia beddomei (5.6/11.1), Calophyllum acidus (4.9/6.1), Casearia “zeylanica” (3.1/7.1)
Hayes 2 (132 trees)	Ratnapura District, Hayes Estate, Longford Div., Field no. 4A	6°22′ N, 80°39′ E	1050 m	S-facing convex slope (16°), to edge of ravine	28 Aug 1984	Doona (Shorea) zeylanica (19.6/6.9), Cryptocaria wightiana (19.4/18.3), Calophyllum acidus (9.8/7.6), Dillenia triquetra (6.2/3.0), Myristica dactyloides (5.3/5.3), Fahrenheitia zeylanica (3.2/5.3), Diplospora erythrospora (2.6/5.3), Hortonia floribunda (2.5/8.4)
Hayes 3 (91 trees)	Ratnapura District, Hayes Estate, Longford Div., Field no. 4A	6°22′ N, 80°39′ E	1050 m	S-facing ravine	29 Aug 1984	Doona (Shorea) zeylanica (35.7/15.4), Calophyllum acidus (12.4/5.5), Elaeocarpus glandulifer (8.5/2.2), Cryptocarya wightiana (8.4/13.2), Hortonia floribunda (5.2/12.1). Acronychia pedunculata (2.1/6.6), Myristica dactyloides (2.0/5.5)

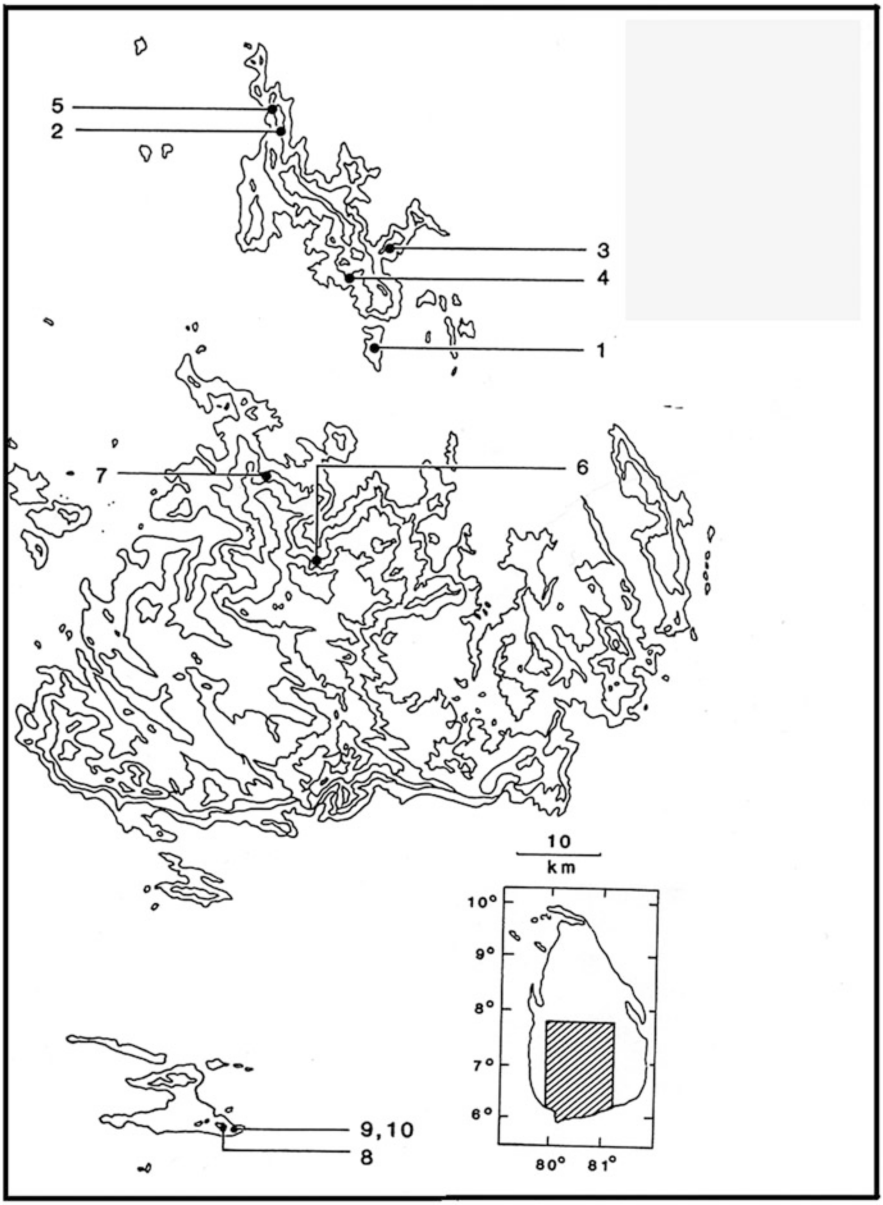

Fig. 2 Map of Sri Lanka showing locations of samples. Key: 1, Woodside; 2, Midcar; 3, Corbet's Gap; 4, Rangala; 5, Laggala; 6, Kabaragala; 7, Kondagala; 8, Hayes-1; 9, Hayes-2; 10, Hayes-3

Climatic data for two stations of lower-montane mixed evergreen forest are as follow. For Diyatalawa (1247 m), CM = 18.2 °C; WM = 21.4 °C, MAT = 20.2 °C; W(ET) = 18.3 °C; and MAP = 173.1 cm/year; for Passara (1006 m), CM = 19.2 °C, WM = 22.7 °C; MAT = 21.3 °C; W(ET) = 19.0 °C; and MAP = 227.4 cm/year. Greller and Balasubramaniam (1988, Table 6) analysed the climates of three stations representative of their Notophyllous Evergreen Mixed (lower montane) Forest: Diyatalawa, Passara, and Talawakelle (1220 m), characterizing the climates as Very Warm, Temperate to Very Temperate, and Humid (Diyatalawa, Passara) or Perhumid (Talawakelle).

The lower-montane forests sampled in Sri Lanka measured 15–20 m in height, with occasional emergents reaching 30 m. The canopy was closed, and a sub-canopy layer was evident. In areas where *Doona* species were present (Loolkandura and Hayes), characteristic cauliflower or mushroom-like crowns could be recognized from a distance. Mid-elevation Evergreen Mixed (MEM) forests apparently were the choice lands for cultivation of cardamom (*Elettaria cardamomum*), which requires cooler temperatures than in the lowland, abundant moisture, and shade. Undisturbed forests between the specified altitudes in accessible areas were scarce. All areas investigated were cultivated with cardamom, and natural undergrowth was largely absent. However, moderately dense undergrowth was observed in adjacent patchy forests, especially on steep slopes. Several rare shrubs and herbs were encountered in this undergrowth vegetation (Jayasuriya et al. 1993).

Methods

In Sri Lanka and south India, exclusive of Ponmudi, each site was sampled by a belt transect, usually 100 m × 5 m, lying more or less parallel to the contour of the land. Individuals over 10 cm DBH (diameter at breast height) within each belt transect were measured. We aimed to record at least 50 individuals on each transect. If the tree composition changed radically at some point on the transect, though, we stopped and gave a new number to the trees recorded beyond that point. This procedure sometimes yielded samples of fewer than 50 individuals. On Ponmudi Mountain we censused 12 sholas. Representative specimens of all species encountered were collected for identification in the herbarium, and duplicate specimens were deposited at the National Herbarium, Peradeniya; University of Peradeniya; Queens College of the City University of New York; Arnold Arboretum of Harvard University, Massachusetts; and the Missouri Botanical Garden, St. Louis. Taxonomy follows Ashton et al. (1997), Balasubramanyan et al. (1985), Mabberly (2008), and The Plant List (2010).

Figure 3 is a dendrogram showing all Lower Montane stands. It was produced, using the UPGMA method (SAS 1985), from a matrix of percentage dissimilarity

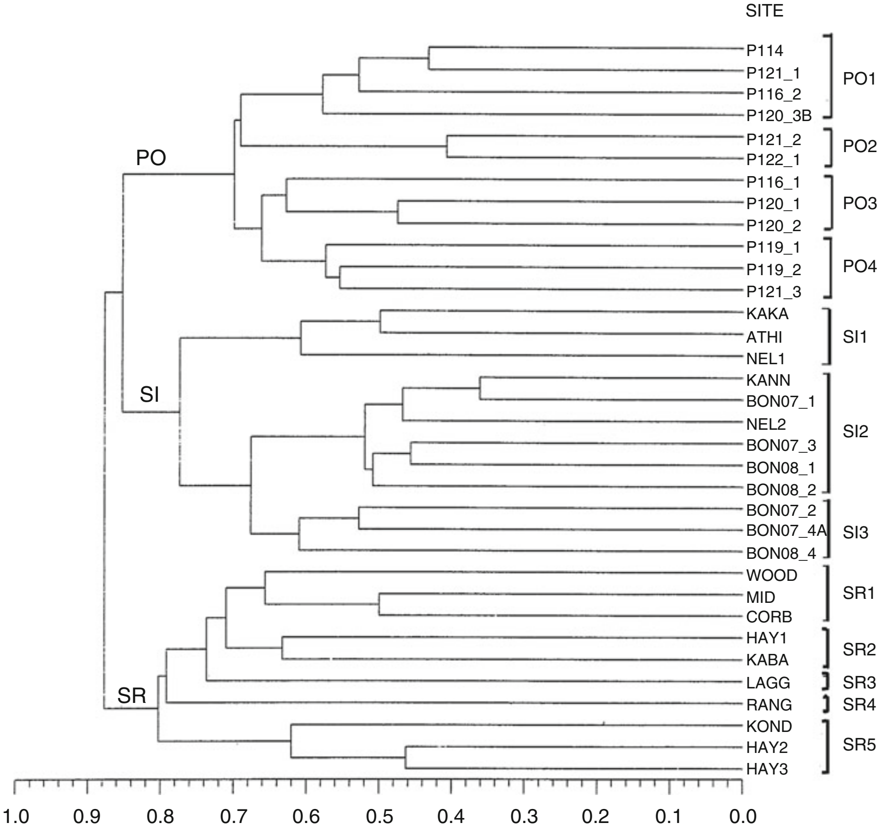

Fig. 3 Dendrogram (Bray-Curtis; UPGMA) of forest stands in South India (including Ponmudi) and Sri Lanka

values derived by the following Bray-Curtis formula: 2 W/(A + B), where W is the lesser of two values of percentage basal area for taxa in stands A and B. Figure 4 is an ordination of those stands to show relationships in three dimensions. Each stand is shown connected by a line to the centroid of the stand.

Because contiguous stands in Sri Lanka (Hayes-2 and Hayes-3) showed only 0.46 % dissimilarity, it was decided that comparisons of the composition of vegetation composition in Sri Lanka versus Kerala, at the species level, would give less useful information than at the genus level. This is because both areas are high in endemic species, while the number of endemic or unshared genera is relatively low. An additional consideration is that many of the dominant genera are represented by only one dominant species (in south India: *Syzygium densiflorum, Cullenia exarillata, Vateria indica,* etc.), so little information is lost when genera are compared.

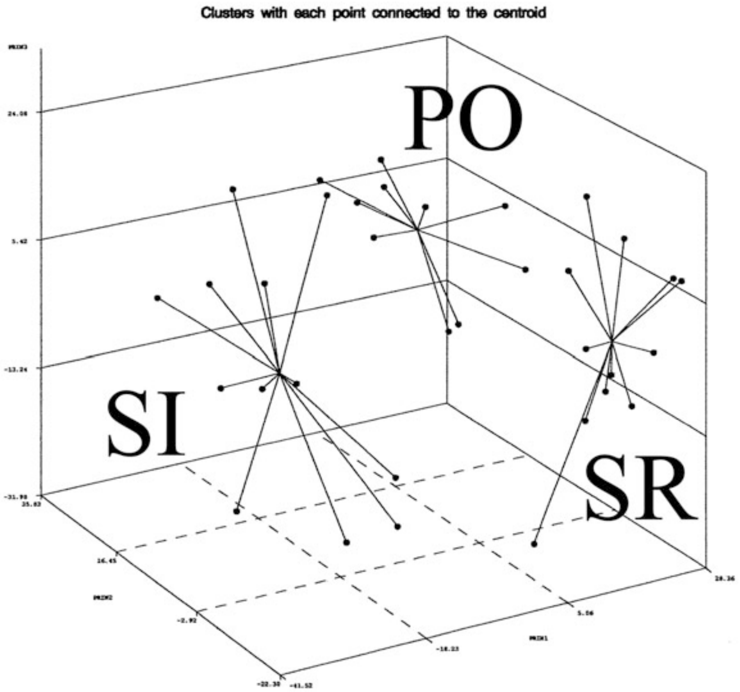

Fig. 4 Three-dimensional ordination of the forests stands listed in Fig. 3. Note that every point (stand) in the three clusters is connected to the centroid of its cluster. Code: *SI* South India, *PO* Ponmudi, Travancor, Kerala, India; *SR* Sri Lanka

Syntaxonomy (Plant Communities or Associations)

Walter (1985) divides the earth ("Geo-biosphere") into nine climate zones that are "large and uniform environments…ecologically designated as Zonobiomes (ZB)." In the terminology of Walter, "Evergreen tropical rainforest" is the "zonal vegetation" of Zonobiome I ("Equatorial with diurnal climate"). Because vegetation and flora of mountain ranges differ in the different ZB's, Walter designates the mountain vegetation as "Orobiomes" (OB) and numbers them according to the zonobiome in which they are located. Thus, Walter designates tropical upland vegetation as OB I and uses the term "Biome" to refer to the subdivisions of the Orobiome. Whitmore and Burnham (1975) distinguish four altitudinal belts of vegetation in the equatorial tropics: lower montane, upper montane, subalpine and alpine. In Whitmore's terminology we consider all of our stands to be Lower Montane Forest. Referring to the charts in Greller and Balasubramaniam (1988) that show the relationship of average leaf size of evergreen forest trees to elevation in Sri Lanka, we characterize the Lower Montane, Orobiome I in Sri Lanka-Kerala, as Evergreen Tropical Notophyllous Rainforest. Greller and Balasubramaniam (1993), describing composition of vegetation in the lower montane belt of Sri

Lanka, use Walter's system to classify as OB I/2-1, the notophyllous evergreen forest of mixed tropical families there. Walter labels the subdivision below "individual Altitudinal Belts" (i.e., orobiome levels) as "Synusiae" (parts of ecosystems). This level of classification appears to be the same as Braun's (1950) "Association" and is perhaps the equivalent of Meher-Homji's "Series plesioclimax".

Results

In South India, we sampled stands in Kerala (21) and Tamil Nadu (3). Of the stands in Kerala, 12 were located on Ponmudi Mountain. In all, we recorded 117 species in 98 genera belonging to 40 families. MEM forests are classified by cluster analysis into four types on Ponmudi and three, additional types in the other locations sampled in South India. The following families are represented as canopy dominants in one or more of the seven Lower Montane (MEM) types in south India: Myrtaceae, Clusiaceae, Sapindaceae, Ebenaceae, Bombacaceae, Anacardiaceae, Sapotaceae; as well as understory dominants in the Xanthophyllaceae, Fabaceae and Euphorbiaceae.

In Sri Lanka we recorded a total of 120 species of flowering plants, in 80 genera and 40 families, in 10 stands. Of these, 49 species (41 %) are endemic to Sri Lanka. Our MEM stands are classified into five forest types by cluster analysis. The following families are dominants in our Sri Lanka stands of Lower Montane Forest: Myrtaceae, Anacardiaceae, Clusiaceae, Elaeocarpaceae, Moraceae, Myristicaceae, Lauraceae, Euphorbiaceae, Sapotaceae, Bombacaceae, and Ebenaceae. All of the 11 families of Sri Lankan dominants can be considered characteristic dominants of Lower Montane forests in the adjacent Western Ghats.

The 34 stands of lower montane forest were compared by genera, using the Bray-Curtis Dissimilarity Index for relative basal-area data, and the dendrogram in Fig. 3 was generated, using the UPGMA method. Three major clusters are readily distinguished. A Sri Lankan cluster separates from the other two clusters at a dissimilarity value of 0.88. This cluster is labeled SR (Sri Lanka). The two Indian clusters separate at the dissimilarity value of 0.86. One Indian cluster, labeled SI (South India), comprises the Kerala and adjacent Tamil Nadu stands. The other cluster, labeled PO (Ponmudi), comprises all of the Ponmudi stands. The average diameter (dbh) of the trees sampled is roughly similar for the three major clusters (30–36 cm dbh), with the "shola" forests of Ponmudi having the smallest average size (30 cm dbh).

Three Regional Clusters: Dominant Trees

South India Except Ponmudi Table 4 summarizes dominance and density data for the South India stands, exclusive of Ponmudi Mountain. In our samples the major

Table 4 Phytosociological data for forest stands in South India (Kakachi, Kannikatti, Athirmala, Nelliampathy and Bonaccord; ≥0.04 % BA)

Species	BA	RBA	D	RD
Cullenia exarillata	357,958.94	30.77	106	15.49
Palaquium ellipticum	243,637.82	20.94	75	10.96
Mesua ferrea	47,567.34	4.09	42	6.14
Syzygium densiflorum	46,937.71	4.04	34	4.97
Gluta travancorica	40,323.81	3.47	12	1.75
Myristica malabarica	35,271.50	3.03	3	0.44
Persea macrantha	34,679.85	2.98	13	1.90
Agrostistachys borneensis	32,298.16	2.78	40	5.85
Diospyros bourdillonii	22,707.14	1.95	1	0.15
Dimocarpus longan	21,806.15	1.87	15	2.19
Garcinia morella	20,783.32	1.79	29	4.24
Humboldtia unijuga	15,227.70	1.31	39	5.70
Myristica dactyloides	15,036.02	1.29	18	2.63
Drypetes elata	13,056.21	1.12	4	0.58
Hydnocarpus alpina	12,276.79	1.06	1	0.15
Albizia procera	11,672.38	1.00	15	2.19
Elaeocarpus tuberculatus	10,927.92	0.94	9	1.32
Unidentified sp.	10,903.16	0.94	17	2.49
Holigarna arnottiana	10,217.82	0.88	14	2.05
Litsea sp.	9856.00	0.85	1	0.15
Diospyros sp.	8534.28	0.73	2	0.29
Cinnamomum verum	7930.02	0.68	8	1.17
Melicope lunu-ankenda	7832.59	0.67	9	1.32
Calophyllum apetalum	7745.57	0.67	5	0.73
Garcinia rubro-echinata	7715.24	0.66	10	1.46
Litsea wightiana	7563.29	0.65	5	0.73
Garcinia echinocarpa	7196.55	0.62	6	0.88
Michelia (Magnolia) nilagirica	7113.07	0.61	3	0.44
Artocarpus heterophyllus	6532.43	0.56	5	0.73
Syzygium sp.	5248.41	0.45	7	1.02
Knema attenuata	5152.13	0.44	11	1.61
Psydrax (Canthium) sp.	5078.66	0.44	9	1.32
Elaeocarpus munronii	4957.71	0.43	4	0.58
Pongamia pinnata	4642.79	0.40	4	0.58
Myrcia bracteata	4439.29	0.38	4	0.58
Antidesma ghaesembilla	4398.43	0.38	5	0.73
Poeciloneuron indicum	4327.71	0.37	6	0.88
Heritiera papilio	3690.50	0.32	4	0.58
Lophopetalum wightianum	3314.37	0.28	2	0.29
Diospyros ebenum	3243.23	0.28	13	1.90
Coffea canephora	3118.50	0.27	1	0.15
Aglaia “anamalayana”	2533.93	0.22	19	2.78

(continued)

Table 4 (continued)

Species	BA	RBA	D	RD
Semecarpus “anacardium”	2242.63	0.19	3	0.44
Carallia brachiata	2207.07	0.19	2	0.29
Breonia sp.	1964.29	0.17	1	0.15
Macaranga peltata	1687.71	0.15	4	0.58
Antidesma sp.	1555.91	0.13	1	0.15
“Thuvara”	1521.14	0.13	1	0.15
Memecyclon randeriana	1268.14	0.11	4	0.58
Cryptocarya wightiana	1189.57	0.10	2	0.29
Olea dioica	1144.03	0.10	2	0.29
Cyathocalyx zeylanica?	1021.43	0.09	2	0.29
Gomphandra coriacea?	1006.70	0.09	2	0.29
Holigarna grahamii?	990.79	0.09	2	0.29
Garcinia sp.	990.20	0.09	1	0.15
Elaeocarpus sp.	868.21	0.07	2	0.29
Actinodaphne bourdillonii	829.91	0.07	2	0.29
Calophyllum tomentosum	805.36	0.07	2	0.29
Symplocos sp.	797.11	0.07	3	0.44
Litsea “hookeri”	707.14	0.06	1	0.15
Lasianthus ciliatus	616.79	0.05	2	0.29
Mallotus resinosus	572.79	0.05	1	0.15
Cinnamomum sp.	491.07	0.04	1	0.15
Phoebe wightii	491.07	0.04	1	0.15
Rubiaceae	464.55	0.04	3	0.44
Alseodaphne semecarpifolia	452.57	0.04	1	0.15
Psychotria nigra	446.29	0.04	3	0.44
Lauraceae	433.91	0.04	1	0.15
Xanthophyllum arnottianum	427.43	0.04	3	0.44
Leea indica	415.64	0.04	1	0.15
Totals	1,163,063.89	100.00	684	100.00

Code: *BA* basal area (cm^2), *RBA* relative basal area, *D* density, *RD* relative density

dominants are: *Cullenia exarillata* (30.8 % basal area) and *Palaquium ellipticum* (20.9 %). Lesser dominants are *Mesua ferrea* (4.1 %), *Syzygium densiflorum* (4.0 %), *Gluta travancorica* (3.5 %), *Myristica malabarica* (3.0 %) and *Persea macrantha* (3.0 %). In the understory, *Agrostistachys borneensis* accounts for 5.6 % of all density, *Humboldtia unijuga* 5.5 %, and (subcanopy) *Garcinia morella* 4.1 %.

Ponmudi Mountain Table 5 summarizes dominance and density data for all Ponmudi stands. The only major dominant is *Syzygium densiflorum* (16.7 % basal area). Lesser dominants are *Vateria indica* (6.8 %), *Gluta travancorica* (6.7 %), *Holigarna arnottiana* (6.6 %) and *Diospyros* sp. (6.3 %). *Xanthophyllum flavescens* dominates the understory with 10.9 % density. *Gomphandra polymorpha,* also in the understory, accounts for 4.2 % density and *Gordonia obtusa* for 3.5 % density.

Table 5 Phytosociological data for all Ponmudi, Travancore, Kerala, India stands

Species	BA	RBA	D	RD
Syzygium densiflorum	182,055.70	16.77	166	14.32
Vateria indica	73,928.05	6.81	39	3.36
Gluta travancorica	73,314.61	6.75	56	4.83
Holigarna arnottiana	71,350.91	6.57	59	5.09
Diospyros sp.	68,091.38	6.27	66	5.69
Cullenia exarillata	52,035.50	4.79	37	3.19
Garcinia gummi-gutta	48,303.95	4.45	60	5.18
Olea dioica	46,114.16	4.25	46	3.97
Xanthophyllum flavescens	46,044.63	4.24	127	10.96
Dimocarpus longan	44,279.71	4.08	36	3.11
Ficus sp.	43,269.09	3.99	30	2.59
Elaeocarpus munronii	38,553.82	3.55	51	4.40
Gordonia obtusa	30,177.71	2.78	40	3.45
Poeciloneuron indicum	24,618.98	2.27	27	2.33
Schefflera racemosa	23,572.41	2.17	35	3.02
Calophyllum apetalum	22,172.27	2.04	11	0.95
Persea macrantha	20,377.11	1.88	23	1.98
Gomphandra tetrandra	19,334.07	1.78	49	4.23
Ficus retusa	18,849.09	1.74	6	0.52
Canthium dicoccum	18,030.96	1.66	11	0.95
Mesua ferrea	15,858.27	1.46	11	0.95
Cinnamomum verum	12,960.95	1.19	22	1.90
Amygdalus (Heritiera) papilio	11,578.29	1.07	6	0.52
Palaquium ellipticum	11,309.77	1.04	8	0.69
Unidentified sp.	7537.75	0.69	5	0.43
Elaeocarpus tuberculatus	7460.75	0.69	3	0.26
Litsea floribunda	7368.04	0.68	15	1.29
Glochidion zeylanicum	4718.61	0.43	11	0.95
Lannea coromandelica	4419.64	0.41	1	0.09
Wendlandia thyrsoidea	4264.66	0.39	20	1.73
Artocarpus heterophyllus	3687.16	0.34	6	0.52
Mallotus paniculatus var. paniculatus	3461.86	0.32	7	0.60
Sapindaceae	3396.05	0.31	5	0.43
Bischofia javanica	3146.39	0.29	2	0.17
Antidesma montanum var. montanum	3010.66	0.28	9	0.78
Vernonia travancorica	2351.84	0.22	3	0.26
Clerodendrum inerme	2319.43	0.21	9	0.78
Kydia calycina	2085.48	0.19	3	0.26
Melicope lunu-ankenda	1591.07	0.15	1	0.08
Melia dubia	1257.14	0.12	1	0.09
Dillenia pentagyna	1059.34	0.10	4	0.35
Humboldtia decurrens	881.96	.0.08	4	0.35

(continued)

Table 5 (continued)

Species	BA	RBA	D	RD
Scleropyrum pentandrum	664.91	0.06	2	0.17
Agrostistachys borneensis	623.86	0.06	3	0.26
Erythrina variegata	616.00	0.06	1	0.08
Isonandra lanceolata	602.84	0.06	4	0.35
Ficus hispida	387.36	0.04	2	0.17
Symplocos sp.	375.77	0.03	3	0.26
Symplocos cochinchinensis var. laurina	330.20	0.03	1	0.09
Flacourtia indica	311.54	0.03	2	0.17
Myristica sp.	268.91	0.02	1	0.09
Macaranga peltata	240.62	0.02	1	0.08
Neolitsea cassia	201.34	0.02	2	0.17
Albizia procera	182.48	0.02	2	0.17
Psychotria sp.	176.78	0.02	1	0.09
Euonymus crenulatus	132.78	0.01	1	0.08
Aporosa cardiosperma	103.91	0.01	1	0.09
Vitex sp.	78.57	0.01	1	0.08
Total	1,085,497.09	100.00	1159	100.00

Code: *BA* basal area (cm^2), *RBA* relative basal area, *D* density, *RD* relative density

Sri Lanka Table 6 summarizes dominance and density data for all of the Sri Lanka stands. The only major dominant (≥10 % basal area) for these stands is *Myristica dactyloides* (12.9 % basal area). A lesser dominant (5–10 % basal area) is *Elaeocarpus glandulifer* (6.1 %). Dominants with 3–5 % basal area are the understory trees *Bhesa ceylanica* (5.0 %) and *Fahrenheitia zeylanica* (4.7 %). The latter tree is second in relative density with 5.5 %. Other lesser dominants are *Doona zeylanica* (3.6 % basal area) and *Cryptocarya wightiana* (3.3 % basal area).

Associations Recognized from the Dendrogram

(Dominants in the same stratum are shown with a dash, dominants of different strata are shown separated by a slash.)

South India Except Ponmudi

Referring to the dendrogram (Fig. 3), we see that at a dissimilarity level of 0.66 there are three clusters on the South India (SI) branch, designated SI1, SI2 and SI3. These are treated as “Associations” of the lower montane forest belt, and tables of their floristic composition are available by request from the senior author. Webb

Table 6 Phytosociological data for all Sri Lanka stands

Species	BA	RBA	D	RD
Myristica dactyloides	202,166.94	12.88	94	7.48
Elaeocarpus glandulifer	96,498.33	6.15	54	4.30
Bhesa ceylanica var.montana	78,320.50	4.99	34	2.70
Fahrenheitia zeylanica	74,139.41	4.72	72	5.73
Doona (Shorea) zeylanica	56,149.59	3.58	24	1.91
Cryptocarya wightiana	51,376.47	3.27	59	4.69
Syzygium aqueum	45,373.43	2.89	14	1.11
Aglaia congylos	44,442.55	2.83	36	2.87
Syzygium amphoraecarpus	42,915.71	2.73	14	1.11
Pseudocarapa championii	42,103.03	2.68	23	1.83
Ficus fergusonii	41,204.43	2.63	4	0.32
Gordonia ceylanica	42,402.52	2.70	31	2.47
Syzygium gardneri	36,538.07	2.33	18	1.43
Cullenia rosayroana	34,261.86	2.18	13	1.04
Litsea gardneri	24,725.91	1.58	21	1.67
Prunus ceylanica	26,724.54	1.70	27	2.15
Ficus callosa	23,942.29	1.53	4	0.32
Nothopegia beddomei	23,631.97	1.51	53	4.22
Ficus sp.	22,757.43	1.45	6	0.48
Semecarpus nigro-viridis	22,359.46	1.42	39	3.10
Neolitsea fuscata	20,920.00	1.33	12	0.96
Neolitsea cassia	20,828.06	1.33	20	1.59
Palaquium grande	19,600.60	1.25	18	1.43
Schefflera wallichiana	19,448.79	1.24	4	0.32
Syzygium batadamba	15,946.40	1.02	15	1.19
Persea macrantha	15,297.88	0.97	5	0.40
Acronychia pedunculata	15,255.44	0.97	38	3.03
Ficus microcarpa	14,288.56	0.91	4	0.32
Calophyllum acidus	13,823.13	0.88	16	1.27
Hortonia floribunda	13,802.79	0.88	42	3.34
Myrsine “viridiflora”	13,655.71	0.87	12	0.96
Calophyllum trapezifolium	13,331.41	0.85	6	0.48
Semecarpus obscura	13,244.00	0.84	16	1.27
Calophyllum tomentosum	12,930.50	0.82	12	0.96
Dimocarpus longan	12,363.91	0.79	14	1.11
Turpinia malabarica	12,183.36	0.78	17	1.35
Garcinia morella	11,793.57	0.75	13	1.04
Scolopia crassipes	10,288.84	0.66	12	0.96
Cedrela toona	10,182.86	0.65	10	0.80
Filicium decipiens	9150.43	0.58	8	0.64
Doona (Shorea) gardneri	8969.18	0.57	9	0.72
Cinnamomum sp.	8895.86	0.57	6	0.48

(continued)

Table 6 (continued)

Species	BA	RBA	D	RD
Dillenia triquetra	8792.73	0.56	8	0.64
Syzygium micranthum	8650.09	0.55	5	0.40
Erythrina subumbrans	8562.71	0.55	4	0.32
Eurya ceylanica	8387.89	0.53	4	0.32
Canthium coromandelicum	7754.64	0.49	7	0.56
Macaranga peltata	7383.63	0.47	20	1.59
Mallotus rhamnifolius	7304.01	0.47	13	1.04
Fagraea ceilanica	8727.71	0.56	8	0.64
Semecarpus gardneri	6647.17	0.42	12	0.96
Eurya japonica	6636.34	0.42	10	0.80
Flacourtia sp.	6558.36	0.42	7	0.56
Symplocos cochinchinensis	6536.36	0.42	20	1.59
Adinandra lasiopetala	5714.53	0.36	6	0.48
Annonaceae	5646.14	0.36	4	0.32
Bhesa ceylanica	5418.07	0.35	3	0.24
Mangifera zeylanica	5174.71	0.33	4	0.32
Syzygium megacarpum	5119.71	0.33	2	0.16
Flacourtia inermis	4903.05	0.31	3	0.24
Doona (Shorea) disticha	4721.52	0.30	4	0.32
Ochnaceae	4618.43	0.29	6	0.48
Aporosa fusiformis	4361.69	0.28	9	0.72
Syzygium sp.	4194.93	0.27	3	0.24
Cleistocalyx operculatus	4128.73	0.26	6	0.48
Syzygium hemisphericum	3850.00	0.25	1	0.08
Psydrax (Canthium) dicoccus	3743.98	0.24	5	0.40
Syzygium sp.	5996.57	0.38	4	0.32
Diplospora erythrospora	3544.70	0.23	9	0.72
Melicope lunu-ankenda	3390.66	0.22	13	1.04
Syzygium rubicundum	3264.48	0.21	4	0.32
Glochidion moonii var. moonii	3130.29	0.20	5	0.40
Vitex pinnata	3076.86	0.20	6	0.48
Ficus nervosa	3039.80	0.19	1	0.08
Cinnamomum litseifolium	2933.59	0.19	6	0.48
Casearia “zeylanica”	2781.42	0.18	9	0.72
Homalium “zeylanicum”	2617.41	0.17	2	0.16
Gomphandra tetrandra	2474.76	0.16	4	0.32
Palaquium hinmolpedda	2430.60	0.15	3	0.24
Syzygium umbrosum	2415.58	0.15	4	0.32
Celtis timorensis	3216.05	0.20	2	0.15
Michelia (Magnolia) champaca	2390.14	0.15	2	0.16
Michelia (Magnolia) nilagirica	2376.79	0.15	1	0.08
Semecarpus “coriacea”	2343.03	0.15	4	0.32

(continued)

Table 6 (continued)

Species	BA	RBA	D	RD
Unknown 81020-23	4249.14	0.27	2	0.16
Schefflera sp.	2019.29	0.13	4	0.32
Carallia brachiata	1898.68	0.12	4	0.32
Ficus aspera	1886.50	0.12	1	0.08
Symplocos “obovata”	1882.02	0.12	5	0.40
Diospyros sp.	1610.51	0.10	3	0.24
Gyrinops walla	1603.32	0.10	7	0.56
Actinodaphne elegans	1451.43	0.09	4	0.32
Isonandra montana	1371.68	0.09	2	0.15
Allophylus zeylanicus	2284.58	0.15	8	0.64
Caryota urens	1232.00	0.08	2	0.16
Cinnamomum dubium	1187.95	0.08	5	0.40
Memecylon “sylvaticum”	1005.71	0.06	2	0.15
Glochidion zeylanicum	945.80	0.06	3	0.24
Syzygium sp.	908.29	0.05	1	0.08
Cullenia sp.	804.57	0.05	1	0.08
Others				
Total	1,569,537.05	100.00	1256	100.00

Code: *BA* basal area (cm^2), *RBA* relative basal area, *D* density, *RD* relative density

and Tracey (1994) would consider them as “fasciations,” i.e. local variations of the regional association.

Association SI1 comprises samples at Kakkachi, Athirmala and Nelliampathy 1 (see Table 1). This type can be designated the *Cullenia exarillata*/*Humboldtia unijuga* Association. The major dominant tree (≥10 % basal area) is *Cullenia exarillata* (36.3 %); other dominants are *Humboldtia unijuga* (9.7 % understory), *Syzygium densiflorum* (8.6 %), *Aglaia anamaliensis* (7.1 %), and *Dimocarpus longan* (5.6 %). Lesser dominants are *Garcinia morella* (3.7 %), *Elaeocarpus tuberculatus* (3.4 %), *Euodia lunu-ankenda* (3.4 %), and *Persea macrantha* (2.6 %).

Association SI2 comprises samples at Kannikkati, Bonaccord 7-1, Nelliampathy 2, Bonaccord 7-3, Bonaccord 8-1 and Bonaccord 8-2. This type can be designated the *Palaquium ellipticum*-*Cullenia exarillata*/*Agrostistachys borneensis* Association. The major dominants are *Palaquium ellipticum* (canopy tree, 35.0 % basal area) and *Cullenia exarillata* (canopy tree, 32.7 %); lesser dominants are *Mesua ferrea* (canopy, 5.0 %), *Agrostistachys borneensis* (understory, 4.3 %), *Diospyros bourdillonii* (canopy, 3.3 %), and *Gluta travancorica* (2.6 %).

Association SI3 comprises samples at Bonaccord (Bon 7-2, Bon 7-4A, Bon 8-4). This type can be designated the *Gluta travancorica*-*Mesua ferrea*/*Garcinia morella*/*Agrostistachys borneensis* Association. The major dominant trees are *Gluta travancorica* (canopy, 24.2 % basal area), *Mesua ferrea* (canopy, 15.2 %) and *Garcinia morella* (lower canopy, 11.4 %). Other dominant canopy trees are *Albizia procera* (9.2 %), *Myristica dactyloides* (8.1 %), and *Cullenia exarillata*

(5.7 %). Lesser dominants are *Holigarna arnottiana* (canopy, 4.0 %), *Poeciloneuron indicum* (canopy, 3.4 %), and the understory trees *Humboldtia unijuga* (3.3 %) and *Agrostistachys borneensis* (3.0 %; relative density 10.5).

Ponmudi Mountain, Kerala

At Ponmudi Mountain we can recognize four clusters at or above the 0.66 dissimilarity level (Fig. 3). For convenience these are designated Ponmudi (PO) 1–4. The following taxa are dominants (tables of floristic composition are available by request from the senior author).

Cluster PO1 (Ponmudi samples 114, 121-1, 116-2, 120-3B). This type can be designated the *Syzygium densiflorum/Garcinia morella/Xanthophyllum flavescens* Association. The major dominant is *Syzygium densiflorum* (canopy, 37.2 % basal area). Other dominant trees are *Garcinia morella* lower canopy, 7.9 %), *Cullenia exarillata* (canopy, 7.6 %), *Ficus retusa* (6.8 %), *Gluta travancorica* (canopy, 6.8 %) and *Xanthophyllum flavescens* (understory, 6.7 %).

Cluster PO2 (Ponmudi samples 121-2, 122-1). These are lower-montane stands that are transitional to the lowland mixed tropical evergreen forests. The major dominants are *Vateria indica* (canopy, 21.6 % basal area) and *Gluta travancorica* (canopy, 13.4 %). Other dominant trees are *Diospyros* sp. (lower canopy, 9.4 %), *Syzygium densiflorum* (canopy, 9.4 %), *Calophyllum apetallum* (canopy, 6.0 %) and *Mesua ferrea* (lower canopy, 5.7 %). Also noteworthy here is *Xanthophyllum flavescens* (understory, 4.9 %).

Cluster PO3 (Ponmudi samples 120-1, 120-2, 116-1). This type can be designated the *Dimocarpus longan*-mixed tropical hardwoods/*Diospyros* Association. The major dominants are *Dimocarpus longan* (16.1 % basal area), *Diospyros* sp. (lower canopy, 12.6 %) and *Ficus* sp. (canopy, 10.2 %). Other dominant trees are *Syzygium densiflorum* (canopy, 9.4 %), *Olea dioica* (lower canopy, 9.0 %), *Poeciloneuron indicum* (canopy, 7.8 %), *Gomphandra polymorpha* (lower canopy, 7.1 %), *Cullenia exarillata* (canopy, 6.9 %) and *Heritiera paplio* (canopy, 5.8 %).

Cluster PO4 (Ponmudi samples 119-1, 119-2, 121-3). This forest type can be designated the *Holigarna arnottiana-Syzygium densiflorum* Association. The major dominants are *Holigarna arnottiana* (canopy, 16.5 % basal area) and *Syzygium densiflorum* (canopy, 10.8 %). Other dominant trees are *Elaeocarpus monronii* (lower canopy, 6.6 %), *Canthium dicoccum* (lower canopy, 6.3 %), *Persea macrantha* (canopy, 6.2 %), and *Olea dioica* (lower canopy, 5.6 %). In addition there are 11 other trees with percentage basal area in the range 1–5 %.

Sri Lanka

Referring once again to the dendrogram (Fig. 3), we see that the Sri Lanka cluster can be divided at the 0.66 level of dissimilarity into five branches, which are labeled

SR1-SR5. We combined data for samples within each of the five (tables of their floristic composition are available by request from the senior author).

SR1 comprises Midcar, Woodside and Corbet's Gap. We can designate this type as the *Myristica dactyloides-Syzygium/Bhesea montana* Association. It has as the major dominant *Myristica dactyloides* (19.2 % basal area); another dominant is *Bhesa montana* (understory, 8.4 %); lesser dominants are *Syzygium aqueum* (4.9 %), *Aglaia congylos* (4.5 %), *Fahrenheitia zeylanica* (understory, 4.5 %), *Syzygium* sp. (4.5 %), *Ficus fergusonii* (4.5 %), *Pseudocarapa championii* (4.3 %), *Elaeocarpus glandulifer* (3.5 %), *Cullenia rosayroana* (3.5 %) and *Gordonia ceylanica* (3.0 %). When basal areas of all the *Syzygium* species are summed (12.8 %), it is clear that *Syzygium* is a major dominant. This is an association of deep soils on well-drained slopes or rich flatlands.

Cluster SR2 comprises Hayes 1 and Kabaragala. We can designate this type as the *Palaquium hinmolpedda*-mixed tropical hardwoods/*Fahrenheitea zeylanica* Association. It has as major dominants *Palaquium hinmolpedda* (11.0 % basal area) and *Fahrenheitia zeylanica* (understory, 11.2 %). Dominant trees include *Elaeocarpus glandulifer* (8.5 %), *Myristica dactyloides* (8.4 %), *Semecarpus nigro-viridis* (6.2 %) and *Nothopegia beddomei* (lower canopy and understory, 5.7 %). Lesser dominants are *Eurya ceylanica* (understory, 4.8 %), *Cryptocarya wightiana* (4.7 %), *Litsea gardneri* (understory, 4.5 %), *Scolopia crassipes* (4.3 %) and *Syzygium batadamba* (4.0 %). The two stands occupy S-facing slopes on shallow or deep soils.

Cluster SR3 comprises only the stand at Laggala. We can designate this type as the *Schefflera racemosa-Persea macrantha/Fahrenheitia zeylanica* Association. In this stand the major dominants are *Schefflera racemosa* (19.5 % basal area) and *Persea macrantha* (14.4 %). Other dominant trees are *Fahrenheitia zeylanica* (understory, 8.3 %), *Bhesa ceylanica* (understory, 5.4 %) and *Canthium coromandelicum* (understory, 5.1 %). Lesser dominants are *Flacourtia inermis* (understory, 4.8 %), *Dimocarpus longan* (4.6 %), *Cedrela toona* (4.5 %) and *Ficus microcarpa* (4.4 %).

Cluster SR4 comprises only the stand at Rangala. We can designate SR4 as the *Elaeocarpus glandulifer-Prunus ceylanica*-mixed tropical evergreen hardwoods Association. The major dominants are *Elaeocarpus glanduifer* (21.7 % basal area) and *Prunus ceylanica* (14.9 %). Other dominant trees are *Syzygium gardneri* (9.4 %), *Myrcia* (*Rapanea)* sp. (9.1 %), *Gordonia ceylanica* (8.1 %), *Semecarpus obscura* (6.6 %) and *Cinnamomum* sp. (5.9 %). Lesser dominants are *Fagraea ceilanica* (4.7 %), *Flacourtia inermis* (3.4 %) and *Eurya japonica* (3.4 %). This is a low, gnarled stand that occurs on an exfoliating igneous rock dome. In south India this would be called a Hilltop Evergreen Community.

Cluster SR5 comprises three stands: Kondagala, Hayes 2, and Hayes 3. We can designate this cluster as the *Doona-Cryptocarya wightiana Calophyllum* Association. The major dominants are *Doona zeylanica* (23.6 % basal area) and *Cryptocarya wightiana* (12.0 %). Other dominant trees are *Calophyllum acidus* (9.4 %) and *Elaeocarpus glandulifer* (5.5 %). Lesser dominants are *Doona gardneri* (3.8 %), *Hortonia floribunda* (understory dominant, 3.2 %) and *Myristica* *dactyloides* (3.2 %). These three stands dominated by Dipterocarpaceae (i.e., *Doona* spp.) are transitional in composition to the lower-montane dipterocarp forests, in which dipterocarps are nearly the only canopy trees. Dipterocarp forests dominate in regions of the highest rainfall. It is likely that these three stands receive more rainfall than is typical for the mixed-family forests of the lower montane belt.

The ordination of our sampled stands is given in Fig. 4. We see that the Sri Lanka stands are nearly all closely related compositionally. There is a great deal of variation in the South India cluster. The Ponmudi cluster, comprising stands on just one mountain, shows a smaller range of variation that resembles the Sri Lanka cluster more closely, with the exception of one stand, PO 116-1, which is dominated by *Olea dioica*. A classification of the forest types that can be recognized from these clusters is given in Table 7.

Discussion

Altitudinal Zonation of Tropical Evergreen Forests in South India and Sri Lanka

Based on Whitmore and Burnham (1975), three altitudinal belts of evergreen forest can be recognized as life zones or orobiomes near the southern tip of the Indian Peninsula: (1) Lowland Tropical Evergreen ("Tropical Wet Evergreen Forests" of Chandrasekharan 1962); (2) Tropical Lower Montane Evergreen Forests (Montane Sub-Tropical Forests of Chandrasekharan 1962); and (3) Tropical Upper Montane Evergreen Forests (Montane Temperate Forests of Chandrasekharan 1962). These can be characterized as follows.

Lowland Tropical Evergreen Forests are "... lofty, dense, evergreen forests, 150 feet or more... large numbers of trees which occur together. Consociations (gregarious dominants) are rarely met with and two-thirds or more of the upper-canopy trees are species [whose individual] contribution [is] not more than one percent of the total number; a few species may be met with semi-gregariously but this is not typical. Some species of the top story are trees with clear boles 100 ft long and 15 ft or more in girth, and may be deciduous or semi-deciduous without affecting the evergreen nature of the forest as a whole. The canopy is extremely dense... [with] scattered giants that project well above the general canopy...[and no other] differentiation into definite canopy layers."

"[E]piphytes are numerous... aroids, ferns, mosses and orchids. Climbers [may be] conspicuous but often [are] not so. Ground vegetation may be absent [or there may be] a carpet of *Strobilanthes* or *Selaginella* and ferns may occur; grasses are absent. The undergrowth is often a tangle of canes, creeping bamboos and palms, which may replace high forest as cane brake along streams. Erect bamboos are unusual but may occur locally. Long cylindrical boles usually with thin smooth bark are typical, but plant buttresses are also frequently seen. The leaves are thick

Table 7 Associations and series of lower montane forests in South India and Sri Lanka

Series		Associations (a-z)	Faciations(1-X)	Author
Mesua-Palaquium- Cullenia	India I	a1	Cullenia (Durio) exarillata-Mesua [ferrea]-Palaquium ellipticum	Ramesh et al. *in* Varghese and Balasubramanyan (1999)
		a2	Cullenia (Durio) exarillata-Mesua [ferrea]-Palaquium ellipticum- Gluta travancorica	Ramesh et al. *in* Varghese and Balasubramanyan (1999)
		a3	Cullenia (Durio) exarillata-Aglaia sp.-Palaquium ellipticum	Chandrasekharan (1962)
		a4	Palaquium ellipticum- Cullenia (Durio) exarillata/ Agrostistachys borneensis	Greller et al., present study
		a5	Cullenia exarillata/ Humboldtia unijuga	Greller et al., present study
		a6	Mesua [ferrea]-Palaquium ellipticum	Ramesh et al. *in* Varghese and Balasubramanyan (1999)
		a6	Palaquium [ellipticum]-Mesua [ferrea]	Chandrasekharan (1962)
		a7	Ficus hispida- Bischofia javanica-Mesua [ferrea]-Cullenia (Durio) exarillata	Greller et al. after Varghese and Balasubramanyan (1999)
		a8	Cullenia (Durio) exarillata-Aglaia sp.-Palaquium ellipticum	Ganesh et al. (1996)
		b1	Poeciloneuron indicum- Palaquium ellipticum	Chandrasekharan (1962)
		c1a	Mesua [ferrea]-Calophyllum sp.	Chandrasekharan (1962)
		c1b	Gluta travancorica-Mesua [ferrea]/Garcinia morella/ Agrostistachys borneensis	Greller et al., present study
Persea macrantha-Holigarna spp.-Diospyros spp	India II/Sri Lanka	a1	Persea macrantha- Diospyros spp.-Holigarna spp.	Greller et al., present study
		a2	Diospyros spp.-Dysoxylum malabaricum- Persea macrantha	Greller et al., present study
		a3	Dimocarpus longan-Holigarna sp.- Olea dioica-Syzygium sp./Diospyros sp.	Greller et al., present study
		b1	Holigarna arnottiana- Syzygium densiflorum	Greller et al., present study
		c1	Schefflera racemosa- Persea macrantha/ Fahrenheitia zeylanica	Greller et al., present study

(continued)

Table 7 (continued)

Series		Associations (a-z)	Faciations(1-X)	Author
Syzygium arnottiana	India III	a1	Syzygium densiflorum/ Garcinia morella/ Xanthophyllum flavescens	Greller et al., present study
Lowland Vateria-Hopea/Lower Montane Ecotonal	India IV	a1	Vateria indica- Cullenia (Durio) exarillata	Chandrasekharan (1962)
		a2	Vateria indica-Mesua [ferrea]	Chandrasekharan (1962)
		a3	Vateria indica- Gluta travancorica	Greller et al., present study
		b1	Poeciloneuron indicum- Palaquium ellipticum-Hopea ponga	Ramesh et al. *in* Varghese and Balasubramanyan (1999)
Lower Montane/Upper Montane Knema-Litsaea Ecotonal	India V	a1	Knema attenuata-Litsaea oleoides ecotonal	Varghese and Balasubramanyan (1999)
Myristica dactyloides	Sri Lanka I	a1	Myristica dactyloides-Syzyzgium spp./Bhesa ceylanica montana	Greller et al., present study
		a2	Palaquium hinmolpedda- Myristica dactyloides-Elaeocarpus glandulifer/Fahrenheitia	Greller et al., present study
Lower Montane Hilltop Elaeocarpus glandulifer	Sri Lanka II	a1	Elaeocarpus glandulifer- Prunus ceylanica-mixed tropical evergreen	Greller et al., present study
Lower Montane Doona-Cryptocarya Ecotonal	Sri Lanka III	a1	Doona (Shorea) spp.-Cryptocarya wightiana-Calophyllum sp.	Greller et al., present study

and glossy, only rarely finely pinnate or hairy, and are often white or pink when young. Cauliflory is relatively common." (Champion, in Chandrasekharan 1962).

It is clear from climate data that evergreenness in forests is a function of high rainfall, at any elevation in extreme south India/Sri Lanka. Thus, lowland tropical mixed evergreen forests (Lowland Evergreen Mixed Families LEM) and tropical dipterocarp-dominated lowland forests (Lowland Evergreen Dipterocarp-dominated, LED) are present as well as lower-montane mixed tropical forests (Mid-elevational Evergreen Mixed Families, MEM), on the Western Ghats. These have traditionally been distinguished roughly as Low and High Level Evergreen Forests, respectively (Chandrasekharan 1962). From our data, this transition occurs at around 900 m above sea level, at the southern tip of India and in adjacent Sri Lanka. Pascal (1984) recognized the transition at 600–700 m; Chandrasekharan (1962) recognized the distinction at 450 m. The following forest types can be taken as examples of regional lowland evergreen tropical forests: (1) *Dipterocarpus bourdilloni-Dipterocarpus indicus-Anacolosa densiflora* (Olacaceae) (40 km N of Shenkottah Gap to 80 km N of Palghat Gap; Pascal 1984); (2) *Dipterocarpus indicus/Vateria indica* (Dipterocarpaceae*)/Myristica dactyloides/Humboldtia brunonis* Forest (at 500–600 m in the Kadamakal Reserve of Kodagu District; Pascal and Pelissier 1996); and (3) *Lophopetalum wightianum-Vateria indica-Mangifera indica* (on water courses below 900 m; Pascal 1984).

Nevertheless, floristically transitional forests have been described as "High Level" by Chandrasekharan (1962); e.g. at Kottayam, where the dominant trees include such lowland taxa as *Dipterocarpus indicus, Anacolosa densiflora, Kingiodendron pinnatum* (Caesalpiniaceae)*, Vateria indica, Canarium strictum, Artocarpus hirsutus, Hopea parviflora* and *Polyalthia fragrans*; as well as the more strictly lower-montane trees that are dominants in our present study: *Cullenia exarillata, Poeciloneuron indicum, Persea macrantha, Gluta travancorica,* and, possibly*, Calophyllum elatum* (and *Mesua ferrea*, as well). At Ponmudi, as well as at Kulathuhepugha and Shendurni, Chandrasekharan described a "High Level Forest" dominated by such lowland taxa as *Anacolosa, Artocarpus* spp., *Dysoxylum malabaricum, Lophopetalum wightianum, Dipterocarpus* spp., *Kingiodendron*, and *Hopea*; as well as by taxa that are dominant in our lower-montane stands: *Palaquium ellipticum, Cullenia exarillata*, *Gluta travancorica,* and *Persea macrantha.*

Tropical Lower Montane Evergreeen Forests have trees of lower stature (15–33 m) than the lowland forest, and they lack buttresses (Greller et al. 1997). Blasco (1971, p. 147) recognizes forests of middle elevations as having three woody strata. The dominant stratum is discontinuous with (uncommon) emergents 25–35 m tall, having clear boles to 10–15 m, or somewhat twisted. Upper branches and terminal branches show decided twisting. Crowns in all the strata are broad and deep. This type has the largest percentage of trees bearing notophyllous (20.25–45.0 cm^2) leaves of any altitudinal belt. The leaves are largely entire and simple (Greller and Balasubramaniam 1988). The liana community is rich in species, although woody climbers are sparse; root climbers are present and can be prominent (e.g., *Freycinetia*, Pandanaceae) in wet forests at this altitude. Canopies are often festooned with mosses and herbaceous epiphytes. Understory layers have variable density, with shrubs (3–9 m tall, especially *Strobilanthes*) and tall and short herbs.

All of our stands in Kerala and Sri Lanka should be considered variants of notophyllous evergreen forest of mixed tropical families. They are part of the tropical lower-montane orobiome or, in a few cases, transitional from lowland rainforest to notophyllous evergreen forest of mixed tropical families (which could be labeled an oro-ecotone), or from lower-montane mixed families (MEM) to lower-montane dipterocarp-dominated (MED).

The statistics given for the three major clusters should be taken only as an indication of the role of certain prominent trees in these samples. It is conceivable that the locating and sampling of other sites might give somewhat different results. Nevertheless, it is noteworthy that the two regions, south India and Sri Lanka, had a different composition of dominant trees, and that Ponmudi Mountain differed strongly from the other south India stands (Agastyamalai Range and Nelliampathy sites, in Kerala-Tamil Nadu), in dominant taxa and in other parameters of vegetation cover.

These lower-montane forests are mainly enriched by taxa common in the lowland "Wet Zone" and, to a markedly lesser degree, by those from the (Upper) Montane Evergreen forests. The occurrence of *Doona* spp. at certain sites represents a variation of the MEM forests, apparently influenced by specific environmental factors. MEM forests have been and still are widely exploited for the cultivation of cardamom (*Elettaria cardamomum*), which has resulted in massive disturbance to a forest type that is unusually rich in endemics. Many potential understory taxa and perhaps some canopy taxa are absent from many sampled stands.

Tropical Upper Montane Forests are "closed… short-boled and branchy… often obtaining considerable girth… Height rarely exceeding 50 to 60 ft (15.2–18.3 m)…[C]rowns are dense and rounded, with entire coriaceous leaves… [showing] red [flush]… [B]ranches are clothed with mosses, ferns and other epiphytes and woody climbers are common… [N]o marked differentiation of canopy layers, but… a continuous series from under-shrub to shrub and shrubs to shoal trees. The forest is usually found in patches in the protected pockets or declivities in the rolling grassland [of the Western Ghats]" (Chandrasekharan 1962).

S. Balasubramaniam (unpublished mss.) characterized the distribution of upper-montane forests in Sri Lanka as comprising 15,800 ha. There are 413 endemic species, 50 % of the total endemics in Sri Lanka. He noted that Perera and, earlier, de Rosayro reported the mass dying of trees (50 % of the population of *Calophyllum* and *Syzygium* species in the upper montane). Gap replacement occurs with such early-successional species as *Syzygium* spp., *Neolitsea fuscata*, *Adinandra lasiopetala*, *Gordonia zeylanica* and *Hedyotis* spp.

Floristic Composition of Lower Montane Forests in Asia

Families of the Lower Montane Evergreen Forests in South India and Sri Lanka

Balasubramaniam and Greller (1981) list the following families as representing dominant genera in lower-montane mixed forests of Sri Lanka: Myristicaceae, Euphorbiaceae, Elaeocarpaceae, Meliaceae, Myrtaceae, Lauraceae, Sapotaceae and Rutaceae. Blasco (1971) lists, in addition, Moraceae (esp. *Ficus*) and Sapindaceae. He states further that the combination of the dominant families Lauraceae and Meliaceae is not observed in any other types of forest in south India, the Lauraceae largely disappearing with lower elevation and the Meliaceae disappearing from the upper montane. Composition of valley forests is richer than in the general uplands, being enhanced by Oleaceae, Celastraceae, Araliaceae, Anacardiaceae, Bixaceae, Arecaceae, Theaceae and others (Blasco 1971). For the Agastyamalai region of southern India, Varghese and Balasubramanyan (1999) list the following dominant families (percentage dominance): Clusiaceae (22.2), Myrtaceae (9.4), Anacardiaceae (7.9), Lauraceae (6.3), Bombacaceae (6.1), Moraceae (5.6), Flacourtiaceae (5.4) and Euphorbiaceae (5.1). Ganesh (1996; in Varghese and Balasubramanyan 1999) calculated percentage importance values for the leading dominant families on the east side of Agastyamalai as: Clusiaceae (48.4), Myrtaceae (25.2) and Lauraceae (21.0). In species richness, the Euphorbiaceae were first with seven species. In 3.82 ha of Kalakad Mundanthurai Tiger Reserve, Agastyamalai, Tamil Nadu, there were 90 tree species in 35 families.

Dominant Genera in the Previously Recognized Lower Montane Evergreen Forest Types of South India

Meher-Homji recognized two "series" of montane forests for south India, at or below 1500 m, namely a "*Dipterocarpus-Mesua-Palaquium-Cullenia* Evergreen" series and a "[*Persea*]-*Holigarna-Diospyros* Evergreen"series. Pascal and Pelissier (1996), working in the Uppangala Forest in the Kadamakal Reserve (12°30′ N, 75°39′ W, Kodagu District, Kerala), found the following dominant taxa at 500–600 m: *Dipterocarpus indicus* (emergent), *Vateria indica* (higher canopy), *Myristica dactyloides* (intermediate layer) and *Humboldtia brunonis* (understory). So, Meher-Homji's *Dipterocarpus-Mesua-Palaquium-Cullenia* forest type appears to be a combination of lowland dipterocarp-dominated forest and a lower-montane forest of *Palaquium, Mesua* and *Cullenia*. The (*Persea*)-*Holigarna-Diospyros* type, an "evergreen low forest," occurs under "high rainfall [where the] dry season extends to 6 months."

Ramesh et al. (1997) recognized the following "medium elevation forest types" in the Western Ghats: (1) *Cullenia exarillata-Mesua ferrea-Palaquium ellipticum-Gluta* *travancorica*; (2) *Cullenia exarillata-Mesua ferrea-Palaquium ellipticum*; (3) *Mesua ferrea-Palaquium ellipticum*; (4) (rare) *Poeciloneuron indicum-Palaquium ellipticum-Hopea ponga*; and (5) (in Mahabaleshwar) *Memecylon umbellatum–Syzygium cumini-Actinodaphne angustata*. We also include the following types, which range from 600 to 900 m: (6) *Persea macrantha-Diospyros* spp.-*Holigarna* spp.; and (7) *Diospyros* spp.-*Dysoxylum malabaricum-Persea macrantha*.

George and Varghese (1987) reported the following "subtropical hill forests" for the Nilgiri Range (Tamil Nadu, 11°15′–11°25′ N and 76°30′–76°55′ E): (1) *Hydnocarpus alpina*-(*Syzygium densiflorum*) (13–18 m tall) at 1400–1800 m; and (2) *Daphniphyllum neilgherrense*-(*Syzygium densiflorum*) (10–15 m tall) above 1800 m.

Working at 600–1200 m elevation in the Agastyamalai Range of southern Kerala, Varghese and Balasubramanyan (1999) recognized a West Coast Evergreen Forest (600–1000 m) of the *Mesua-Cullenia-Dimocarpus* type, dominated (percentage basal area) by *Ficus hispida, Bischofia javanica, Mesua* (*ferrea*) and *Cullenia exarillata*. Dominant trees are listed as: *Ficus hispida* (11.3 % basal area), *Bischofia javanica* (8.7 %), *Mesua* (*ferrea*) (6.0 %), *Cullenia exarillata* (5.7 %), *Calophyllum apetalum* (4.9 %), *Gluta travancorica* (4.8 %), *Ailanthus triphysa* (4.5 %), and *Hydnocarpus macrocarpa* (4.5 %). They consider this forest to be classified under the ***Cullenia-Dimocarpus-Mesua*** type, a sub-type of the *Cullenia-Mesua-Palaquium* Series. Varghese and Balasubramanyan (1999) report a ***Knema attenuata-Litsaea oleoides*****transitional association**, the "Hilltop Evergreen Forest," on exposed flat rock at Chemungimottai (1200 m). Dominants (relative basal area) are: *Knema attenuata* (13.0 %), *Litsaea oleoides* (10.1 %), *Mastixia arborea* spp. *meziana* (9.5 %) and *Gluta travancorica* (6.8 %); and the small trees *Actinodaphne bourdillonii* (6.5 %) and *Xanthophyllum arnottianum* (5.4 %). This stand contains upper-montane as well as lower-montane dominant taxa. Also in that Series is a ***Cullenia-Aglaia-Palaquium*** sub-type observed in the Kalakad-Mundanthurai Sanctuary (1250–1450 m) of Agastyamalai by Ganesh et al. (1996).

Varghese and Balasubramanyan (1999) reviewed the literature and reported Shannon–Wiener diversity indices for these middle-elevation forests of southern Kerala that ranged around 3.5, from 2.8 (Indukki) to 4.0 (Attapadi). By contrast, Pascal and Pelissier (1996) recorded a diversity index of 4.56 for the *Dipterocarpus*/*Vateria*/*Myristica*/*Humboldtia* lowland evergreen forest of the Kadamakal Reserve.

Giriraj et al. (2008) censused 3 ha of forest at "1170 to 1306 m. In the study plot 5624 individuals (mean density 1875/ha) covering 68 woody species belonging to 52 genera and 27 families were enumerated. The mean basal area was 47.01 m^2/ha and the Shannon and Simpson diversity indices were 4.89 and 0.95, respectively. Of these woody species, nearly 51 % are endemic to the Western Ghats. The four dominant species, *Cullenia exarillata, Palaquium ellipticum, Aglaia bourdillonii* and *Myristica dactyloides,* account for 34 % of the trees and 67 % of the basal area, and five species assemblages corresponding to altitudinal gradient were identified using correspondence analysis."

Earlier reports of lower montane forest types in South India include that of Chandrasekharan (1962) for Palghat (Silent Valley, Attapadi):

- ***Cullenia-Palaquium*** **association** ("low elevation climatic climax")
- ***Palaquium-Mesua*** **association** ("medium elevation climatic climax")
- ***Poeciloneuron-Palaquium*** **association** ("optimum moisture climatic climax")
- ***Mesua-Calophyllum*** **association** (" high elevation climatic climax")
- ***Vateria-Cullenia*** **association** ("edaphic variant" of *Cullenia-Palaquium* type)
- ***Vateria-Mesua*** **association** ("edaphic variant" of *Poeciloneuron-Palaquium* type).

In later estimations for Silent Valley National Park, Kundali Hills of the Nilgiri Hills in Palakkad (Palghat) District, Kerala (11°04′–11°13′ N, 76°24′–76°29′ E), the following forest types were also recognized: *Mesua-Cullenia, Ochlandra-Calophyllum*, and *Ochlandra-Poeciloneuron* (KFD 1990; Unnikrishnan 1989, in Varghese and Balasubramanyan 1999).

Chandrasekharan (1962, pp. 66–74) also reports forest classifications for the Kulathupugha Valley above 3500 ft; for Goodrigal, far eastern portions of Kowni Reserve, and for Anamalai Reserve above 3000 ft. When upper slopes and ridges and crests, with extreme climate, high wind and poor soil, occur in the lower montane life zone, they are occupied by "'Low' Tropical Ghat Evergreen Forests". Chandrasekharan lists the following dominants: *Mesua ferrea, Dysoxylum malabaricum, Cullenia exarillata, Holigarna beddomei, Calophyllum elatum, Cedrela toona, Canarium strictum, Artocarpus heterophyllus, Palaquium ellipticum, Hopea parviflora* and *Elaeocarpus* with an undergrowth of *Ochlandra-travancorica, Pandanus, Calamus* and *Strobilanthes.*

Lower Montane Evergreen Forest Types Recognized in this Study of South India and Sri Lanka.

Table 7 gives a summary of the forest types we derived from the sampled data, with previously recognized forest types for South India and Sri Lanka.

South India

On the most mesic sites *Cullenia exarillata* is the only major dominant, with a rich mixture of other taxa showing dominance values (RBA) greater than 5.0 %. *Gluta travancorica* and *Mesua ferrea* are leading major dominants in a few stands. Other major dominants are: *Myristica dactyloides, Holigarna arnottiana, Garcinia morella, Albizia procera, Syzygium densiflorum* and *Humboldtia unijuga* (understory dominant at the lowest elevations of the lower montane belt).

- ***Cullenia exarillata/Humboldtia unijuga* association**. Cluster SI1 comprises samples at Kakkachi, Athirmala and Nelliampathy 1 (see Table 1). This *Cullenia(-Persea)* type occurs on moist slopes and flat uplands at 1000–1310 m.
- ***Palaquium ellipticum-Cullenia exarillata/Agrostistachys borneensis* association**. Cluster SI2 comprises samples at Kannikkati, Bonaccord 7-1, Nelliampathy 2, Bonaccord 7-3, Bonaccord 8-1 and Bonaccord 8-2. The *Palaquium-Cullenia* type occurs on convex topography and adjacent valleys at 900–1100 m.
- ***Gluta travancorica-Mesua ferrea/Garcinia morella/Agrostistachys borneensis* association**. Cluster SI3 comprises samples at Bonaccord (Bon 7-2, Bon 7-4A, Bon 8-4). The *Gluta-Mesua (-Albizia)* type occurs at the lower elevations of the association; only on ridges at 945 m.

Ponmudi, Trivandrum, India

When all samples are combined, the only major dominant is *Syzygium densiflorum* (16.7 % basal area). Other, lesser dominants are *Vateria indica* (6.8 %), *Gluta travancorica* (6.7 %), *Holigarna arnottiana* (6.6 %) and *Diospyros* sp. (6.3 %). *Xanthophyllum flavescens* dominates the understory with 10.9 % density. *Gomphandra polymorpha,* also in the understory, accounts for 4.2 % density, and *Gordonia obtusa*, 3.5 % density.

- ***Syzygium densiflorum/Garcinia morella/Xanthophyllum flavescens* association**. Cluster PO1 (Ponmudi samples 114, 121-1, 116-2, 120-3B). This type occurs in shola ravines and upland flats.
- ***Vateria indica-Gluta travancorica* ecotonal association**. Cluster PO2 (Ponmudi samples 121-2, 122-1). These are lower-montane stands that are transitional to the lowland mixed tropical evergreen forests. The major dominants are *Vateria indica* (canopy, 21.6 % basal area) and *Gluta travancorica* (canopy, 13.4 %). Other dominant trees are *Diospyros* sp. (lower canopy, 9.4 %), *Syzygium densiflorum* (canopy, 9.4 %), *Calophyllumapetallum* (canopy, 6.0 %) and *Mesua ferrea* (lower canopy, 5.7 %). Also noteworthy here is *Xanthophyllum flavescens* (understory, 4.9 %). The *Vateria-Gluta* type is transitional to the lowland mixed evergreen forest.
- ***Dimocarpus longan*-mixed tropical hardwoods/*Diospyros* association**. Cluster PO3 (Ponmudi samples 120-1, 120-2, 116-1). This *Dimocarpus*(*-Holigarna-Olea-Syzygium*) type occurs on convex or steep slopes or on dry, rocky sites.
- ***Holigarna arnottiana-Syzygium densiflorum* association**. Cluster PO4 (Ponmudi samples 119-1, 119-2, 121-3).

Sri Lanka

The only overall major dominant (≥10 % basal area) in these stands is *Myristica dactyloides* (12.6 % basal area). Another dominant (5–10 % basal area) is *Elaeocarpus glandulifer* (6.1 %). Lesser dominants (3–5 % basal area) are the understory trees *Bhesa ceylanica* (4.9 %) and *Fahrenheitia zeylanica* (4.7 %). The latter tree is second in relative density with 5.5 %. The general type comprises a large number of sub-dominants, such as: *Aglaia congylos, Culleniazeylanica, Syzygium* spp., *Pseudocarapa championii, Ficus, Persea macrantha, Canthium coromandelicum, Flacourtia inermis, Garcinia morella, Nothopegia beddomei*, and *Scolopia crassipes*. Sri Lanka has a great diversity of associations. First dominance is also exhibited by species such as *Schefflera racemosa*, *Ficus fergusonii*, and *Palaquium hinmolpedda*. Other, local dominants are *Doona zeylanica* (3.5 % basal area) and *Cryptocarya wightiana* (3.2 % basal area). These occur in the higher-rainfall areas and form stands that are transitional to the lower-montane dipterocarp (*Doona*) consociation.

- ***Myristica dactyloides-Syzygium/Bhesea ceylanica montana* association**. SR1 comprises the Sri Lanka stands Midcar, Woodside and Corbet’s Gap.
- ***Palaquium hinmolpedda*-mixed tropical hardwoods/*Fahrenheitea zeylanica* association**. Cluster SR2 comprises Hayes 1 and Kabaragala, Sri Lanka.
- ***Schefflera racemosa-Persea macrantha/Fahrenheitia zeylanica* association**. Cluster SR3 comprises only the stand at Laggala, Sri Lanka.
- ***Elaeocarpus glandulifer-Prunus ceylanica*-mixed tropical evergreen hardwoods association**. Cluster SR4 comprises only the stand at Rangala, Sri Lanka. On dry ridge tops, on shallow soils, we recognize this low, gnarled type.
- ***Doona-Cryptocarya wightiana-Calophyllum* association**. Cluster SR5 comprises three stands: Kondagala, Hayes 2, and Hayes 3, Sri Lanka. In the wetter climates of the lower montane zone we recognize this type, dominated by *Doona* spp. with a number of co-dominants (*Cryptocarya* and *Calophyllum acidus* or *Acronychia pedunculata* and *Aporusa fusiformis*).

Lower Montane Evergreen Forest in Malesia

Oak-Laurel Forests of East Indies Mountains

Ohsawa (1991) recorded family composition in the oak-laurel type of lower montane forests. He found the following taxa as dominants: Myrtaceae, Fagaceae, Theaceae, Moraceae, Elaeocarpaceae, Hamamelidaceae, Flacourtiaceae and Magnoliaceae on Sumatra; and Fagaceae, Theaceae, Podocarpaceae, Lauraceae, plus Elaeocarpaceae, Myrtaceae, and Aceraceae on Java. Kitayama (1992), working on Mount Kinabalu, Borneo, recognized a lower-montane rainforest between 1200 and 1800 m elevation. This forest type showed a 9.9 % similarity to the lowland rainforest. In Kitayama's lower-montane forest the following families were dominants: Fagaceae, Lauraceae, Theaceae, Myrtaceae and Elaeocarpaceae. He noted further that "… the families Lauraceae and Fagaceae… have broad altitudinal ranges extending both to the lowland and the subalpine" belt. Among the genera and species listed for Lower Montane 2a are *Adinandra, Schima, Lithocarpus, Elaeocarpus, Calophyllum, Horsfieldia, Dacrycarpus* (Podocarpaceae), *Garcinia, Eugenia* (=*Syzygium*?), *Prunus, Neolitsea*, and *Ternstroemia*; and for Lower Montane 2b, *Palaquium, Eugenia, Lithocarpus* and *Litsea*. Referring to Mabberly (2008), one can see that a majority of important species belong to the Fagaceae and Theaceae, with lesser representation by Lauraceae. There is, as well, a representation of south Indian lower-montane dominants such as *Palaquium, Elaeocarpus, Calophyllum, Garcinia* and *Prunus*.

Lower-montane rainforests in Java, Sumatra and the Philippines are constituted by Oak-Laurel Forests. Dipterocarpaceae dominate the lowland forests of those East Indies islands.

Malesian (East Indies) Forests of Mixed Tropical Families Related to Lower Montane Forests of South India

Lowland rainforests of the East Indian islands from the Andamans (Champion and Seth 1968) to Borneo (e.g. Cannon and Leighton 2004) are characterized by the dominant role of Dipterocarpaceae. In these forests, species of such lower-montane genera as *Palaquium* and *Xanthophyllum* are restricted to extreme habitats such as swamp and peat (Cannon and Leighton 2004). Hommel (1990), working in West Java (Indonesia) in a mountainous region of lowland semi-deciduous mixed tropical forest, described a "telescoping effect" on this low, isolated mountain complex (maximum elevation 500 m) reflecting the "[condensed] zoning of higher mountains." He listed the following taxa that are also dominants of lower-montane forests of south India-Sri Lanka: *Myristica, Diospyros, Xanthophyllum, Ficus, Elaeocarpus, Aglaia, Garcinia, Syzygium, Cryptocarya* and *Bischofia javanica*. Many of the latter are also represented in the lower-montane mixed evergreen forests of northern Queensland, at 15–19° S latitude (complex evergreen notophyll vine forests, Tracey 1982), including also *Planchonella, Polyalthia* and S*terculia.*

New Guinea Rainforests: A Mosaic of Indo-Malesian, Antarctic and Laurasian Dominants

Paijmans (1976) reviewed the forest types of New Guinea and listed the following broad-leaved evergreen types: (lowland) mixed alluvial, mixed hill, Dipterocarp, *Casuarin*a, and *Araucaria* forests; (lower montane) mixed lower-montane, *Castanopsis*, *Nothofagus* and coniferous forests; and upper-montane forest. He described the lower montane mixed evergreen forest as reaching 20–30 m tall, with a densely closed and regular canopy; leaves simple, leathery, shiny, dark green, with entire or serrate margins. Dominant families he listed as: Fagaceae, Lauraceae, Cunoniaceae, Elaeocarpaceae, and Myrtaceae, with "conifers in the upper levels." Among the leading genera of the upper strata of the forest he listed *Ilex, Dryadodaphne* and *Planchonella* (*Pouteria*). In the lower level of the tree layer he listed: *Garcinia, Astronia, Polyosma, Symplocos, Sericolea, Drimys, Prunus, Pittosporum* and Araliaceae. He noted that frequency and duration of cloud cover constituted one major factor depressing the elevation at which the lower-montane evergreen forest appears. At 900 m, on a ridge, he described a "mossy" forest of *Nothofagus, Phyllocladus* and *Astronia*. Under usual conditions the lower-elevation stands of lower-montane forest are dominated by Fagaceae, *Castanopsis acuminatissimum* and *Lithocarpus*, where sparsely populated shrub and herb layers. Forests of *Nothofagus* (with 19 species) occur from 600 to 3100 m elevation, assuming dominance at 1500 m (upper montane belt).

Hyndman and Menzies (1990) reported on the forests in the high country at the center of New Guinea. The climate at Bakonabip (1500 m), with a warm-month average of 21.5 °C, and a cold-month average of 18.4 °C, can be characterized as very warm and temperate (after Bailey 1960). Above the foothill rainforest, at 1000 m, begins the Lower Montane Rainforest, which extends to 1800 m. This is a mixed forest 20–30 m tall. It has a two-tiered canopy in which the upper canopy has *Castanopsis, Urophyllum* (Rubiaceae)*, Ficus* (Moraceae)*, Cryptocarya* (Lauraceae)*, Canarium* (Burseraceae)*, Podocarpus* (Podocarpaceae)*, Cyathocalyx* (Annonaceae)*, Symplocos* (Symplocaceae)*, Talauma* (Magnoliaceae)*, Syzygium* (Myrtaceae)*, Litsea* (Lauraceae)*, Sterculia* (Sterculiaceae)*, Erythroxyum* (Erythroxylaceae)*, Casuarina* (Casuarinaceae)*, Conandrium* (Myrsinaceae)*, Fagraea* (Gentianaceae)*,* Arecaceae*,* and *Pandanus* (Pandanaceae); the lower canopy has *Lithocarpus* (Fagaceae), *Elaeocarpus* (Elaeocarpaceae), *Dysoxylum* (Meliaceae)*, Prunus* (Rosaceae)*, Garcinia* (Clusiaceae)*, Pandanus, Euodia* (Rutaceae)*, Caldcluvia* (Cunoniaceae)*, Timonius* (Rubiaceae)*, Duckera* (Anacardiaceae), *Glochidion* (Euphorbiaceae), *Bubbia* (Winteraceae), *Cryptocarya*, *Perrottetia(*Celastraceae)*, Schuurmansia* (Ochnaceae)*, Myristica* (Myristaceae), *Phaleria* (Thymeleaceae), *Psychotria* (Rubiaceae)*, Saurauia* (Actinidiaceae), *Baccaurea* (Euphorbiaceae*), Helicia* (Proteaceae), *Pavetta* (Rubiaceae) *and Aceratium* (Elaeocarpaceae*)*. Trees ferns are prevalent, including *Marattia*, as well as the tall herb *Alpinia*. Ground ferns are also common. Lianas, including *Schefflera, Freycinetia, Costus, Ficus, Peperomia, Mussaenda, Uncaria, Entada, Piper, Asplenium, Smilax, Cissus, Vaccinium, Sabia* and many others, festoon the trees. Thus the flora of the lower-montane rainforests of central New Guinea has a rich mixture of Malesian dominant genera, as well as the Laurasian Fagaceae, *Castanopsis* and *Lithocarpus,* and the Antarctic (Subantarctic) genera *Caldcluvia* (Cunoniaceae) and the conifer*Podocarpus*. Many of the Indo-Malesian genera occur as dominants in the MEM forests of south India and Sri Lanka.

Lower Montane Evergreen Forest in Eastern Australia

Webb (2005) recognized 16 “structural types” of “rainforest” (i.e. non-sclerophyll forest) in Australia, in New South Wales, Queensland and Northern Territory, mainly along the coasts. Webb (1959) grouped the rainforests of Australia into three floristic types: (1) Tropical Rainforest, with mesophyllous leaves on canopy trees; (2) Subtropical Rainforest, with notophyllous leaves, and often *Araucaria* as a dominant; and (3) Temperate Rainforest, with Subantarctic floristic affinities. Under the category “notophyll,” where notophyll was defined as “[evergreen, lance-shaped or elliptical] leaves longer than 7.5 cm (3 in), but less than 25 cm (5 in),” Webb (2005) listed six forest types.

In attempting to find a homologous type with our Indian/Sri Lankan lower-montane mixed evergreen forests, we referred to the descriptions and photographs in Webb’s (1959, 1968) papers. Webb (1968, Fig. 1) listed only two “strictly evergreen” notophyllous forests, (1) “mixed… vine” and (2) “simple … vine.” Of these two notophyllous types, Webb (1959, plate 15, photo 7) described a “Simple Notophyll Vine forest (subtropical Lower Montane) near Coff’s Harbour, N.S.W. Note simplified strata, absence of robust lianes and vascular epiphytes, and single species dominance by *Ceratopetum apetalum* [Cunoniaceae].” Webb (1959, plate 15, photo 6) pictured the “Interior of Notophyll Vine forest at Mt. Glorious, south Queensland; (caption) “Note plank buttresses of *Argyrodendron* (*Heritiera*) *actinophyllum* [Sterculiaceae], robust liane (*Pipernovae-hollandiae*) and trunk spaces obscured by epiphytic *Pothos longipes*.” Webb (1959) further described the Complex Notophyll Vine Forest as “notophylls and microphylls most common; robust lianes, vascular epiphytes, plank buttresses and compound entire leaves prominent…stem diameters irregular, many average 2–4 ft. (60–120 cm) dbh, canopy level uneven, average 50–120 ft. (15–36 m) with mixed evergreens (e.g., *Ficus*) and rare deciduous emergents.” It is clear that only the Australian complex notophyllous vine forest corresponds in floristics (Indo-Malesian), composition (mixed dominants) and structure (notophylls, and diverse life forms) to the Indian/Sri Lankan lower-montane mixed evergreen notophyllous forests (MEM). Climates for two stations of lowland notophyll vine forest, Brisbane (Complex NVF) and Sydney (Simple NVF), were given by Axelrod and Bailey (1969); both are cooler (W = 16.9 °C; W = 15.6 °C, respectively) than Sri Lanka MEM stations.

Environmental Relations of Australian Evergreen Complex Notophyll Vine Forest

In Webb (1959, Fig. 1) we see that (complex) notophyll vine forests (NVF) first appear as an important forest type at sea level, at 21° S latitude, and become a dominant forest type in lowlands at 23° S latitude. In Webb (1968, Fig. 3) we see that percentages of notophyllous rainforest species increase rapidly (1) south of about 38° latitude, (2) from 1200 to 1500 m elevation at 17° S latitude, and (3) above 900 m elevation at 30° S latitude.

Floristic Composition of Some Complex Notophyll Vine Forests

The TSSC website (from J. G. Tracey 2005) gave a list of the flora by synusia in the Mabi Forest (Complex Notophyll Vine Forest 5b), on highly fertile, basalt-derived soils, in the moist lowlands, foothills and uplands of the Atherton Tablelands, near Cooktown, in northern Queensland, where annual precipitation varies between 1300 and 1600 mm. The canopy has as dominants *Aleurites moluccana* (Euphorbiaceae), *Alstonia scholaris* (Apocynaceae), *Argyrodendron* (*Heritiera*) *peralatum* (Sterculiaceae), *Castanospermum australe* (Fabaceae), *Diploglottis cunninghamii* (Sapindaceae), *Elaeocarpus grandis* (Elaeocarpaceae), *Ficus virens, Ficus obliqua* (Moraceae), *Melia azederach* (Meliaceae), *Myristica muelleri* (Myristicaceae), *Terminalia sericocarpa* (Combretaceae), and *Toona australis* (Meliaceae). Subcanopy dominants are listed as: *Acronychia acidula* (Rutaceae), *Aglaia sapindina* (Meliaceae), *Alangium villoxum* (Alangiaceae-Cornales), *Arytera divaricata* (Sapindaceae), *Cupaniopsis serrata* (Sapindaceae), *Daphnandra dielsii* (Monimiaceae), and (*Melicope*) *bonwickii* (Rutaceae). There are listed, in addition, an understory layer, a liana synusia, and an epiphyte synusia. On an area of the Evelyn Tableland, between Atherton and Tully Falls, on Koolmon Creek, on basaltic kraynozem, Tracey (1982) listed some additional canopy genera for Complex Notophyllous Vine Forest with small palms and rattans: *Xanthostemon pubescens* (emergent, Myrtaceae), *Beilschmiedia* (Lauraceae), *Caldcluvia* (Cunoniaceae), *Cardwellia* (Proteaceae), *Cryptocarya* (Lauraceae), *Darlingia* (Proteaceae), *Doryphora* (Monimiaceae), [*Syzygium*] (Myrtaceae), *Flindersia* (Rutaceae), *Geissois* (Cunoniaceae), *Opisthiolepis* (Proteaceae), *Sloanea* (Elaeocarpaceae) and *Sterculia* (Sterculiaceae). In the subcanopy are also: *Alphitonia* (Rhamnaceae), *Athertonia* (Proteaceae), *Bubbia* (*Zygogynum*, Winteraceae), *Castanospora* (Sapindaceae), *Endiandra* (Lauraceae), *Helicia* (Proteaceae), and *Litsea* (Lauraceae). Also listed for this forest are an understory, lianas, epiphytes and hemi-epiphytes and a ground layer.

Comparison of Lower Montane Evergreen Forests in Eastern Australia and in South India-Sri Lanka

Dominant Families

- Family compositions of south Indian and Sri Lankan forest dominant trees are nearly identical: Anacardiaceae, Bombacaceae, Clusiaceae, Elaeocarpaceae, Euphorbiaceae, Flacourtiaceae, Lauraceae, Meliaceae, Moraceae (esp. *Ficus*), Myristicaceae, Myrtaceae, Sapindaceae, Sapotaceae and Rutaceae

(Balasubramaniam and Greller 1981; Blasco 1971; Varghese and Balasubramanyan 1999).

- The taxonomic composition of MEM suggests Gondwanan affinities. Important families of MEM forests, such as Myristicaceae, Sapotaceae, Euphorbiaceae, Elaeocarpaceae, Anacardiaceae, Meliaceae and Rutaceae, are shown to have strong roots in West Gondwanaland (Raven and Axelrod 1974). However, rare occurrences of genera such as *Cinnamomum, Litsea* (Lauraceae), *Michelia* (*Magnolia*, Magnolicaceae), *Symplocos* (Symplocaceae) and *Celtis* (Ulmaceae) suggest remote Laurasian relationships. This is in accordance with the widely accepted view of general enrichment of the Sri Lanka flora from Laurasian land masses of the present Malesian region during the late Tertiary Period (Hora 1949) and, no doubt, during the Pleistocene, when lower temperatures and higher rainfall (Antevs 1928) enabled tropical montane (subtropical) floras to spread widely into lowlands.
- The tropical and subtropical families that are dominants in Australian CNVF are largely shared with the MEM forests of South India-Sri Lanka. But the Australasian lower-montane forests also include dominant genera from other geofloras, viz., the Laurasian (e.g., Alangiaceae), and what are now considered Antarctic (Austral, Subantarctic) Geoflora families of Cunoniaceae, Monimiaceae, Proteaceae and Winteraceae; as well they retain, as local dominants, the archaic Gondwanan endemic families Himantandraceae, Amborellaceae and Eucryphiaceae. Webb et al. (1986) notes that this "autochthonous," mainly "subtropical" Australian rainforest "floristic element" of mixed families has a fossil record that pre-dates Australia's connection to the Malesian region, and they argue strongly that it can be traced back to the [late] Cretaceous.

Generic Distinctiveness of the MEM and CNVF Lower Montane Rainforests

A Sri Lankan MEM cluster, based on shared tree genera, separates from the two south-Indian clusters at a dissimilarity value of 0.88. Thus, these two regions on the Deccan Plate share only 12 % similarity in composition of dominant genera. Although no cluster analysis of dominant genera was attempted between Deccan MEM and Australasian CNVF, these two floras are unlikely to be as similar as the 12 % similarity that marks Sri Lankan and south Indian MEM. The Australian complex notophyll vine forest (CNVF) shares a few dominant genera with Sri Lanka MEM, such as *Acronychia, Aglaia, Elaeocarpus, Ficus, Litsea, Heritiera, Myristica, Syzygium* and *Toona*. Other dominant genera of Australia CNVFR are found at lower elevations and/or drier habitats in Sri Lanka: *Alstonia, Aleurites* (naturalized), *Melia, Polyalthia,* and *Terminalia*. Still others, such as *Beilschmiedia* and *Melicope* (*Euodia*) are more common at higher elevations in Sri Lanka (Ashton et al. 1997). Most of the dominant genera of CNVF are absent from India-Sri Lanka (see section above, "Lower Montane Evergreen Forest Types Recognized in this Study of South India and Sri Lanka"), being Queensland or Australasian endemics of the Proteaceae, Monimiaceae, Winteraceae and Rutaceae; as well as genera of the paleoendemic families such as Himantandraceae, Amborellaceae, and Eucryphiaceae.

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Dynamics of the Hawaiian Rainforest at Multiple Scales

Dieter Mueller-Dombois and James D. Jacobi

Abstract This paper is a short version of a recently published book *‘Ōhi’a Lehua Rainforest*, which resulted from studies of vegetation at multiple scales in space and time. The objective of this short version is not only to demonstrate some of these changes in scale, but also to show that different perspectives through scale changes were needed for synthesizing the subject matter into a coherent story. In other words, any vegetation study that aims at comprehensive explanations needs to view the subject matter from several different perspectives or scales. The five decade-long research on native Hawaiian rainforest is such a study. Following the introduction, this study is summarized under five subheadings:

- A rainforest born among volcanoes
- Turnover by auto-succession
- From rainforest to bog and stream formation
- Fragmentation into smaller units as islands age
- Conclusion: the rainforest on Windward O’ahu

Space and Time, the Two Scale Dimensions

To understand forest vegetation dynamics, which involves different temporal scales, it is necessary first to study the forest ecosystem at several spatial scales. If a rainforest is the study objective, as here, a forested landscape unit must be defined at a broad scale spanning many kilometers. This landscape unit must be exposed to a wet climate year-round. Then a checklist of trees, shrubs, ferns, and other plant life forms must be made. Concurrently with check-listing of plants, a number of sample stands (relevés) must be laid out and analyzed. These are

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at the scale of a few meters, perhaps the size of a house lot. A sufficient number of trees must be measured for diameter at breast height (DBH) and sub-sampled by height and recorded by species. Then all other plants should be listed, preferably in horizontal strata, such as trees taller than 5 m, shrubs and smaller trees 2–5 m high, all plants shorter than 2 m and forest-floor plants, including mosses that occupy decaying wood, soil and rocks. Thereafter, species quantities may be assigned using the Braun-Blanquet cover-abundance scale, or their cover may be measured by the point-frequency method (see Mueller-Dombois and Ellenberg 2002). The quantification method depends on the level of detail needed. To understand vegetation dynamics, the underlying soil profile must also be examined and soil samples collected for laboratory analyses of essential soil parameters. A further need is the establishment of permanent plots (sample stands or relevés) to be revisited periodically and monitored at certain intervals of time.

This sort of basic field study provided an initial understanding of the Hawaiian rainforest.

For assessing the long-term functioning of this community, we also had to study the rainforest at several dynamic scales. These will be summarized here under the following headings:

- A rainforest born among volcanoes
- Turnover by auto-succession
- From rainforest to bog and stream formation
- Fragmentation into smaller units as islands age
- Conclusion: the rainforest on Windward O’ahu

A Rainforest Born Among Volcanoes

The first focus is on the rainforest near the active Kilauea volcano on the Big Island Hawai’i (see location in Fig. 1). From here to Hilo and Mauna Loa, the native rainforest is fragmented periodically by new lava flows. Such a situation is shown on Photo 1.

A recent study by molecular methods (Percy et al. 2008) has shown that colonization of the Hawaiian Islands by *Metrosideros* had a very ancient beginning. The ancestral colonization apparently began about 5 million years ago, coincident with the emergence of the oldest high island Kaua’i (shown in Fig. 1 as 4.4–5.7 million years ago).

The developmental sequence of the Hawaiian rainforest is likely also very ancient and repeated in similar manner over millions of years. As a *Metrosideros* cohort grows, its trees grow taller but the branches remain short and remain deployed along the full length of the trunks. This early tree architecture allows much direct sunlight to reach the forest floor. The open, juvenile forest attracts heliophilic ferns, which become dominant in the undergrowth, replacing the lichen

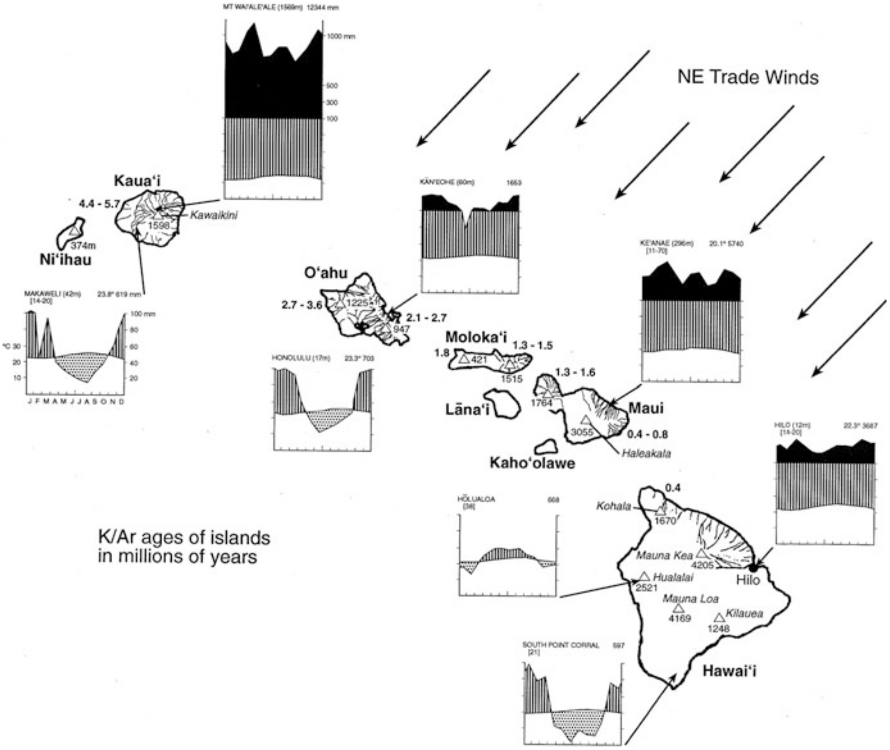


Fig. 1 Map of the main Hawaiian Islands indicating year-round wet climate on the windward northeast Trade Wind sides of the four high islands. The climate diagrams with *black* shadings show precipitation data in excess of 100 mm/month. These data indicate rainforest territory, but local field observations are required to find out if rainforest is actually present

cover. The most aggressive among these is *Dicranopteris linearis*, a stoloniferous mat former (Photo 2).

It takes about 200 years in the rainforest climate of Hawai'i for the forest born on new volcanic surfaces to become mature. Stand maturity is indicated by crown closure and the shedding of most lateral branches. Also, with that growth process, *Dicranoptris* ferns are displaced by shade-tolerant tree ferns (*Cibotium* spp.).

Metrosideros rainforest development on new volcanic surfaces in Hawai'i can be summarized as progressing in three stages, from (1) a *Stereocaulon* lichen-forest stage with young saplings, to (2) a *Dicranopteris* mat-forming fern stage under open juvenile forest, to (3) a *Cibotium* tree-fern stage under closed mature forest.

Thus, while the time scale for development of mature forest from barren lava flows in rainforest environments is about 200 years, the primary successional sequence, as here outlined, has evolved and likely been repeated as such over several millions of years.

Photo 1 Developing *Metrosideros polymorpha* cohort on the 1955 *Kamaile* lava flow, with a dense *Stereocaulon vulcani* lichen cover on basalt rock surfaces. Kipuka forest, an island of older surviving mature forest, is seen in background

Photo 2 A young, typically open *Metrosideros* forest with a dense fern undergrowth of mostly *Dicranopteris linearis*

Turnover by Auto-Succession

By measuring many sample stands throughout the Hawaiian rainforest on the windward slopes of Mauna Loa and Mauna Kea, we found that there were hardly any saplings of *Metrosideros polymorpha* in closed mature forests, because the saplings of this species are shade-intolerant. In addition to the dominant tree ferns, there were numerous native shrubs and smaller shade-tolerant tree species, such as *Cheirodendron trigynum*, *Myrsine lessertiana*, *Perrotetia sandwicensis*, *Coprosma rhyncarpa*, *C. ochracea*, and *Ilex anomala*, to name a few.

We considered the absence of sub-canopy *Metrosideros* saplings to represent a “sapling gap” under the mono-dominant *Metrosideros* canopy. Stand structure analyses in terms of size frequency showed that the population of canopy trees over 5 m high was distributed in the form of normal bell-shaped curves relative to their diameter distribution. This pattern is similar to that found in even-aged plantation stands.

Photo 3 A mature Hawaiian rainforest in an early stage of canopy dieback, near Mile 15 on Saddle Road, Big Island Hawai'i. Photo courtesy of Roger Baldwin, 1965

By synthesizing the structure-analysis results from many stand samples we came to the conclusion that the native Hawaiian rainforest is comprised of a mosaic of cohort stands. Our effort to measure so many tree stands (Mueller-Dombois et al. 1980) was necessary in order to try to understand the collapse or dieback of forest segments that happened on the windward side of Hawaii during the 1970s and into the early 1980s (Photo 3).

This dynamic behavior has now been recognized as "cohort senescence," a major form of predisposition to canopy dieback. Habitat constraints, such as changes in soil water regime and nutrient imbalances, may increase with advancing stand age to result in "premature senescence." It only requires a trigger factor to bring about synchronized collapse of a senescing cohort. In the absence of disease, a sapling wave is generated that coincides with the opening of the canopy (as shown in Fig. 2b).

Dieback is defined here as the loss of tree-crown foliage over a whole stand without any significant replacement of leaves or re-growth. Such dieback can be a rapid or long, drawn-out process, but it ends with death of the trees affected. The same phenomenon has also been called "forest decline". The difference is that forest decline may be recognized as resulting from disease or illness, whereas canopy dieback is recognized as a normal process in the life cycle of the canopy species.

Turnover by auto-succession is a common pattern in mono-dominant forests built from cohorts (more details in Mueller-Dombois et al. 2013). The time scale for full canopy recovery was found to be less than 30 years.

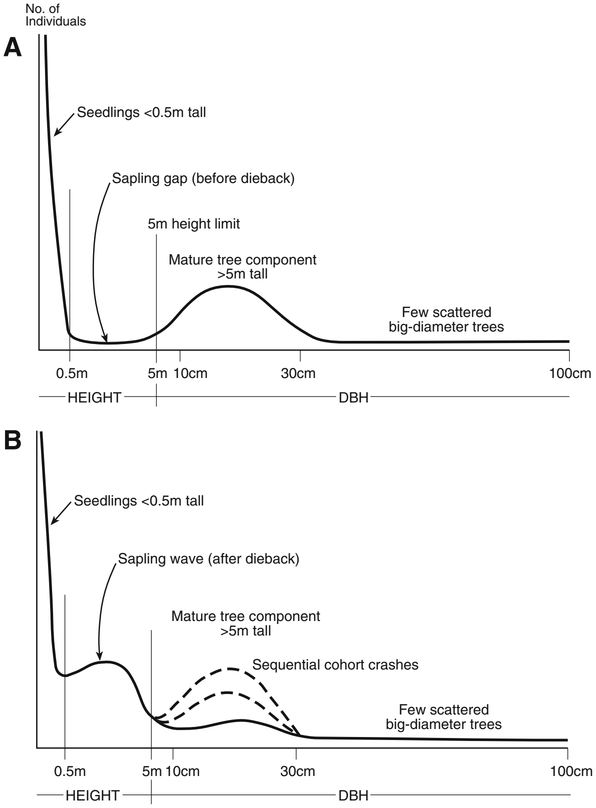


Fig. 2 Generalized population structure of *Metrosideros* stands: (**a**) before canopy dieback, with a sapling gap; and (**b**) after dieback, with a sapling wave. DBH = tree diameter at breast height (From Mueller-Dombois 1987:580)

From Rainforest to Bog and Stream Formation

Recovery after canopy collapse is a relatively short-term event that has been monitored at approximately 5-year intervals over a 25-year period in 25 permanent plots (Boehmer et al. 2013). This time scale is typical of "secondary succession."

The new forest stand that recovered from a sapling wave may last 2–4 centuries, depending on cohort lifespan. The phenomenon of collapse and recovery can be recognized in the pollen diagram shown in Fig. 3, extending over a time span of 10,000 years.

The pollen diagram shows about 2–3 depressions per 1000 years, approximating the time required for completing the life cycle of a *Metrosideros* cohort. The diagram shows clearly that the *Metrosideros* rainforest near the Moloka'i bog has persisted, with oscillations, over the past 10,000 years, i.e. since the retreat of the last ice age.

A still much longer time scale of *Metrosideros* rainforest existence is demonstrated in Fig. 4.

The checkmark-like symbols on each curve resemble the recurring canopy breakdown and recovery phases, as were shown in more detail in Fig. 2a, b.

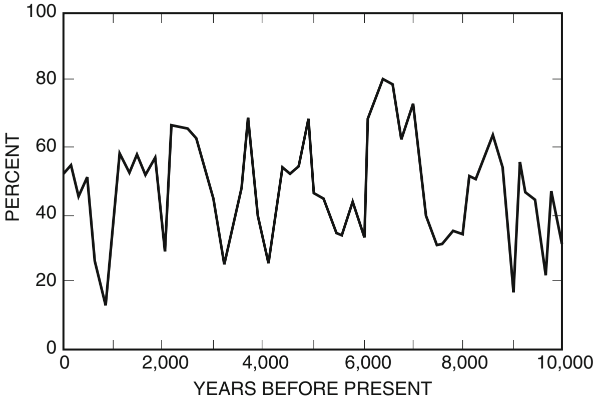


Fig. 3 The fluctuating abundance of *Metrosideros* pollen in a 325 cm-deep soil core in a Hawaiian rainforest bog on Moloka'i (after Selling 1948). The time axis is based on carbon-dating the core base. (Reproduced with permission from Annual Review of Ecology & Systematics 1986:233)

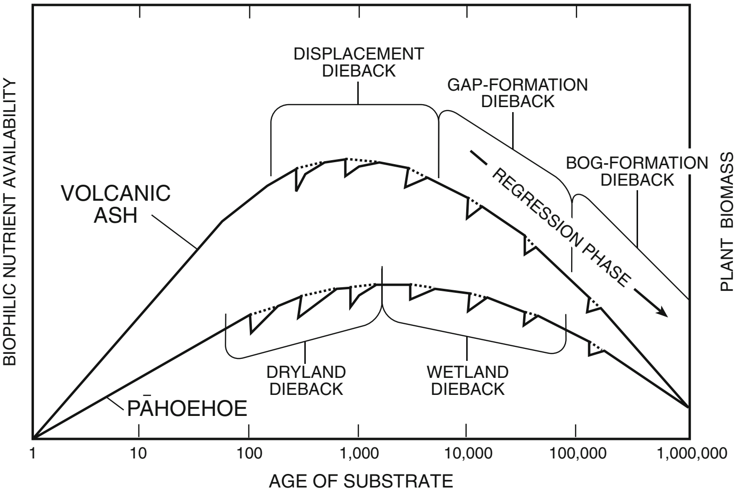


Fig. 4 Long-term primary succession on the two prevailing substrates of Hawai'i, with five dieback types superimposed. (Reproduced with permission from Annual Review of Ecology & Systematics 1986:234)

The breakdown and recovery phases relate to the oscillations in *Metrosideros* pollen abundance (2–3 per 1000 years), as indicated on the bog-soil core of Fig. 3.

The types of dieback identified during this study relate to the substrate ages as they change in biophilic nutrient availability with weathering and soil formation over time. The "Dryland" and "Wetland" diebacks were found mostly on shallow soils, so-called histosols, which are pāhoehoe rock substrates overlain with shallow mats of decomposing organic matter. Both were also identified as "*replacement dieback types*" on account of re-invasion with sapling cohorts of the same canopy species. The term "Displacement dieback" relates to the delayed *Metrosideros* sapling recovery after canopy dieback. This type of dieback was restricted mostly to the nutritional climax on pyroclastic soils from volcanic ash to a'ā lava flows. Here, treeferns (*Cibotium* spp.) formed a vigorous sub-canopy layer, densely shading and thereby preventing re-development of sapling generation. More recently, displacement dieback has expanded due to the invasion of aggressive alien tree species, such as strawberry guava (*Psidium cattleianum*).

In the regression phase of primary succession we encountered two more types of dieback, "Gap-formation dieback" and "Bog-formation dieback." Nutrient impediments such as loss of cations and immobilization of phosphorus resulted in less vigorous recovery by *Metrosideros*. This was designated structurally as "*stand-reduction dieback*". Trees in the follow-up generation never grew quite as tall as in the previous generation. Gap-formation dieback also resulted in more uncertain outcomes, occasionally developing into fern savannas. Bog-formation dieback was only recognized originally as a trend in soil aging to hydromorphy with iron toxicity (Lyon 1919). However, bog-formation dieback relates not only to this type of soil aging but more broadly to geomorphologic aging. It involves a change in the whole landscape from forest to bog ecosystem. *Metrosideros* still survives in bogs, but the trees become dwarfed. This is an interesting evolutionary adaptation that has as yet to be investigated further (Photo 4).

Bog formation is often associated with slow lateral drainage, the beginning of stream formation. Along the drainage pathway one finds, initially, complete die-off of *Metrosideros* trees. Where the stream is forming a regular pathway by cutting more deeply into the soil substrate, *Metrosideros* becomes reestablished on the slope. This demonstrates an unexpected tenacity of this colonizer species, a common pattern also observed by Lyon (1919).

Not all rainforest substrates end in bogs, as Fig. 4 may indicate. Studies along the high island chain from the young island Hawai'i to the oldest high island Kaua'i have shown that sites at 1200 m along an isohyet of 2500 mm of mean annual rainfall end merely in short-statured *Metrosideros* forests (Vitousek 2004). Sites at the same elevation along 4000 mm isohyets end in *Metrosideros* shrub bogs (Kitayama and Mueller-Dombois 1995).

Photo 4 Dwarf *Metrosideros* growing in Pepe'ōpae bog in an area of upland rainforest on Moloka'i Island. The bog profile diagram (Fig. 3) with the oscillating abundance of *Metrosideros* pollen came from this location

Fragmentation into Smaller Units as Islands Age

When we proceed from Hawai’i and Maui, with their great shield volcanoes, we can see windward O’ahu as a fragmented shield volcano with very different landscapes (Fig. 5).

The long duration of precipitation typical of the rainforest climate, in combination with faulting of the original basaltic shields, shows its effect in the three profiles drawn from west to east over the Ko’olau mountain range.

On windward O’ahu the large area of rainforest that once stretched across windward Mauna Loa and Mauna Kea has disappeared. Instead, with geologic aging, the rainforests have become fragmented into smaller units related to topography (Photo 5).

The summit of the former Ko’olau volcano is projected to have reached only about 1200 m above sea level, according to Fig. 5. That would put the Ko’olau summit into the middle of the rainforest belt on Mauna Kea and at the same height as the currently active Kilauea volcano.

Thus, when the Ko’olau summit became fragmented into its present geomorphologic state, its summit retained native rainforest. That is still very

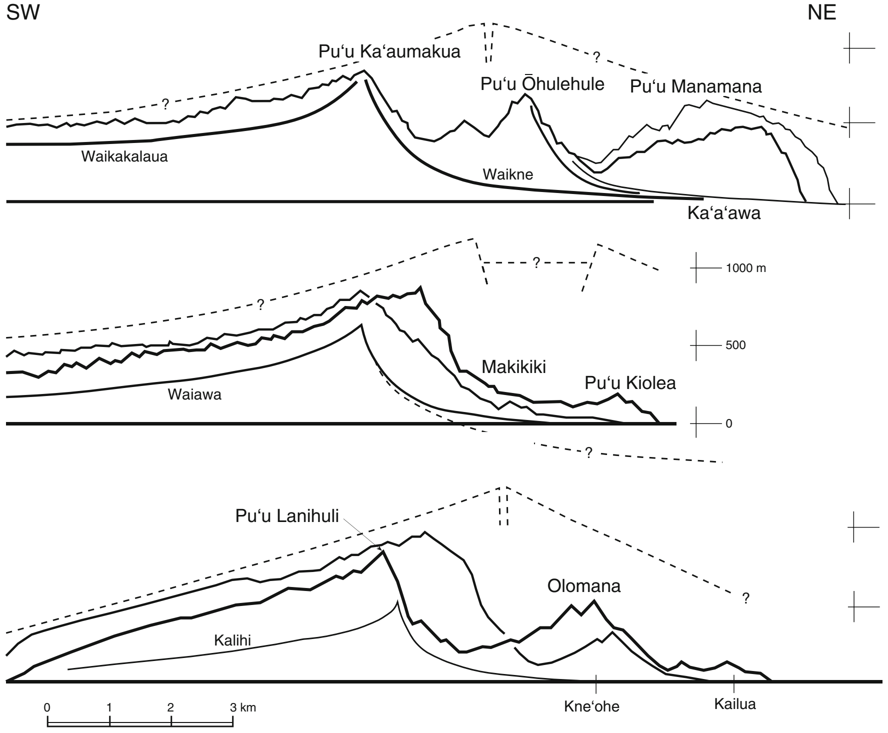


Fig. 5 Three profiles through east O’ahu showing the geomorphic change over 2 million years of erosion of the Ko’olau shield volcano (after Wirthmann and Hueser 1987)

Photo 5 View of the windward slope of the huge Mauna Kea shield volcano on a cloudless day. The summit, at 4205 m (13,796 ft), reaches far above the inversion zone at 1900 m, which marks the upper limit of the *dark green* belt, the *Metrosideros*-dominated rainforest

much in evidence today, in spite of its fragmentation. This demonstrates the native resilience of that forest type—it kept pace with the aging process of the volcanic islands.

The breakdown of the Ko’olau volcanic shield resulted in smaller ecosystem units. Typical are the windward valleys with freshwater streams which, known as Ahupua’a, formed the traditional resource system of the indigenous Hawaiian population.

An example of a windward rainforest valley is the Kahana Ahupua’a (Photo 6).

A centrally located transect from the back of the valley to the coast shows the different resource zones, which were clearly distinguished and named by the Hawaiians (Fig. 6).

Native *Metrosideros* rainforest is confined to the back of the valley known as Wao kele (unit B). Another ecosystem dominated by native trees is Wao koa (unit C). Units D & E contain mostly human-introduced and modified vegetation. This is not surprising considering the strong human influence in this valley since the arrival of the first Hawaiian colonizers, from 300 AD (Allen 1997; Kirch 2000). Before European contact, Kahana valley supported an indigenous Hawaiian population estimated at 720–1000 (Stauffer 1990). During World War II, Kahana valley served as a military training area.

An ecological study of Kahana valley conducted in the 1970s revealed 13 vegetation types. These are outlined from aerial photographs with ground surveys and relevés. They are projected here as a fine-scale vegetation map (Fig. 7).

Details of the vegetation units are discussed in Mueller-Dombois and Wirawan (2005).

Photo 6 Kahana Valley as seen from a low-flying aircraft, with a restored fishpond at *lower left*, the Kahana estuary next to it, the coastal ironwood (*Casuarina equisetifolia*) forest, the lush central marsh, land scars on frontal slopes, forested bottomlands and back slopes. Pu'u Ka'aumakua (at 880 m) marks the back range behind Pu'u o Kila (at 467 m) on the *left* of the photo. Photo courtesy of Douglas Peebles. *Metrosideros polymorpha* is still the dominant forest tree in the ridge and back-slope system of the valley, while the native *Pandanus tectorius* and *Acacia koa* are the dominating trees in the middle part of the valley (see Fig. 6)

Conclusion: The Rainforest on Windward O'ahu

On O'ahu Island, native *Metrosideros polymorpha* rainforest still survives as low-stature or "shrub" forest on ridges and upper slopes, albeit with different varieties of the parent species. A second species, *M. rugosa*, grows as low, gnarled trees or shrubs on the windiest ridge sites. It has small, thick leaves with revolute margins and reddish brown hairs underneath. On wet slopes, a small tree variety *M. polymorpha* var. *newellii*, with glabrous leaves, is found along mountain streams. Upper slopes with stony, shallow soils are the sites where *Metrosideros* species and varieties display their native resilience as the original tree colonizers on volcanic substrates. Here, however, the introduced Strawberry guava (*Psidium cattleianum*) now threatens to become a serious competitor.

The lower windward slopes of windward O'ahu are now mostly dominated by exotic trees, such as the Octopus tree (*Shefflera actinophylla*), the Java plum (*Syzygium cumini*), and the Charcoal tree (*Trema orientalis*), among others. The gentler lower slopes are also planted with Norfolk Island pine (*Araucaria heterophylla*), swamp mahogany (*Eucalyptus robusta*), and other *Eucalyptus* species, as well as with Paperbark trees (*Melaleuca quinquenervia*). One of the first exotic trees brought by the Hawaiians, which thereafter became naturalized, is the Kukui tree (*Aleurites mollucana*). This tree took hold of the gulches and today

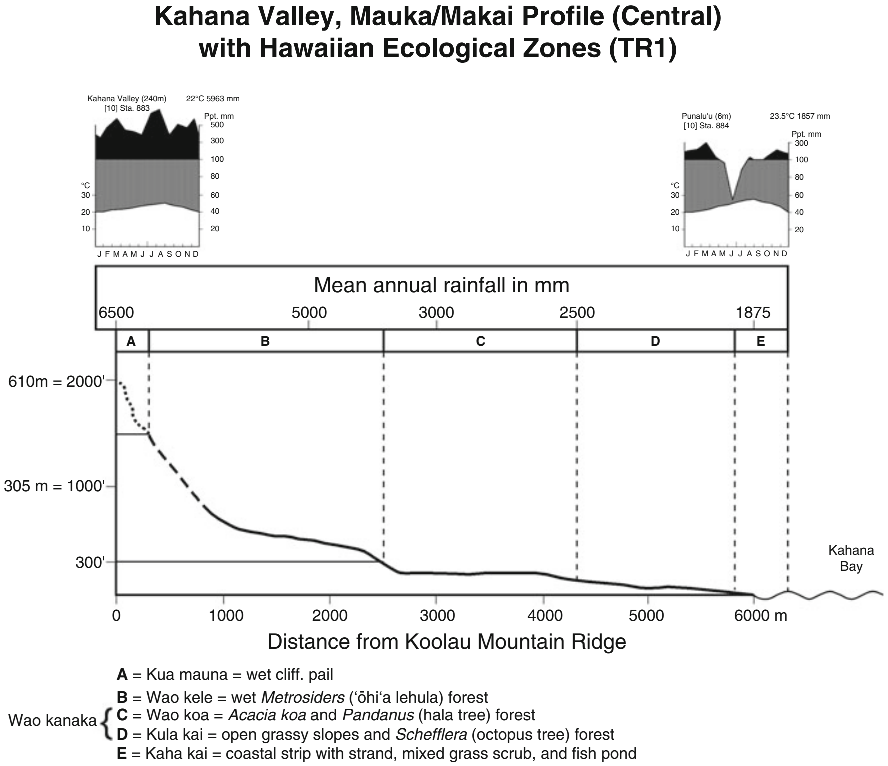
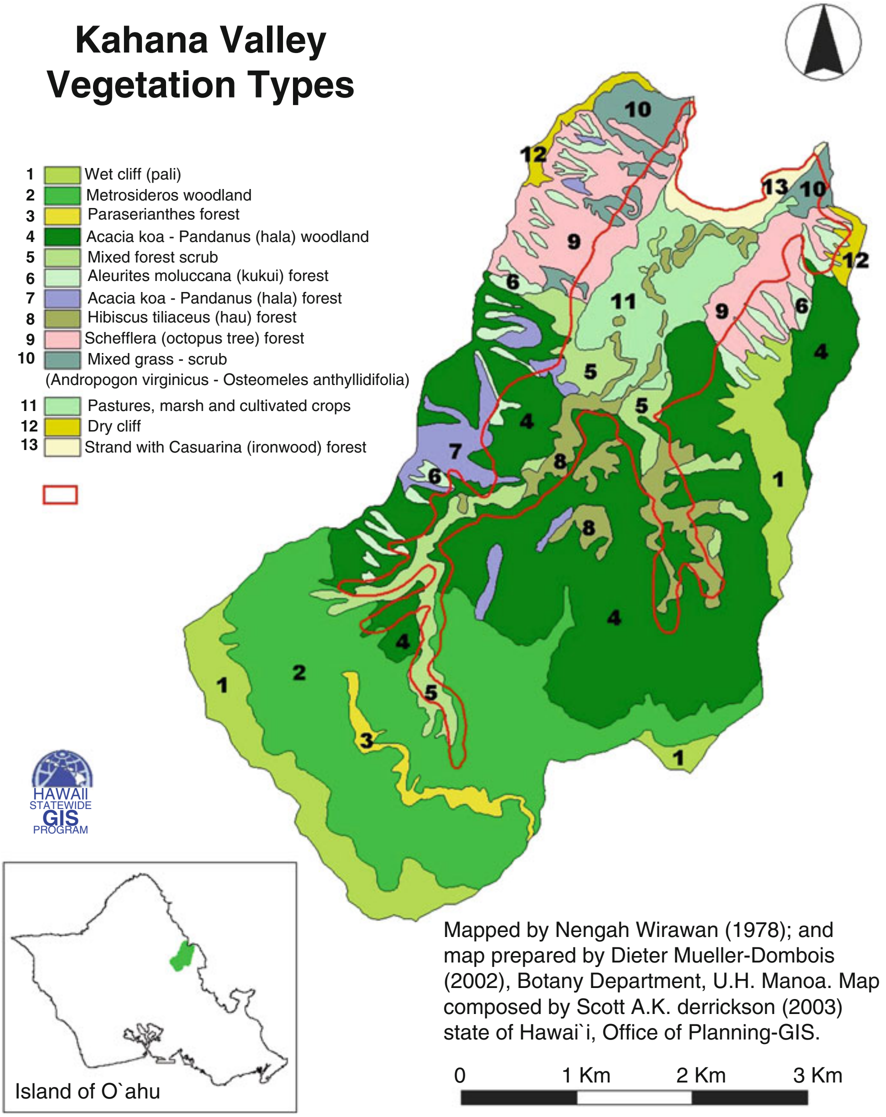


Fig. 6 Topograhic profile from mountain to sea (mauka-makai) in central Kahana Valley, a rainforest valley on the windward side of O'ahu. The rainforest climate is documented here by two Walter-type climate diagrams. They show a steep gradient of mean annual rainfall from 1.9 to 5.9 m over the short distance of 6 km, from the coast to the back of the valley. Along this profile one can distinguish five Hawaiian ecological zones. (From Mueller-Dombois, D. and N. Wirawan 2005:305)

forms narrow, vertically extending stands on the steep valley slopes, easily spotted by their metallic-green foliage. The Hawaiians also brought the Breadfruit tree (*Artocarpus altilis*), now sporadically present in the rainforests of windward O'ahu, including Kahana valley. Other fruit trees, such as Mango (*Mangifera indica*), Mountain apple (*Syzygium malaccense*), Java plum (*S. cumini*) and Guava (*Psidium guava* and *P. cattleianum*), were introduced in the 1800s as replacement watershed forest in rainforest environments. Mid-slopes still contain the second-most important native tree, Koa (*Acacia koa*), which is often found as a sporadic companion among other canopy trees. In Kahana valley the original Koa forest grows mixed also with the native Hala tree (*Pandanus tectorius*). Here on the gentler, colluvial lower-slope substrates, the slowly decomposing foliage of the Hala tree limits the regeneration of Koa, which is in the process of declining from its original dominance.



Kahana Valley Vegetation Types

Mapped by Nengah Wirawan (1978); and map prepared by Dieter Mueller-Dombois (2002), Botany Department, U.H. Manoa. Map composed by Scott A.K. derrickson (2003) state of Hawai`i, Office of Planning-GIS.

Fig. 7 Vegetation map of Kahana Valley 2005

Now often prevailing on lower slopes is the aggressive, invasive alien Albizia tree (*Albizia moluccana* = *Paraserianthes falcataria,* now renamed *Falcataria moluccana*), which grows fast and tall. Originally hailed as a good tree for watershed protection, it is now seen as a curse because of its great potential height overtopping other trees, its poor soil-binding capacity, its high breakability and the danger that it will crash down in stormy weather.

Today there is much concern about preventing mistakes such as the introduction of damaging species, including disease organisms. At the same time much thought is given to the restoration of ecosystems. A current question is: What is a desirable state of restoration under the given circumstances, which include climate change? Research in vegetation ecology can help elucidate this question. To do this correctly, the vegetation needs to be explored at different scales in space and time. The example presented here can claim to be such a study.

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On the Steppes and Shrub Thickets in Onon Dahuria

Irina Safronova and Ekaterina Golovina

Abstract Onon Dahuria is a mountain area with ranges of 1000–1700 (rarely to 2500) meters oriented mainly from southwest to northeast. The ranges are separated by wide inter-mountain depressions with rolling hills and plains. Two vegetation belts are differentiated in these mountains, namely taiga (smaller area) and forest-steppe (larger, reaching up to 1000–1500 m). In the forest-steppe belt, forests dominated by *Larix dahurica, Pinus sylvestris* and *Betula platyphylla* grow mainly on the much more humid northern slopes. Steppes are confined to low mountain massifs and the lower parts of mid-height ranges, where they occupy southern, southwestern and southeastern slopes, and sometimes north slopes in the southern part of the region. A specific feature of the forest-steppe belt of Onon Dahuria is the presence of plant communities with many shrubs, i.e. shrub steppes and shrub thickets.

General Characteristics of Natural Environments in the Region

Dahuria is part of southern Siberia, just north of Mongolia, and Onon Dahuria is a mountainous part, near the Onon River. The mountain ranges run mainly from southwest to northeast, reach 1000–1700 m above sea level (rarely 2000–2500 m), and are separated by wide inter-mountain depressions with rolling hills and plains. As altitudinal belts, one can distinguish taiga and forest-steppe. Forest-steppe covers the larger area and reaches up to 1000–1500 m (see Figs. 1 and 2).

The climate of Onon Dahuria is ultra-continental, characterized by an extreme contrast between the cold and warm seasons. The mean air temperature is −26 °C in January, the coldest month, 17.5 °C in July, the warmest month. The mean annual temperature is negative, so permafrost occurs in some places. Air and soil temperature both fluctuate widely over the course of a day, and average annual precipitation is only 350 mm. The specific peculiarity of the Dahurian climate is the low air

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Fig. 1 The forest-steppe belt in the Onon Dahuria. Irina Safronova's photo

Fig. 2 The forest-steppe belt in the Onon Dahuria. Irina Safronova's photo

humidity, especially in spring and early summer (35 %, with minima as low as 5–10 %). Warmth and moisture also depend strongly on slope steepness and aspect (exposition).

The widespread occurrence of permafrost has led to the formation of different types of soil (Ufimtseva 1967). Steppe soils in Dahuria are frozen deeply (up to 3–3.5 m), due to their thin snow cover (Nogina 1964).

In the forest-steppe belt of Onon Dahuria, forests dominated by *Larix dahurica*,[1] *Pinus sylvestris* and *Betula platyphylla* grow mainly on the much more humid northern slopes, much less often on eastern or western and even southern slopes. Steppes are confined to low mountain massifs and the lower parts of mid-height ranges, where they occupy southern, southwestern and southeastern slopes, and

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[1] Plant names are given by S. K. Cherepanov (1995).

Fig. 3 Steppe communities of the forest-steppe belt in the Onon Dahuria. Irina Safronova's photo

Fig. 4 The forest-steppe belt in the Onon Dahuria. Communities of *Pulsatilla tenuiloba* and *Arctogeron gramineum* are in the foreground. Irina Safronova's photo

sometimes north slopes in the southern part of the region (see Figs. 3 and 4). Communities with shrubs, such as *Armeniaca sibirica*, *Spiraea aquilegifolia* and others, are also characteristic elements of the landscape (Dulepova 1993; Safronova and Golovina 2013).

Steppe Plant Communities

Forb and Grass-Forbs Steppes

On slopes of various steepness, the lower slopes and small flat-bottom valleys within the slopes have widespread forbs steppes with abundant *Adenophora gmelinii, Allium tenuissimum, Bupleurum scorzonerifolium, Eremogone capillaris,* *Galium verum, Gypsophila dahurica, Filifolium sibiricum, Lespedeza hedisaroides, Lilium pumilum, Polygonum angustifolium, Potentilla acervata, P. tanacetifolia, Pulsatilla turczaninovii, Rhaponticum uniflorum, Saussurea salicifolia, Schizonepeta multifida, Scutellaria baicalensis, Stellera chamaejasme, Thymus dahuricus*, *Youngia tenuifolia* and some others. Their projective cover reaches 30–40 % out of the overall projective cover of 50–65 %. The number of species per relevé is 25–40.

As a rule, grasses compose the herb layer, mainly *Koeleria cristata* and *Poa botryoides*—in places *Stipa baicalensis* and *S. sibirica*, sometimes also *Carex pediformis*.

Sedge-forb communities, with *Pulsatilla turczaninovii, Stellera chamaejasme, Artemisia commutata, Carex pediformis*, etc., form at forest edges and in small flat-bottom valleys on the gentle slopes. These include not only steppe species, but also more mesophilous species such as *Artemisia tanacetifolia, A. sericea, Campanula glomerata, Dendranthemum zavadskii, Polygonatum odoratum*, *Pulsatilla patens, Sanguisorba officinalis*, *Trifolium lupinaster* and *Vicia unijuga*. These species are typical for meadows and forests of the forest-steppe belt and lower part of the taiga belt.

Petrophytic steppes are also widespread, and forbs communities with dominance of *Filifolium sibiricum* are common (Golovina 2009). These are most characteristic of 20–40° slopes with rocky soils and sporadic rock outcrops. Less often they occur on upper slopes, on flat tops and on lower slopes.

The projective cover of *Filifolium sibiricum* is 10–20 %, whereas the overall projective cover is 25–40 %. Besides *Filifolium sibiricum* in the herb layer, there are also such species as *Bupleurum scorzonerifolium, Galium verum, Potentilla tanacetifolia*, *Pulsatilla turczaninovii, Schizonepeta multifida* and *Scutellaria baicalensis*. There are few grasses, only *Stipa baicalensis*, *S. sibirica*, *Poa botryoides* and *Koeleria cristata* (see Figs. 5 and 6).

Forbs are not so numerous on the quite rocky soils of upper slopes and hilltops, and a significant role belongs to *Festuca lenensis* and *Artemisia monostachya*. The amount of forbs and grasses increases on gentle slopes with less rocky soils and on the lower parts of slopes.

Wormwood communities (*Artemisia monostachya*) develop on upper slopes and on tops with rocky soils (see Fig. 7). The projective cover of *Artemisia monostachya* is 10–15 %, with overall projective cover of 30–40 %. The wormwood communities are characterized by the presence of such species as *Arctogeron gramineum, Bupleurum bicaule, Filifolium sibiricum*, *Phlojodicarpus sibirica, Pulsatilla tenuiloba, Eremogone capillaris* and the dwarf semi-shrub *Thymus dahuricus*; the grasses *Festuca lenensis* and *Poa botryoides* are common.

Besides the widespread steppe coenoses mentioned above, there are also rare-plant communities dominated by obligate petrophyte species *Chamaerhodos trifida*, *Orostachys spinosa* and *Arctogeron gramineum* (see Figs. 8 and 9). These species are highly tolerant against humidity and temperature fluctuations, but as weak competitors they increase their abundance only under conditions least favorable for most other plants—on dry rocky substrates, where soil has hardly

Fig. 5 Fether-grass-forb (*Filifolium sibiricum*, *Potentilla acervata*, *P. tanacetifolia*, *Stipa baicalensis, Stipa sibirica*) steppes. Irina Safronova's photo

Fig. 6 Grass-forb (*Filifolium sibiricum*, *Arctogeron gramineum*, *Orostachys spinosa*, *Festuca lenensis*, *Koeleria cristata*) steppes on stony soil. Irina Safronova's photo

developed at all. So, communities of *Chamaerhodos trifida*, *Orostachys spinosa* and *Arctogeron gramineum* form on the highly insolated upper slopes and hilltops with skeletal soil, which consists of a very thin (1–5 cm) layer of pebbly silt. It seems that these communities represent an early stage of the steppe vegetation development on the windswept rock.

Herb stands are sparse, with overall projective cover of 40–50 %. In the herb layer one can distinguish two sublayers. *Chamaerhodos trifida*, *Orostachys spinosa* and *Arctogeron gramineum* are concentrated in the surface sublayer about 5–7 cm high. Besides dominants, there are also other low petrophytes: *Eremogone capillaris*, *Potentilla leucophylla*, *Patrinia sibirica*, *Potentilla sergievskajae*, *Thymus dahuricus* and *Festuca litvinovii*. The projective cover of most of them is not more than 1–2 %. These communities also include some slightly taller plants: *Aconogonon angustifolium*, *Pulsatilla tenuiloba*, *Silene jenesseensis*, *Stellera*

Fig. 7 Wormwood communities (*Artemisia monostachya*) on upper slope. Irina Safronova's photo

Fig. 8 The community of *Orostachys spinosa*. Ekaterina Golovina's photo

chamaejasme and some others. Altogether they form a very sparse first herb sublayer about 15–20 cm high, where only petrophyte *Pulsatilla tenuiloba* is significant, with projective cover of 5–10 %. Usually few low individuals of the shrub *Pentaphylloides parvifolia* are also present and characteristic.

The communities of *Orostachys spinosa* and *Arctogeron gramineum* can be found throughout the forest-steppe area of Onon Dahuria. Coenoses that also contain *Chamaerhodos trifida* as at least a co-dominant occur only in the most arid eastern part of the region, in the basin of the Aga river (a left tributary of the Onon River) and in the Onon-Aga interfluve. It seems that these communities are determined by climatic conditions: the area of mass distribution of *Chamaerhodos trifida* in the Eastern Transbaikal region is confined to its most arid, warmest eastern part only. Besides the Onon-Aga interfluve, there is also a territory lying east of the investigated area (Siberian Flora 1988). Thus, in Onon Dahuria, *Chamaerhodos trifida* communities are near the western boundary of their range.

Fig. 9 The community of *Chamaerhodos trifida* and *Orostachys spinosa*. Ekaterina Golovina's photo

Grass Steppes

Grass steppes are presented by *Festuca lenensis* and feather-grass (*Stipa baicalensis, Stipa sibirica*) communities. Steppes of *Festuca lenensis* seem attracted to sites with rocky soil and rock outcrops (see Fig. 10). The projective cover of *F. lenensis* is 8–12 %, with a general projective cover of 20–30 %. Frequently *Artemisia monostachya* is co-dominant here, and petrophyte species are characteristic, including *Arctogeron gramineum, Eremogone capillaris*, *Potentilla leucophylla, Pulsatilla tenuiloba* and *Saxifraga spinulosa*.

Feather-grass (*Stipa baicalensis*) steppes (see Fig. 11), together with steppes of *Stipa sibirica*-*Stipa baicalensis* and *Stipa baicalensis*-*Stipa sibirica*, occur on gentle slopes, in depressions on slopes, and on the lower parts of slopes, on less rocky soils. The projective cover of the grasses is 20–35 %, with a general projective cover of 50–70 %. As a rule, forbs are significant, such as *Adenophora stenanthina, A. gmelinii, Bupleurum scorzonerifolium, Filifolium sibiricum, Galium verum, Gypsophila dahurica, Lespedeza hedisaroides* and *Thalictrum appendiculatum*. *Carex pediformis* also occurs often.

On the lower parts of slopes and partly on the bottoms of folds, there are relatively large areas of all-aged deposits with plant communities of *Artemisia tanacetifolia* and of *Leymus chinensis*. Coenoses of *Artemisia frigida* occur on slope areas that are subjected most to grazing by livestock (Safronova 2005) (see Fig. 12).

Fig. 10 Steppes of *Festuca lenensis* on the upper slope with the stony soil. Irina Safronova's photo

Fig. 11 Feather-grass (*Stipa baicalensis*) steppes. Irina Safronova's photo

Fig. 12 Overgrazing on the bottom of small valley. Irina Safronova's photo

Shrub Steppes

A specific feature of the forest-steppe belt of Onon Dahuria is the presence of communities with shrubs: shrub steppes and shrub thickets (Safronova 2008; Belikovich et al. 2009). Shrub steppes are characterized by a more or less even scattering of shrubs across the terrain, whereas shrub thickets are characterized by high density of shrubs (see Fig. 13).

Five shrub species participate in shrub steppes of the region: *Armeniaca sibirica, Pentaphylloides parvifolia*, *Spiraea aquilegifolia, S. pubescens* and *Ulmus macrocarpa*. Their projective cover is 5–15 %. The most common species is *Armeniaca sibirica*, which occurs in almost all of the shrub-steppe communities (see Fig. 14).

These shrub steppes occur mainly on upper slopes exposed to the south, southeast or southwest, with primitive rocky-scree soils. These shrub steppes are physiognomically indistinct in the landscapes, due to the relative short stature of the shrubs (60–80 cm on average).

The shrub steppes are diverse: the grass-forb type predominates, with forb-grass and grass-forb-wormwood types found much less often. About 80 species of vascular plants have been recorded in the shrub steppes. The general objective cover is 50–60 %, in places up to 70 %. The cover of the shrubs is 5–15 %, with herb cover of 30–40 %.

The bunch grasses are easily distinguished, covering from 10–20 % to 40–50 %. In all coenoses the notable role belongs to *Koeleria cristata*, usually together with *Stipa sibirica* and rarely with *Festuca lenensis*. Sometimes communities occur with *Stipa baicalensis* as the dominant. Characteristic but less abundant species are such grasses as *Cleistogenes kitagawae* and *Poa botryoides*; very rare are *Cleistogenes squarrosa* and *Festuca sibirica*. In shrub steppes there is always some species of wormwood, often notably *Artemisia monostachya*.

Fig. 13 Shrub steppes (in the foreground) and shrub thickets (in the background). Irina Safronova's photo

Fig. 14 Forb-fether-grass (*Stipa baicalensis*, *S. sibirica, Filifolium sibiricum*, *Lespedeza juncea*) steppe with *Armeniaca sibirica*. Irina Safronova's photo

Forb-shrub steppe communities are also characteristic, in which shrubs and forbs have almost equal projective cover. The general projective cover changes from 40 to 55 %, and the abundance of shrubs from 20 to 30 %. Usually one or another species prevails in the shrub layer of these communities, but locally there may be coenoses with co-dominance by two or three shrub species. Such forbs as *Galium verum*, *Lespedeza dahurica, Patrinia rupestris*, *Potentilla tanacetifolia*, and *Saussurea salicifolia* are common.

Shrub Thickets

Shrub thickets are dominated by the same five shrubs (*Armeniaca sibirica*, *Spiraea pubescens, S. aquilegifolia, Pentaphylloides parvifolia* and *Ulmus macrocarpa*). These are restricted to broad gullies, depressions on slopes, and also to rather rocky parts of slopes with rock outcrops, i.e. to sites that are more moist than those occupied by steppes (see Fig. 15). Shrub thickets are 60–120 cm tall, their coenoses include more than 70 species, and their projective cover is generally about 90 %. In the shrub layer of these communities, four species play almost equal roles, namely *Armeniaca sibirica*, *Spiraea pubescens, S. aquilegifolia* and *Ulmus macrocarpa*. Sometimes a fifth shrub, *Pentaphylloides parvifolia*, plays a smaller part in the composition of these coenoses. Coenoses with co-dominance by two or three shrub species occur locally.

In the shrub thickets, there is a distinct layer constituted by the wormwood semi-shrub *Artemisia gmelinii*. Its height is 40–50 cm and projective cover 5–20 %.

Under the shrubs, in the herbaceous layer, there are more than 50 species. They are not abundant, though, and have small projective cover (10 %). Grasses are not important, neither in abundance (projective cover 5–10 % or less) nor in species

Fig. 15 Shrub communities on the steep stony slopes. Irina Safronova's photo

diversity. *Stipa sibirica* occurs in all communities, and *Koeleria cristata, Cleistogenes kitagawa* and *Agropyron cristatum* show high constancy. *Carex pediformis* is always present in small abundance.

Conclusion

Steppes plant communities in the forest-steppe belt of Onon Dahuria are very specific. There is a huge role for communities with quite variable forb composition. Peculiar features of the vegetation cover are both shrub-forb and forb-shrub steppes and shrub thickets.

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The Vegetation Series of Italy and Applications in Biodiversity Conservation

Carlo Blasi

Abstract The *Series of the Vegetation of Italy* represents the synthesis of a national project that produced the first detailed document on the potential heterogeneity of Italian vegetation. The map and regional monographs of the *Series of the Vegetation of Italy* are of fundamental importance for understanding the natural capital of the entire country and are also useful for understanding and assessing environmental heterogeneity. This information represents the current state of knowledge on the Italian vegetation, in terms of diversity and spatial distribution.

This is an extraordinary collection of useful data in different areas of interest, such as: taxonomy, syntaxonomy, and syndynamics; analysis and monitoring of biodiversity for environmental planning and management; analysis of gaps in protected areas; definition and assessment of ecological networks and ecoregions; and ecological analysis of the landscape.

Currently this *Map* represents the essential reference for the construction of the Map of Ecosystems of Italy and of the Synthetic Map of the potential vegetation, both at a scale of 1:100,000.

Consistently with the adopted scale, the *Map* describes territorial areas (environmental units) characterized by the same type of vegetation series and by the same potential natural vegetation, defined as "*the vegetation a given site can host under the current climatic and pedological conditions, in absence of any disturbance*" [Tüxen (Angewandte Pflanzensoziol 13:5–42, 1956)]. Therefore, the *Map* highlights the potential heterogeneity of the Italian vegetation, and the monograph at regional scale analyzes the actual vegetation, describing the individual stages of each vegetation series.

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Introduction

In 1998 the Italian Ministry for the Environment decided to update and assess systematically all the natural and environmental data available for Italy. Prof. Carlo Blasi, director of the Department of Environmental Biology at the Sapienza University of Rome, was asked to be the scientific co-ordinator of this programme. The aim of this programme, which involved hundreds of researchers from many Italian universities, was the "Complete overview of the basic Naturalistic Knowledge in Italy". Bearing in mind the primary objective of the conservation of biodiversity, for the very first time in Italy, the team attempted to summarise all the data available on the climate, flora, vegetation, fauna, landscape and land use, with particular attention to coastal areas.

One of the most noteworthy outcomes of this project was the Map of the Vegetation Series of Italy, at a scale of 1:250,000, accompanied by a monograph for each region. This summary is of fundamental importance, not only for the information it provides on the vegetation heritage of the whole country, but also for the definition and mapping of its environmental heterogeneity, achieved by integrating phytosociology (synphytosociology) with ecological land classification. Indeed, a paper on the hierarchical classification of the Italian territory published in 2000 (Blasi et al. 2000) was a highly significant event in the development of landscape ecology that has led recently to the mapping of the ecoregions of Italy.

A first draft of the map was submitted to the Ministry in 2005. Revision and updating of the project continued until 2010, when the volume "The Vegetation of Italy", accompanied by the Map of the Vegetation Series of Italy, was published (Blasi et al. 2004; Blasi 2010).

This map, which accompanies the volume on the vegetation of each administrative region, consists of three sheets printed at a scale of 1:500,000; the map is based, though, on mapping scales ranging from 1:50,000 to 1:100,000.

The creation of the map was overseen by a scientific committee composed of Carlo Blasi (co-ordinator), Livio Poldini, Edoardo Biondi, Giovanni Sburlino and Roberto Venanzoni; they were in turn supported by three young researchers, Leonardo Rosati, Daniela Gigante and Goffredo Filibeck. Scientific supervisors, who were selected in each region, were asked to invite a total of 68 expert phytosociologists to take part. Besides representing the highest level of vegetation knowledge in Italy, this team of experts served as a means of validating the project at the national level. The project itself contains an extraordinary wealth of data that are indispensable for updating knowledge of floristic and vegetation biodiversity, for land planning and biodiversity assessment and monitoring, as well as for defining and evaluating connectivity and assessing the structural and functional topology of the ecological networks, particularly the land network. The maps and regional monographs combined thus provide an overview of the current state of knowledge of Italian vegetation in terms of diversity and spatial distribution.

Historical Framework and Methodology

The application of phytosociology to the analysis and spatial distribution of vegetation in Italy, in the 1940s, led to the publication of a local-scale physiognomic map (Sappa and Chiarrer 1949). The first phytosociological map was published by Giacomini in 1954, followed in 1955 by Giacomini and Pignatti's vegetation map of the Spluga region.

The whole of Italy was mapped at broader scales (<1:1,000,000) by the following authors:

Fiori A. (1908): Botanical map of Italy. (1:5,000,000);
Fiori A. (1936): Map of plant formations (1:2,500,000);
Beguinot A. (1933): Map of the vegetation areas in Italy (1:5,000,000);
Giacomini V. and Fenaroli L (1958): Vegetation map of Italy (1:6,000,000);
Giacomini V. (1973): Forest landscape map of Italy (1:250,000);
Tomaselli (1973): Forest vegetation map of Italy (1:2,000,000); and
Fenaroli L. (1970): Map of actual vegetation (1:1,000,000).

More recently, Pedrotti (1992), with the collaboration of several local experts, published a Map of the Actual Vegetation of Italy (1:1,000,000), which includes 54 physiognomic vegetation types.

The vegetation series analysed in the volume co-ordinated by Blasi describe both the plant community that constitutes the mature stage of each unit mapped (Härdtle 1995; Biondi and Blasi 2004a, b) and the coenoses that replace that community when it is disturbed (serial stages).

Indeed, all the plant communities that are spatially present within the same environmental unit and that share the same potential vegetation constitute a "vegetation series" (Rivas-Martínez 1976; Géhu 1986, 1991).

The Map of the Vegetation Series of Italy may be considered the first concise detailed document on the heterogeneity of the vegetation potential in Italy and is also very likely to be richer than many similar maps created for other European regions. The accompanying volume includes regional monographs, each with its own bibliography, which analyse the present vegetation by describing each stage of every vegetation series. As might be expected, for national coverage, there are unfortunately still considerable discrepancies in knowledge between different regions. However, this nation-wide mapping project has yielded an extraordinary amount of data that have been used to identify and map vegetation series covering both extremely limited and very extensive areas.

With regard to methodology, the Map of the Vegetation Series of Italy combines, for the very first time at an international level, the inductive approach of the European School of Phytosociology with the deductive approach of the ecoregion classification developed in the United States in the mid-twentieth century.

The classification of ecoregions, over more than 10 years (Blasi et al. 2000; Capotorti et al. 2012a, b), has led to the definition of land units (environmental units) characterised, depending at the scale adopted, by the same type of vegetation series, i.e. by the same potential natural vegetation. This is defined as the vegetation a given site can host, under the current climatic and pedological conditions, in the absence of any disturbance (Tüxen 1956). The deductive, spatially explicit approach of such classification can thus help to establish a spatial framework of varying vegetation potential. The inductive approach alone, which is based on the synthetic analysis of phytosociological relevés, is in fact often insufficient to map vegetation series, especially where the significant expansion of agricultural and urban areas limits the occurrence of natural and semi-natural vegetation and masks boundaries between different natural settings. Once the spatial framework is set, though, the traditional analysis and classification of phytosociological relevés, based on field and/or literature data, enable one to characterise and typify the potential vegetation and all the related serial stages for each land unit.

This methodology, designed by the Laboratory of Plant Ecology and Conservation of Nature directed by Blasi (Department of Environmental Biology, Sapienza University of Rome), has proved to be effective even at finer scales (Blasi et al. 2000, 2005). In addition to the innovative integration of deductive and inductive processes, another original element of this methodology is the exclusive use, even for the vegetation series, of the classical phytosociological relevés, as opposed to the synrelevés, which would make it even more difficult to recognise and map homogenous land units (in terms of vegetation potential) inductively.

The preparation of the Map of the Vegetation Series was thus based on a hierarchical ecological approach to land classification that led to the creation, as an underlying reference layer for the whole country, of areas that share the same geomorphological and bioclimatic features, obtained by integrating, in a GIS environment, geological and morphological maps as well as the Phytoclimatic Map of Italy (scale 1:250,000) (Fig. 1). The contributions of the experts involved in the project were indispensable insofar as they improved the definition of homogeneous areas, characterised the environmental units detected by the hierarchical classification of vegetation, tested the models proposed, and integrated the existing phytosociological data within an organic framework.

The scale adopted is such that there is bound to be a significant degree of heterogeneity within the environmental units. The series for each cell mapped is thus the prevailing one, i.e. the series that covers most of a given environmental unit. Any other series that are present within the same environmental unit but have not been mapped, and are subordinate to the main series, are included in the relevant monograph, in which the differential ecological roles of these other series are also described. In some cases, if the experts thought that a unit considered homogeneous at a scale of 1:250,000 contained two or even more series, but were not able to determine which series prevailed, then the expression “series mosaic” was adopted. When numerous series were linked by an ecological gradient or by particular geomorphological or phytoclimatic units that escaped detection at the scale adopted (e.g. vegetation in river valleys or low sandy coasts), then the mapping unit was referred to as a *geosigmetum*, whose features are described in the relevant monograph. The scale 1:250,000 prevents the maps from being used or reproduced at a finer scale. It is widely known that, given the hierarchical nature of

Fig. 1 Map of vegetation series in Italy

environmental heterogeneity, what is considered to be homogeneous at one scale (in this case potential vegetation) may no longer be homogenous as the scale becomes finer to provide greater detail (Klijn and Udo de Haes 1994). Lastly, the definition and detail of the vegetation series may vary from unit to unit, as well as from region to region, owing to differences in current knowledge at the national level. Indeed, the western Alpine sector has been studied considerably less than the central and eastern Alpine sectors, and less is known about the Apennines in Liguria than about those in the rest of the peninsula.

The map legend is laid out hierarchically, with the mapping units (*sigmeta* or *geosigmeta*) grouped according to "macroclimatic region" and the phytoclimatic plan divided according to the thermotype and geographic macro-sectors (Alpine, peninsular and insular). The definition of the series, which is based on that proposed by Rivas-Martínez (1987), contains the following elements: chorology, edaphic features, diagnostic species, and the most evolved community in the series (the "head of the series" association). The geographic terms were selected in such a way as to highlight any differences or vicariances between mapping units in which the physiognomy, structure and ecological characteristics are similar.

The Latin name of the vegetation series (*sigmeta*) derives from the head-of-the-series association (Rivas-Martínez 1987): for example, the *Anemono apenninae-Fago sylvaticae* sigmetum takes its name from the beech forest association (*Anemono apenninae-Fagetum sylvaticae*), which is considered to be the mature stage of the vegetation series. This series is thus defined in the legend as "a southern Apennine neutro-basophilous beech series (*Anemono apenninae-Fago sylvaticae* sigmetum)".

As mentioned in the previous paragraph, the mapping units in which it was impossible to identify a prevailing vegetation series were referred to in the legend as "series mosaics". There may thus be mosaics in which the various series alternate depending on morphological or mosaic-related parameters for which substrate differences affect the presence of one series or the other in the mapping unit, as occurs in unit 82b: "A mosaic of the basophilous western Alpine series of Scots pine (*Ononido-Pino sylvestris* sigmetum) and the acidophilous series of beech (*Luzulo-Fagion*)". Lastly, altitudinal mosaics have sometimes been mapped on steep orographic gradients, as in unit 14b: A mosaic of the basophilous eastern Alpine series of Norway spruce (*Adenostylo glabrae-Piceo excelsae sigmetum*) and of the series of mountain pine shrubland (*Rhododendro hirsuti-Pino prostratae sigmetum*)".

The map legend is made up of 317 mapping units, noted by alphanumeric codes in the cells on the map. These include 240 units with a prevailing vegetation series, 37 series mosaics, 39 *geosigmeta*, and 1 unit without vegetation (code 174 "Volcanic desert"). Since the extent of the *geosigmetum* for aquatic and peri-lacustrine vegetation could not be determined, this was included in the class "lakes". For the sake of clarity, the 317 units were included under 279 entries in the legend, listed in numerical order.

Distribution of the Series in the Geographic Sectors of Italy

The high number of entries in the legend is due to the very detailed basic information provided by local experts.

Eighty-seven mapping units were identified in the Alpine geographic sector, though only three of these extend (partially) into the peninsular northern Apennine sector; 191 units were identified in the peninsular and insular sectors, with 58 being found exclusively on the two largest islands, Sicily and Sardinia. The fact that the units in the Map of the Vegetation Series do not overlap in the different sectors of the country highlights the marked ecological and phytogeographic differences present in Italy.

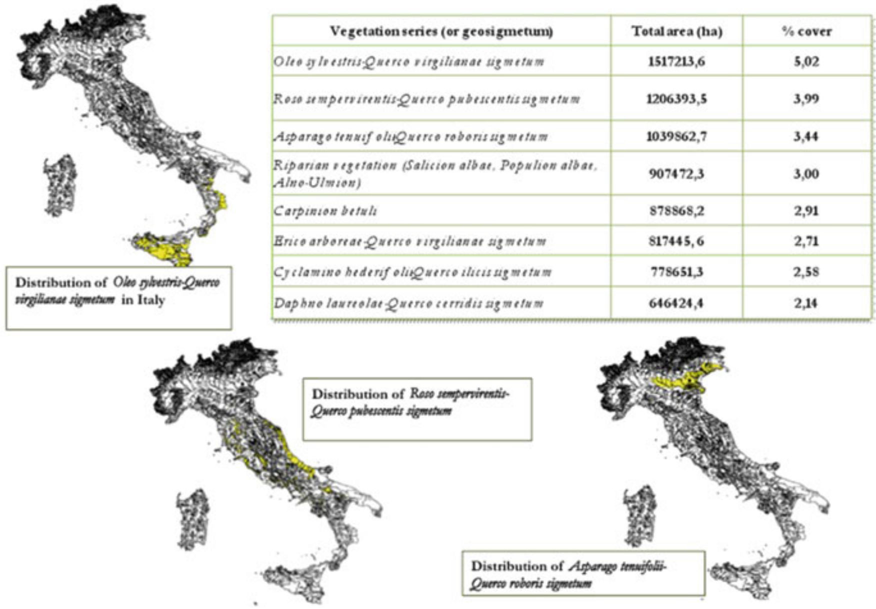
Sardinia and Sicily are the regions with the highest numbers of exclusive vegetation series. Thirty-two of the 40 mapping units identified in Sicily are exclusive to Sicily, including the *Agropyro panormitani-Querco congestae* sigmetum and the *Geranio versicoloris-Querco ilicis* sigmetum; others are shared with other southern Italian regions (e.g. *Anemono apenninae-Fago sylvaticae* sigmetum), particularly with Calabria (e.g. the *Teucrio siculi-Querco ilicis* sigmetum).

The presence of exclusive series in Sardinia is even more marked owing to the more isolated position of this island, as well as to the different palaeographic and tectonic origin of the strait between Sardinia and Corsica. All the mapping units in Sardinia are exclusive to that island, with two exceptions. One is the *Galio scabri-Querco ilicis* sigmetum, which is also present on Elba and which highlights the phytogeographic links between the Tuscan archipelago and the Sardinian-Corsican area; the other is the *Pistacio lentisci-Pino halepensis* sigmetum, which is also present in Puglia.

As regards the phytogeographic, geomorphological and climatic variability and complexity of Italy, all the units in the map differ greatly in both extent and the number of cells that represent them.

As extremes, the *Junipero hemisphaericae-Abieto nebrodensis* sigmetum covers 320 ha and accounts for only 0.001 % of the area of Italy, but the *Oleo sylvestris-Querco virgilianae* sigmetum covers 1,517,000 ha and accounts for approximately 19 % of Italy's surface.

The vegetation series that cover the largest areas of potential vegetation (together 30 % of the whole territory) are the *Oleo sylvestris-Querco virgilianae* sigmetum (just mentioned), the *Asparago tenuifolii-Querco roboris* sigmetum, the *Roso sempervirentis-Querco pubescentis* sigmetum, the hygrophilous peninsular geosigmetum of riparian vegetation (*Salicion albae*, *Populion albae*, *Alno-Ulmion*), the series of *Quercus robur* and *Carpinus betulus* forests in the western Po plain (*Carpinion betuli*), the *Erico arboreae-Querco virgilianae* sigmetum, the *Cyclamino hederifolii-Querco ilicis* sigmetum, the *Daphno laureolae-Querco cerridis* sigmetum, the *Physospermo verticillati-Querco cerridis* sigmetum and the *Anemono apenninae-Fago sylvaticae* sigmetum (Fig. 2). In order to reach 50 % of the overall surface area of Italy, we need to consider the 25 most extensive species.



Vegetation series (or geosigmetum)	Total area (ha)	% cover
Oleo sylvestris-Querco virgilianae sigmetum	1517213,6	5,02
Roso sempervirentis-Querco pubescentis sigmetum	1206393,5	3,99
Asparago tenuifoliiQuerco roboris sigmetum	1039862,7	3,44
Riparian vegetation (Salicion albae, Populion albae, Alno-Ulmion)	907472,3	3,00
Carpinion betuli	878868,2	2,91
Erico arboreae-Querco virgilianae sigmetum	817445,6	2,71
Cyclamino hederifoliiQuerco ilicis sigmetum	778651,3	2,58
Daphno laureolae-Querco cerridis sigmetum	646424,4	2,14

Fig. 2 Potential vegetation types with highest cover

The number of mapped cells that make up each of the series ranges from 173 for the *Roso sempervirentis-Querco pubescentis* sigmetum, which is one of the most extensive series (as mentioned before), to only one for some series that are highly localised, such as the orophilous garrigue series mapped near the summit of Monte Capanne on Elba (*Helichryso italici-Genisto desoleanae* sigmetum, approximately 370 ha).

The mapping units that cover the smallest area include: the northern Apennine geosigmetum of high-altitude primary vegetation (*Sileno exscapae-Trifolietum alpini*, *Oligotricho-Gnaphalietum supini*, *Polytrichetum sexangularis*, *Poo-Cerastietum cerastioidis*, *Salicetum herbaceae*), the Sardinian calcicolous series of *Ostrya* (hop hornbeam) forests (*Cyclamino repandi-Ostryo carpinifoliae* sigmetum) and the calcicolous series of *Quercus cerris* forests in Gargano (*Doronico orientalis-Carpino betuli* sigmetum). None of these units covers an area that exceeds 500 ha.

The afore-mentioned data on the land cover in Italy highlight the remarkable significance of the map. There are, besides the more extensive series, other vegetation types that are of extraordinary importance in both phytogeographic and ecological terms, despite covering very limited areas in Italy. These exceptional results may be attributed to the fact that the original methodology adopted for this project not only integrated the mapping information available, but also assigned a role of particular importance to the local experts.

Viewed physiognomically, most of the vegetation series identified by the *Vegetation Series Map* are forest types. Indeed, in theory, 90 % of our country should be covered by forests. In reality, however, only 30 % of the land is covered by forest communities, while 10 % of the country is covered by primary grasslands or shrublands (Alpine and sub-Alpine sector) or by hydrophytic or aquatic vegetation (fresh or brackish waters).

At national scale, the most widespread vegetation series that correspond to a comparable forest type are: conifer woods dominated by *Picea abies*, *Larix decidua* and/or *Pinus cembra* in the Alpine sector; and the forests of *Quercus robur* and *Carpinus betulus* in the lowland sector of the Po plain.

The physiognomies that display the potential to cover the most extensive areas in the penisular sector are deciduous oak woods with Turkish oak (*Quercus cerris*) and/or downy oak (*Q. pubescens*) and beech (*Fagus sylvatica*) forests. The beech forests occur in 41 different vegetation series, while the deciduous oak woodlands occur in 85. The prevalent potential forest vegetation on the two largest islands, Sicily and Sardinia, is characterised by broad-leaved oakwoods of the Mediterranean type. In Sicily, the vegetation series in the mature stage is dominated by deciduous oakwoods of *Quercus virgiliana*, *Q. gussonei*, etc., which account for approximately 69 % of the region; this is a considerably larger area than that dominated by sclerophyllous trees (*Quercus ilex, Q. suber*) or by shrublands (various kinds of Mediterranean maquis dominated by *Juniperus, Pistacia, Myrtus, Rhus* etc.), which account for barely 22 %. By contrast, evergreen oakwoods (*Q. ilex* and *Q. suber*) play a decidedly dominant role on Sardinia, where they account for 77 % of the potential land cover of the region. Deciduous oakwoods, which account for 16 % of the territory, nevertheless cover a considerable proportion of the region, particularly in the inland areas, and are of extraordinary phytogeographic value.

Vegetation Series and Actual Land Use

The scale that we adopted did not allow us to map the actual vegetation cells. This information may, however, be obtained from the CORINE Land Cover 2000 (APAT 2005). By consulting both maps at the same time, one may observe that the proportion of agricultural and artificial surfaces for each vegetation series rises markedly as the altitude decreases and the terrain becomes less steep.

Most of the series that display a poor "state of conservation" (assessed as cover percentage of residual natural and semi-natural vegetation types) are in fact located on hilly or low-lying terrain, especially in phytoclimatic areas ranging from meso-temperate to meso/thermo-Mediterranean (sensu Rivas-Martínez).

In the Mediterranean region, the *Quercus virgiliana* woods found on the Tavoliere in Puglia (*Irido collinae-Quercetum virgilianae*) have virtually all been replaced by semi-natural woods and olive groves (which cover as much as 96 % of this area) and by artificial surfaces (2 %). Indeed, natural and semi-natural vegetation covers barely 2 % of the overall surface of Puglia. By contrast, the montane (supra-temperate phytoclimatic region) and subalpine and alpine (orotemperate and cryo-orotemperate) areas in the Alps, and to an even greater extent in the

Apennines, are generally characterised by a high level of natural and semi-natural vegetation, with a marked presence of actual vegetation in the mature stage.

The agricultural use of the land may thus be considered to be the primary cause of changes in the vegetation series at the national scale.

Applications of the Map of the Vegetation Series

Several projects have been carried out at national scale in recent years within the context of the Global Strategy of Plant Conservation (GSPC) and the National Biodiversity Strategy of Italy. The National Strategy should be considered a reference framework that may be used to integrate the results of initiatives aimed at conserving biodiversity, to identify any weaknesses that warrant more research and the investment of resources, and consequently to decide what conservation measures need to be implemented at the national, regional and global levels. The National Biodiversity Strategy in Italy foresees the application of a multi-disciplinary scientific approach and a close collaboration between political bodies and regional and central administrations. Implementation of the National Strategy in Italy is planned for the period 2011–2020.

Other research initiatives were also conducted up to 2010, often supported directly or indirectly by the Map of the Vegetation Series and aimed above all at Targets 4, 5 and 7 of the Global Strategy of Plant Conservation.

Target 4 of the GSPC mandates that "At least 10 per cent of each ecological region or vegetation type [be] secured through effective management and/or restoration" To test whether target 4 was fulfilled, gap analysis, based on the protected-area and Natura 2000 networks, was used to investigate to what extent each biodiversity element is represented in existing protected areas and to identify which elements require more protection. This permits assessing what contribution is made by each of these two protection networks.

By using the information provided by the Map of the Vegetation Series and assuming that the various series represent types of potential natural vegetation (PNV), it was possible to overlay PNV data and spatial data for protected areas, with the following results (Fig. 3):

- 78 of the PNV types have less than 10 % protection,
- about 65 % of the PNV types are protected, but the remaining 35 % are not protected sufficiently.

Currently, 12 additional PNV types can be classified as complete gaps. These types are mainly located in the Temperate Region, in the plains and low hilly areas (Rosati et al. 2008).

Target 5 requires that "at least 50 per cent of the most important areas for plant diversity [be] protected with effective management in place for conserving plants". Target 7 requires that "at least 50 per cent of known threatened plant species [be] conserved *in situ*".

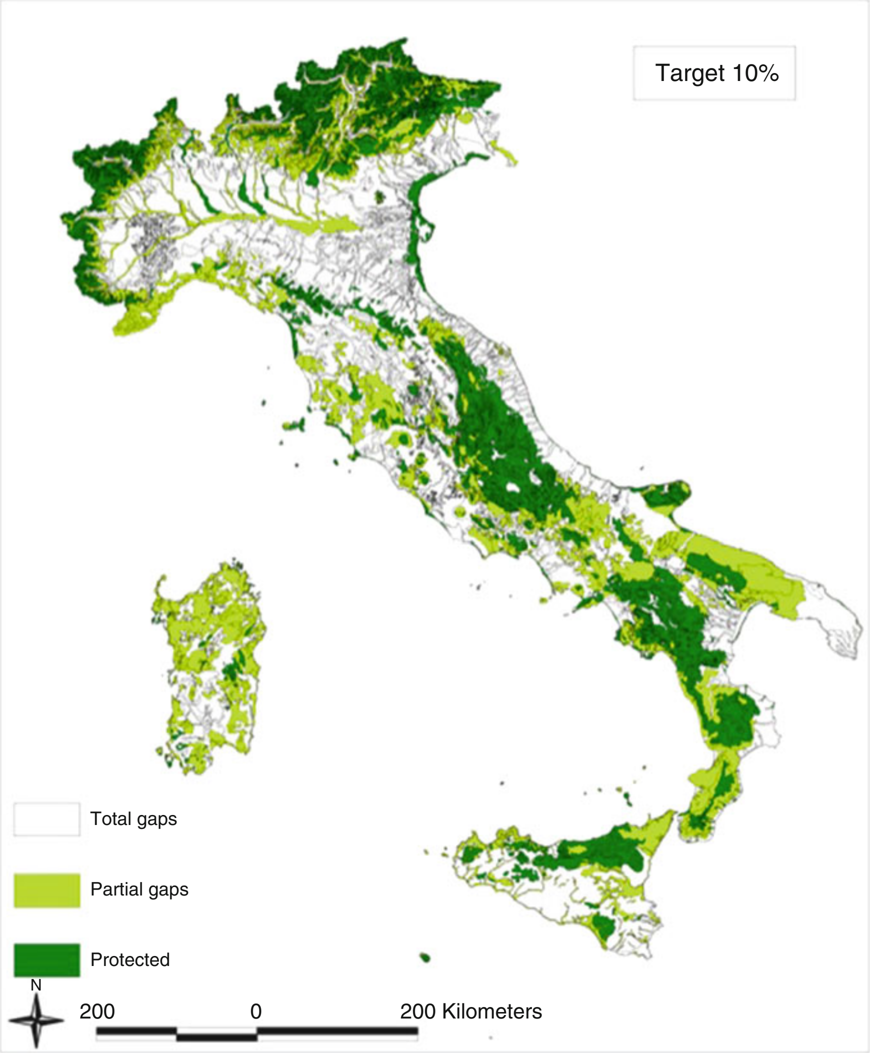


Fig. 3 Gap analysis and potential natural vegetation

The best means of defining these areas is proposed by *Planta Europa* through the Important Plant Areas Programme. An Important Plant Area (IPA) is defined as "a natural or semi-natural site exhibiting exceptional botanical richness and/or supporting an outstanding assemblage of rare, threatened and/or endemic plant species and/or vegetation of high botanical value".

The identification and mapping of IPAs (Fig. 4) can make a major contribution to the global strategy for plant conservation, even within the context of "ecological

Fig. 4 Map of the Important Plant Areas (IPAs) in Italy

connectivity" and "land ecological networks". To qualify as an Important Plant Area, a site needs to satisfy one or more of the following criteria:

- criterion A: The site contains significant populations of one or more species that are of global or European conservation concern;
- criterion B: The site has an exceptionally rich flora within a range of defined habitat types, in relation to its biogeographic zone;
- criterion C: The site is an outstanding example of a habitat type of global or European plant conservation and botanical importance.

The IPA project shows that 70 % of the cells contain at least one record of species or habitat of IPA interest. Vascular species (57 % of the cells) were more widespread than habitats (48 % of the cells), while other taxa were present in only 16 % of the cells. The final ranking of the cells, obtained by combining the relative values, detected 351 top-ranking cells, 798 medium-ranking cells and 1309 low-ranking cells. Although fewer than 50 % of the IPAs are included in the Official List of Protected Areas, only 21 % fall outside the Natura 2000 Network. Approximately 2 % of the IPAs are not afforded any protection by the systems currently in use.

Of the 1394 vascular plants analyzed, 86 % were represented at least once within the protected areas. More than 60 % of the species in each of the threatened categories were recorded in at least one type of protected area. Other taxa represented in the IPAs included 72 % of the total number of bryophyte species, 77 % of the fungus species and 59 % of the lichen species, as well as 19 % of the sites of interest for freshwater algae (Blasi et al. 2011).

Several countries have developed national responses to the GSPC. In some cases this has resulted in the development of national plant conservation strategies with national targets aligned with the global targets. In other countries, national responses have been developed within the context of National Biodiversity Strategies and Action Plans (NBSAPs).

Following the adoption of the Strategic Plan for Biodiversity 2011–2020 and the Aichi Targets, parties are being urged to update and revise their NBSAPs to take into account the 2020 biodiversity targets. The harmonisation and inclusion of national plant conservation targets within the framework of national biodiversity strategies will be an important element in achieving the 2020 GSPC targets. Targets 4, 5 and 7, in particular, have been updated:

Target 4: At least 15 % of each ecological region or vegetation type secured through effective management and/or restoration;

Target 5: At least 75 % of the most important areas for plant diversity of each ecological region protected with effective management in place for conserving plants and their genetic diversity; and

Target 7: At least 75 % of known threatened plant species conserved *in situ*.

Conclusions

Scientific knowledge of the potential natural vegetation of Italy may be considered a milestone in the history of vegetation studies at both the National and European levels. Botanical research had been focused for a long time on extremely detailed analyses, which led to the neglect of more integrative or at least geographic studies at broader scale. The funding provided by the Ministry for the Environment approximately 20 years ago gave rise to several research projects that are now yielding overviews on fundamental topics such as phytoclimatology, ecoregions and landscapes.

On the methodological level, research on vegetation has at last adopted a basic ecological and model-based approach that can be used to tackle problems with equal effectiveness at different scales (Blasi and Frondoni 2011; Biondi et al. 2011). Contemporary knowledge of both actual and potential vegetation can be exploited to assess a wide range of disciplines and, above all, to monitor the environment, as required by the Habitats Directive.

Following a long period of attention being focused on vegetation types, interest has now shifted to the ecological definition of dynamic change. Indeed, modern phytosociology integrates the synchronous approach with the diachronous approach, providing at the same time the quantitative data that are needed to define the corresponding ecological models.

The changes that are currently taking place globally, particularly those related to land use, involve Europe as a whole and need to be interpreted quantitatively; this is a role that research on vegetation is expected to play. In order to be able to address these issues at the various temporal and spatial scales involved, we need to know the structural and functional complexity, at different scales, of vegetation stages all at comparable maturity. It is for this reason that the vegetation series has become the reference model in the assessment of both ongoing changes and the state of conservation of plant communities and of the landscape.

Nor can we ignore the importance of the potential vegetation in any planning intervention, whether it be at the local, regional or national level. Indeed, these maps quantify the heterogeneity of an area, not only distinguishing but also integrating the potential diversity (related above all to physical elements and to the floristic heritage) with effects resulting from human activities, which manifest themselves in the serial stages.

The syndynamic map assumes particular importance for application purposes insofar as it has proved to be highly useful in every sector, from land planning (land ecological network, local and nationwide land planning, transport planning, selection of industrial areas, etc.) to agricultural and forest planning. Never before has the potential of synphytosociology been so evident in the definition of new agricultural models designed to perform multiple functions, including the conservation of biodiversity and the improvement in the quality of life.

These basic studies and vegetation series maps, which contain so much ecological and dynamic information, are likely to lead rapidly to increasing integration among all the people whose work is based on the land, such as urban and landscape planners, agronomists, foresters and phytosociologists. In Italy, following the completion of this basic overview, other studies are under way not only to enhance our basic knowledge, but also to develop integrated application models, and in particular sustainable management models that may be applied to protected areas and, more generally, to urban and extra-urban systems. In this regard, a project aimed at producing a volume entitled "Italian Vegetation Prodromus", funded by the Ministry for the Environment and supervised by Edoardo Biondi and Carlo Blasi, was recently started. Besides being a major achievement, this occasion also marks the ongoing nature of cultural and scientific research in the vegetation field.

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Marcescent *Quercus pyrenaica* Forest on the Iberian Peninsula

Beatriz Vilches de la Serna, Daniel Sánchez-Mata, and Rosario G. Gavilán

Abstract Deciduous forests occur widely in central-western Europe as far south as the Iberian Peninsula. In this area dominated by a Mediterranean-type climate, the marcescent endemic *Quercus pyrenaica* Willd. serves as an indicator of the southern limit of broad-leaved forests. Its distribution area extends from southwest France to northeast Morocco, occupying—at least potentially—large areas of the peninsula and thus covering a wide variety of environments and ecological niches that we will attempt to identify. Different community types will also be identified, based on current classifications and the latest analysis of these forests. Their uniqueness, the current situation of global change, and real threats to their conservation and existence, have made their study a pressing concern.

In Europe, deciduous forests are widely distributed over central-western territories as far south as the Iberian Peninsula. In this area dominated by the Mediterranean climate, the marcescent endemic *Quercus pyrenaica* Willd. serves as an indicator of the southern limit of European broad-leaved forests. Its distribution area extends from southwestern France to northeastern Morocco, occupying at least potentially large areas of the Iberian Peninsula and thus covering a wide variety of sites and ecological niches that we will attempt to show in the present text.

Quercus pyrenaica has been known by several names throughout history: *Quercus tauzin* Pers, *Quercus toza* Bosc ex DC. (perhaps the most common), *Quercus aurin* Bosc, *Quercus brossa* Bosc, *Quercus stolonifera* Lapeyr, etc. However, the assignment of the definitive scientific name *Quercus pyrenaica* by Carl Ludwig von Willdenow in 1805 was due to an unfortunate error in the herbarium label describing the original specimen in the Pyrenees, where its presence is virtually nil. Surprisingly, Christian von Steven once again gave it the same name in 1813 (International Plant Names Index 2014). Because of its variable foliage and the frequent hybridization within the genus, there are even today local discrepancies as to its denomination [e.g. *Quercus pauciradiata*, by López González (2001)]. Its most widely-used vernacular name—"melojo" ("Pyrenean") seems to derive

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Fig. 1 General structure of *Quercus pyrenaica* forests, together with inflorescence and details of young leaves. A particularly eye-catching feature of this species is the *purple colour* of the new shoots during the early stages of foliation

from the numerous root sprouts it generates due to its stoloniferous character. (There are also numerous other names: “marojo”, “black oak”, “tozo”, “roure reboll” in the east, “caxigu” or “toziu” in Asturias; “carvallo negro”, “cerqueiro” or “cerquiño” in Galicia, “ametza” in the Basque Country, and “carvalho negral” in Portugal).

The most common appearance of this *Fagaceae* member is as a tree of moderate height (10–15 m), with a straight trunk, irregular crown, and thin, lobed greyish-brown bark with longitudinal cracks. In the few cases where it has been allowed to grow, the Pyrenean oak can reach heights of up to 25 m and a diameter of 1 m (López González 2001). It usually creates closed formations (Fig. 1), although the overall appearance can range from extremely closed forest to different degrees of openness (and trunk diameter), depending on the level of management. This includes the *dehesa* in some parts of the peninsula and, with *Fraxinus* spp., the so-called *bocage* system of open grassland surrounded by a forest margin with *Prunetalia* species. These forests have been transformed traditionally into areas for cultivation or livestock (Fig. 2), which are partly encouraged as effective formers of fertile soil. Their fragmentation has also been driven by charcoal production and its replacement by the cultivation of fast-growing species such as *Pinus sylvestris* and *Pinus pinaster*. *Castanea sativa*, occasionally present in the canopy, has also been favoured and was cultivated frequently at potential sites of Pyrenean oak, probably before the Romans conquered the Iberian Peninsula, although they propagated its use.

Preference for siliceous soils causes the marcescent oaks to predominate mainly in the northwestern quadrant of the Iberian Peninsula. They have a reduced presence in the south, and particularly towards the east, where the dominant soil types

Fig. 2 Effect of continuous grazing and *dehesa* management on *Quercus pyrenaica* forest in Madrid and Segovia (B. Vilches)

derive from calcareous substrates created by Mesozoic sedimentary processes (López-Gómez and Arche 1992; Alonso et al. 1991). These oaks grow on a variable acidic lithology: granite, slate, schist, gneiss and locally decarbonated basic substrates (Aralar-Bidasoa in the Basque Country), or islands of acidic substrate interspersed with limestone soils, as occur in Barrios de Luna (León) or in the eastern Spanish mountains, where they usually grow on red *Buntsandstein* sandstone and argillites.

The substrate is not the only factor, however, that defines the geographical distribution of this forest in the Iberian Peninsula. A number of authors highlight the transitional character of *Quercus pyrenaica* between temperate and Mediterranean climates, occupying locations defined as sub-Mediterranean. For this reason, its distribution has been used to define Iberian biogeographical areas by several authors, such as Polunin (1977, 1989), who used it to extend the Eurosiberian region to the Iberian Sistema Central mountains. Bolòs (1985) even made it the basis for his definition of the Carpetano [around Madrid]-Atlantic territory (Costa et al. 1997). It forms a differential area of favourable “mediterraneity”, where the plant species most vulnerable to summer drought may take refuge, which also benefits wildlife (Martínez-Lirola et al. 2011). Moreover, the distribution area indicates per se that summer drought is one of the limiting factors, as it avoids the driest sites. The second and perhaps not so obvious limiting factor is winter frost. Both are factors to which this oak appears to be adapted morphologically and physiologically for survival. First, the leaf shape ranges from lobed or pinnatifid to pinnatipartite, a variability probably associated with the level of water stress it can withstand (Sisó et al. 2001); the leaves also have stellate hairs (mainly on the underside of mature leaves) that minimize water loss by evapotranspiration (Charco et al. 2002; Sisó et al. 2001). Second, the tap root is well developed for the extraction of groundwater (also useful for pumping nutrients). Finally, it has a particular type of xylem that is renewed and modified every season: in summer it develops narrower vessels to avoid cavitation, protecting the tree from water stress (Gil-Pelegrín et al. 2005). In addition, the marcescent character of the brown leaves (which remain on the leaf buds during winter until late spring) and delayed foliation serve as protection from late frost, which is common in most of continental Iberia. In fact, we have observed that the main division of the Iberian oaks derives basically from these two factors: continentality and summer aridity.

The background of these forests, their uniqueness as marcescent endemics in southern Europe, the current situation of global change and the real threat to their conservation and particularly to the flora found in their Mediterranean fringe, have made their study a pressing concern. Our studies on *Quercus pyrenaica* forests (Vilches 2014) contain a detailed review of the differences in their distribution in the entire Iberian Peninsula and aim to quantify different levels of conservation and floristic singularity. We set out to develop a methodology to define and analyze local and regional nuances and the connections that allow a certain continuity in their floristic composition (Vilches et al. 2013a; Vilches 2014). Different descriptors highlighted different distinctions at different scales of work, which are briefly included in the present chapter.

Bioclimatic and Floristic Patterns

Quercus pyrenaica forests appear in both temperate (Euro-Siberian) and Mediterranean territories (Fig. 3). They are differentiated by a period of summer drought which is non-existent in the first and is prolonged up to 3 months in the second. The adaptations that allow them to live in Mediterranean areas, usually as mountain forests, drive them to seek out dry or better drained locations in temperate Iberia (sunniest orientations, sandy substrates or steep slopes). The Pyrenean oak occurs therefore over a wide range of altitudes (from 290 m in the Basque Country to 1800 m in the Sierra Nevada) and consequently of thermotypes, always maintaining a minimum summer precipitation of 100 mm and annual rainfall of around 600 mm (Costa et al. 1997; Gavilán et al. 2007). We found them only in territories with ombrotypes ranging from humid to even hyperhumid, and thermotypes from meso- to supra-mediterranean and meso-supra-temperate belts (*sensu* Rivas-Martínez et al. 2011).

Quercus pyrenaica forest distribution covers a large number of biogeographical provinces, from the Atlantic-European (Fig. 3: Orocantabrian and Cantabrian-Atlantic) in the Euro-Siberian (or Temperate) region, to the Mediterranean-Central Iberian (Oro-Iberian, 1c), Balearic-Catalan-Provençal (Catalan-Valencian, 2a), Mediterranean West Iberian (4), Coastal-Lusitanian-Andalusian (5), or Betic (6) in the Mediterranean region. These forests are more frequent in the west-Iberian Mediterranean region.

In all these provinces the Pyrenean oak is in contact with different types of forest. In temperate Iberia it is immersed in an environment dominated by broad-leaved phanerophytes and often forms mixed forests with *Quercus robur* in contact with *Fagus sylvatica* and *Quercus petraea*. However, in Mediterranean Iberia it creates islands of typically marcescent vegetation in a predominantly evergreen

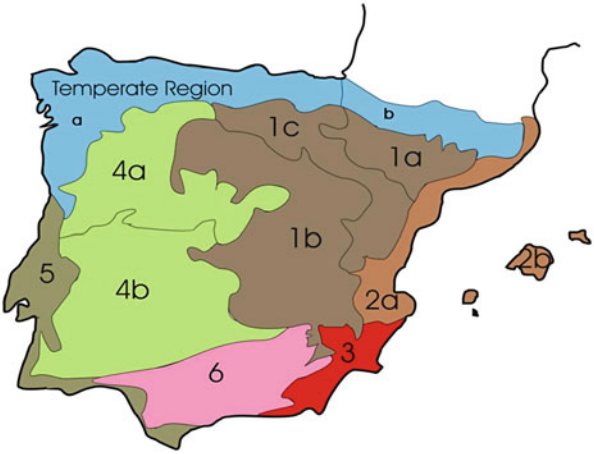
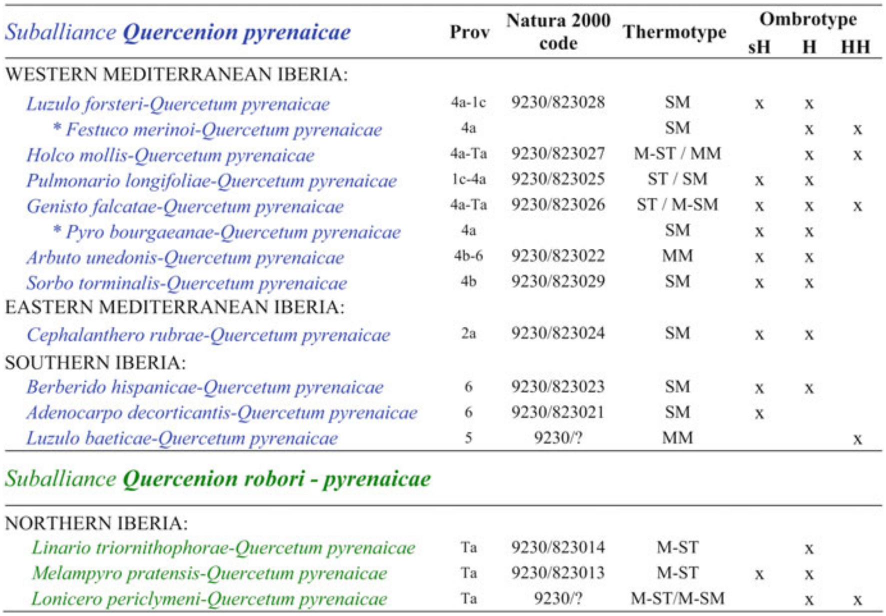


Fig. 3 Iberian biogeographic regions (Rivas-Martínez et al. 2011): *Temperate region*: (a) Atlantic-European Province, (b) Cévennean-Pyrenean Province; *Mediterranean region*: (1) Mediterranean Central Iberian Province (Subprovinces: a. Low Aragonese, b. Castilian, c. Oro-Iberian), (2) Balearic-Catalan-Provençal Province (Subprovinces: a. Catalan-Valencian, b. Balearic), (3) Murcian Almeriensian, (4) Mediterranean West-Iberian Province (Subprovinces: a. Carpetan-Leonese, b. Lusitanan-Extremadurean), (5) Coastal-Lusitanian-Andalusian Province, (6) Betic Province. Map produced by J. M. Blanquer Lorite

environment, contacting (depending on the altitude and geographic location) stands of *Quercus suber*, *Quercus broteroi* or *Quercus rotundifolia* Lam., which may also have conifers such as *Pinus sylvestris* or *Pinus pinaster* (Blanco et al. 2005). The floristic ensembles vary depending on the location. The latest syntaxonomical classification (Rivas-Martínez et al. 2011) divided Iberian Pyrenean oak forests into 15 climate-based associations, included in the class *Querco-Fagetea* Br.-Bl. & Vlieger in Vlieger (1937), alongside other optimal Eurosiberian deciduous forests (Order *Quercetalia roboris* Tx. in Barner (1931), including acidophilous oak and beech forests). These associations define a particular alliance, *Quercion pyrenaicae* Rivas Goday ex Rivas-Martínez (1965), which is subdivided into two suballiances: a purely Mediterranean *Quercenion pyrenaicae* Rivas-Martínez 1974 (Table 1, in blue) and one corresponding to temperate forests in the northern peninsula, called *Quercenion robori-pyrenaicae* (Br-Rl., P. Silva & Rozeira (1956)) Rivas-Martínez (1975) (Table 1, green, Vilches 2014).

We will describe briefly the main distribution areas of *Quercus pyrenaica* together with its most representative associations. Without overlooking various bioclimatic belts, we can confirm that summer drought, continentality and precipitation seasonality are the main climate patterns differentiating peninsular Pyrenean oak communities. There is a widely-known decrease in the range and sequence of precipitation, which is mainly latitudinal from north to south (average rainfall) but also longitudinal from west to east.

Table 1 Phytosociological associations of *Quercus pyrenaica* in the Iberian Peninsula



Suballiance ***Quercenion pyrenaicae***	Prov	Natura 2000 code	Thermotype	Ombrotype		
				sH	**H**	**HH**
WESTERN MEDITERRANEAN IBERIA:						
Luzulo forsteri-Quercetum pyrenaicae	4a-1c	9230/823028	SM	x	x	
** Festuco merinoi-Quercetum pyrenaicae*	4a		SM		x	x
Holco mollis-Quercetum pyrenaicae	4a-Ta	9230/823027	M-ST / MM		x	x
Pulmonario longifoliae-Quercetum pyrenaicae	1c-4a	9230/823025	ST / SM	x	x	
Genisto falcatae-Quercetum pyrenaicae	4a-Ta	9230/823026	ST / M-SM	x	x	x
** Pyro bourgaeanae-Quercetum pyrenaicae*	4a		SM	x	x	
Arbuto unedonis-Quercetum pyrenaicae	4b-6	9230/823022	MM	x	x	
Sorbo torminalis-Quercetum pyrenaicae	4b	9230/823029	SM	x	x	
EASTERN MEDITERRANEAN IBERIA:						
Cephalanthero rubrae-Quercetum pyrenaicae	2a	9230/823024	SM	x	x	
SOUTHERN IBERIA:						
Berberido hispanicae-Quercetum pyrenaicae	6	9230/823023	SM	x	x	
Adenocarpo decorticantis-Quercetum pyrenaicae	6	9230/823021	SM	x		
Luzulo baeticae-Quercetum pyrenaicae	5	9230/?	MM			x
Suballiance ***Quercenion robori - pyrenaicae***						
NORTHERN IBERIA:						
Linario triornithophorae-Quercetum pyrenaicae	Ta	9230/823014	M-ST		x	
Melampyro pratensis-Quercetum pyrenaicae	Ta	9230/823013	M-ST	x	x	
Lonicero periclymeni-Quercetum pyrenaicae	Ta	9230/?	M-ST/M-SM		x	x

The following information is included: biogeographical province thermotype and ombrotype (Rivas-Martínez et al. 2011), and their correspondence with Natura 2000 initiative codes and habitat types of Spain (Atlas y Manual de los Hábitats Naturales y Seminaturales de España). Associations not included as such in the habitat classification, but which are part of the above, are marked with an asterisk

Abbreviations: *MM*/*SM* meso/supra-mediterranean, *MT*/*ST* meso/supra-temperate, *SH* subhumid, *H* humid, *HH* hyperhumid

Mediterranean Macroclimate (Suballiance *Quercenion pyrenaicae*)

Three large areas can be recognized in the region of Mediterranean climate.

A. Western Mediterranean Iberia

Luzulo forsteri-Quercetum pyrenaicae and *Festuco merinoi-Quercetum pyrenaicae* are found in the Sistema Central (mountains), and the first also in the Sistema Ibérico. *Luzulo-Quercetum* constitutes the central association for this oak, with a purely siliceous character. *Genista florida*, *Cytisus scoparius*, and occasionally *Adenocarpus hispanicus*, often appear as replacement shrubs (*Genisto floridae-Cytisetum scoparii*, *Genisto floridae-Adenocarpetum hispanici*). *Festuco merinoi-Quercetum* covers mainly the Sierra de Gredos and includes brooms such as *Cytisus multiflorus*, and also graminoid replacement communities with *Festuca elegans* ssp. *merinoi* (*Thymo mastichinae-Cytisetum multiflori*, Table 2).

Table 2 Phytosociological associations of *Quercus pyrenaica* in the Sistema Central of the Iberian Peninsula. *Pulmonario longifoliae-Quercetum pyrenaicae* (1), *Luzulo forsteri-Quercetum pyrenaicae subass. quercetosum pyrenaicae* (2–6), *subas. genistetosum falcateae* (7–8), *Festuco merinoi-Quercetum pyrenaicae* (9–25) (*Quercenion pyrenaicae*, *Quercion pyrenaicae*, *Quercetalia roboris*, *Querco-Fagetea*)

N. relevé	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Exposure	NE	–	–	–	NE	E	SE	W	–	–	NE	SE	NE	N	NE	SE	SE	SW	NE	NW	–	NW	–	NE	E
Altitude (1 = 10 m asl)	150	119	110	115	124	115	130	100	121	144	120	153	140	116	115	123	135	144	113	119	109	119	142	118	115
Characteristics																									
Quercus pyrenaica	5	5	5	5	5	5	5	5	5	5	4	5	5	3	5	5	4	5	5	5	5	5	5	5	5
Holcus mollis	2	2	2	2	2	1	1	2	1	2	2	2	1	1	2	1	2	2	2	2	2	2	1	3	2
Poa nemoralis	2	1	1	1	1	1	.	1	1	1	.	1	2	2	1	+	.	2	1	2	1	2	1	1	.
Silene nutans	.	+	.	+	.	1	.	+	.	+	1	1	+	+	+	2	1	+	+	1	+	1	+	1	1
Arenaria montana	.	2	1	1	1	1	.	1	.	.	1	+	+	.	.	1	.	.	1	.	1	.	.	1	1
Teucrium scorodonia	1	.	.	.	.	+	.	1	1	+	1	1	1	1	1	.	.	1	1	1	+	2	.	1	.
Viola riviniana	.	.	1	.	.	1	+	1	.	1	.	.	+	1	.	.	.	+	1	.	1	1	.	+	.
Luzula forsteri	.	1	1	.	1	1	1	1	.	.	.	.	1	1	+	1	.	.	1	.	1	1	.	.	.
Hyacinthoides non-scripta	.	.	.	.	+	1	.	+	+	+	.	+	.	.	+	.	.	+	.	1	+	2	.	.	.
Aristolochia paucinervis	.	.	.	.	.	1	.	+	.	.	.	+	.	.	.	.	1	.	+	.	1	+	1	.	.
Sedum forsterianum	.	+	.	.	1	+	.	1	.	.	.	.	+	+	1	.	.	.	1	.	.	.	.	+	1
Festuca aggr rubra	+	1	2	2	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Brachypodium sylvaticum	1	.	2	+	.	+	.	+	.	.	.	.	.	+	.	.	.	1	.	.	.	.	.	.	.
Lathyrus niger	.	.	1	.	.	1	.	.	1	.	.	.	+	1	.	.	.	.	.	.	.	.	.	1	1
Sorbus aucuparia	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Geum sylvaticum	+	+	.	.	.	.	1	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.
Centaurea triumfettii subsp. *lingulata*	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	+	.	+	.	.
Castanea sativa	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	+	.	+	1
Hedera helix	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	+	.	.	.	.	.	.	+

(continued)

Table 2 (continued)

N. relevé	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Exposure	NE	–	–	–	NE	E	SE	W	–	–	NE	SE	NE	N	NE	SE	SE	SW	NE	NW	–	NW	–	NE	E
Altitude (1 = 10 m asl)	150	119	110	115	124	115	130	100	121	144	120	153	140	116	115	123	135	144	113	119	109	119	142	118	115
Primula veris s.l.	.	+	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.
Prunus avium	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	1	.	.	.	.	.	.	+
Helleborus foetidus	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	2	.	.
Veronica officinalis	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	.	.	.
Arum cylindraceum	.	.	.	.	.	.	.	.	1	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.
Malus sylvestris	+	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Melittis melissophyllum	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.
Crepis lampsanoides	.	.	.	.	.	.	.	.	.	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.
Ulmus glabra	.	.	.	.	.	.	.	+	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.
Genista falcata	.	.	.	.	.	.	+	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Festuca elegans subsp. *merinoi*	.	.	.	.	.	.	.	1	+	.	2	2	+	+	.	3	.	+	+	+	.	1	.	1	2
Euphorbia oxyphylla	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	1	+	1	1	+	1
Physospermum cornubiense	.	.	.	.	.	.	.	.	+	1	.	.	1	1	.	+	.	.	.	.	+	.	+	.	.
Viburnum lantana	.	.	.	.	.	.	.	.	.	.	.	.	+	2	.	.	.	.	.	.	.	.	+	.	.
Genista tournefortii	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	1	.	.	.	.
Prunella laciniata	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.
Trifolio-Geranietea and *Rhamno-Prunetea* characteristics																									
Clinopodium vulgare subsp. *arundanum*	1	1	.	.	1	1	+	1	+	1	1	.	+	1	1	1	1	1	1	1	1	.	1	1	1
Silene latifolia	.	.	.	+	.	.	.	+	+	+	+	1	.	+	1	1	+	+	.	.	.	+	1	.	1
Carex lamprocarpa	.	+	.	.	.	+	1	+	.	1	1	1	+	.	1	+	1	1	1	1	.	1	+	1	+

Cruciata glabra	1	+	1	.	1	+	1	1	.	.	.	+	+	1	1	1	.	1	1	1	.	.	1	.	.
Conopodium subcarneum	.	1	+	.	+	1	.	1	.	.	.	.	.	.	1	1	1	.	.	.	+	1	1	1	.
Lonicera periclymenum subsp. *hispanica*	+	+	.	.	.	1	.	.	1	1	1	.	1	1	1	.	+	.	1	1	2	1	1	1	1
Crataegus monogyna	+	+	1	.	.	+	+	.	+	1	.	.	+	1	1	.	.	+	1	.	1	.	.	.	.
Conopodium pyrenaeum	.	.	.	.	.	1	.	1	.	+	.	+	.	.	1	+	.	.	1	.	.	.	1	.	.
Prunus spinosa	.	.	+	1	1	.	.	.	+	.	.	.	.	.	+	.	.	1	.	.	1	+	.	.	.
Rumex acetosa	.	.	.	.	.	+	.	+	.	.	.	+	1	+	1	.	.	+	1	.	.	.	.	.	.
Vicia sepium	.	.	.	.	.	.	.	.	.	.	.	.	2	+	.	.	.	1	1	.	2	.	.	1	.
Viola odorata	.	1	.	.	.	1	.	.	.	.	.	.	.	.	1	.	.	.	.	.	1	.	1	.	.
Hieracium murorum	+	.	.	.	.	.	.	.	.	.	1	.	+	.	.	.	.	.	+	.	.	.	.	+	.
Astragalus glycyphyllos	.	.	.	.	.	+	.	.	+	.	.	.	+	.	.	.	.	1	.	.	.	.	+	.	.
Clinopodium vulgare	.	.	+	1	.	1	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	1	.	.
Rosa corymbifera	.	.	.	.	+	.	.	.	.	.	.	.	1	.	+	.	1	.	.	.	1	.	.	.	.
Ornithogalum pyrenaicum	.	.	.	.	.	.	.	.	1	1	.	.	.	.	1	.	.	+	+	.	.	.	.	.	.
Rosa canina	.	+	1	1	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Aquilegia vulgaris subsp. *hispanica*	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	+	.	+	+	+	.	.	.
Trisetum flavescens	.	1	.	.	.	+	+	.	.	.	.	.	.	.	+	.	.	.	.	.	+	.	.	.	.
Polygonatum odoratum	.	.	.	.	.	.	.	.	1	.	.	+	1	.	1	.	.	.	.	.	.	.	.	.	.
Lathyrus pratensis	.	+	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.	.	+	.	.	.	.
Potentilla sterilis	1	+	1	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Origanum virens	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	1	.	.	.	.	.	.	.	.	1
Tamus communis	.	.	.	.	.	+	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	+
Vicia cracca	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	1	.	.	.	.	1	.	.
Arabis stenocarpa	.	.	.	1	.	.	.	.	.	2	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.

(continued)

Table 2 (continued)

N. relevé	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Exposure	NE	–	–	–	NE	E	SE	W	–	–	NE	SE	NE	N	NE	SE	SE	SW	NE	NW	–	NW	–	NE	E
Altitude (1 = 10 m asl)	150	119	110	115	124	115	130	100	121	144	120	153	140	116	115	123	135	144	113	119	109	119	142	118	115
Trifolium ochroleucon	.	.	.	.	.	+	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Tanacetum corymbosum	.	.	.	.	.	1	.	.	.	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.
Hieracium sabaudum	.	.	.	.	.	.	.	.	.	.	.	.	.	+		.	.	.	.	.	.	.	.	.	+
Cruciata laevipes	.	.	.	+	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Shrub and forest companions																									
Pteridium aquilinum	2	.	.	.	.	+	3	3	.	.	3	1	1	.	.	2	.	1	1	1	+	.	.	2	3
Cytisus scoparius	.	.	.	.	+	1	.	.	+	1	1	2	1	1	1	.	1	1	1	.	+	1	1	1	1
Genista florida	1	.	.	.	.	+	.	+	.	.	+	.	1	+	.	.	.	.	1	.	+	+	.	+	.
Paeonia broteri	.	.	.	.	.	+	1	.	1	.	.	+	.	.	.	.	.	.	.	.	2	.	.	.	.
Paeonia officinalis subsp. *microcarpa*	.	.	.	.	.	.	+	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pinus sylvestris s.l.	+	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.
Juniperus communis subsp. *hemisphaerica*	.	+	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.
Cistus laurifolius	.	+	+	1	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.
Adenocarpus complicatus	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	+	.	.	.	+	.
Erica arborea	1	.	.	1	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Rubia peregrina	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.
Daphne gnidium	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	+	.	.	.	+	.
Genista tinctoria	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.
Lotus corniculatus subsp. *carpetanus*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.	.	.
Bryonia dioica	.	.	.	.	.	.	.	.	.	1	.	+	+	+	.	.	.	1	.	+	+	+	1	.	+

Companions																									
Lapsana communis	+	.	.	.	.	+	.	+	+	1	+	.	1	1	1	.	.	.	+	+	+	1	+	.	.
Dactylis glomerata	.	1	1	1	.	.	.	.	1	1	.	1	.	1	1	2	1	1	1	1	1	+	1	1	1
Poa pratensis	.	.	1	1	.	.	.	.	1	.	1	.	1	1	1	.	.	.	.	1	1	.	.	.	1
Anthoxanthum odoratum	.	.	.	.	1	+.	.	.	.	.	1	1	.	.	+	+	.	.	.	.	+	+	.	1	+
Agrostis castellana	.	.	.	.	.	.	1	.	.	.	1	1	.	+	.	.	1	.	.	.	1	1	1	+	1
Geum urbanum	+	.	+	+	.	.	.	.	.	+	.	.	.	.	.	.	.	1	+	.	+	+	+	.	.
Lactuca viminea	.	.	.	.	.	.	.	+	.	+	.	+	.	.	.	.	.	.	+	.	.	.	.	+	+
Anthriscus sylvestris	.	.	.	.	.	.	.	.	.	.	+	.	+	.	+	.	.	.	.	1	.	+	.	.	+
Campanula rapunculus	.	+	.	.	.	.	.	.	.	.	1	.	.	.	.	1	.	.	.	.	.	+	.	+	.
Arrhenatherum album	.	+	.	.	.	.	.	.	1	2	.	.	.	.	.	.	.	+	.	.	.	.	.	2	.
Centaurea alba	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	1	1	.	.	.	.	+	.	.	.
Thymus pulegioides	.	.	+	.	.	.	.	.	.	.	1	.	.	.	.	+	.	.	.	.	+	.	.	.	.
Luzula campestris	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	1	+	.	.	.	+	.	.	.	.
Festuca rivas-martinezii	.	.	.	2	.	.	.	.	.	.	.	+	.	.	+	.	2	.	.	.	.	.	.	.	.
Acinos alpinus subsp. *meridionalis*	.	.	+	.	.	.	+	+	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.
Hypericum perforatum	.	.	.	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Galium aparine	.	+	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	+	.	.
Luzula lactea	.	.	.	.	1	.	.	1	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
Festuca rothmaleri	.	.	.	.	.	.	2	.	.	.	.	.	.	.	+	.	.	.	.	.	+	.	.	.	.
Sanguisorba verrucosa	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	.	.	.	.	.	.	.	+
Stipa gigantea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+
Galium pumilum subsp. *rivulare*	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
Hypochoeris radicata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+

(continued)

Table 2 (continued)

N. relevé	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Exposure	NE	–	–	–	NE	E	SE	W	–	–	NE	SE	NE	N	NE	SE	SE	SW	NE	NW	–	NW	–	NE	E
Altitude (1 = 10 m asl)	150	119	110	115	124	115	130	100	121	144	120	153	140	116	115	123	135	144	113	119	109	119	142	118	115
Crucianella angustifolia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	+
Thapsia villosa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	+	.	.
Genista anglica	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.
Torilis arvensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	1	.	.	.	.
Heracleum sphondylium	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	+	.	.	.	.	.	.	.
Galium verum	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.
Ranunculus ollisiponensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	.
Asphodelus albus	.	.	.	.	.	.	+	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.
Nepeta coerulea	.	.	.	.	.	.	.	.	+	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.
Cucubalus baccifer	.	.	.	.	.	.	.	.	+	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Other species: *Melica uniflora* 2, *Melampyrum pratense* 1, *Stellaria holostea* 1, *Galium rotundifolium* 1, *Sanicula europaea* 1, *Cystopteris fragilis* +, *Lactuca muralis* +, *Ilex aquifolium* + in 1; *Fragaria vesca* + in 2; *Holcus lanatus* 1 in 3; *Lathyrus linifolius* 2, *Hypericum montanum* + in 6; *Allium massaesylum* + in 7; *Pinus pinaster* s.l. 2, *Milium vernale* 1, *Avenella flexuosa* subsp. *iberica* 1, *Carex distachya* + in 8; *Sorbus aria* 1, *Vincetoxicum nigrum* + in 9; *Genista cinerascens* in 12; *Quercus rotundifolia* +, *Knautia arvensis* +, *Hepipactis helleborine* +, *Lilium martagon* +, *Scabiosa columbaria* + in 13; *Asplenium adiantum-nigrum* +, *Galium mollugo* + in 14; *Helictochloa marginata* +, *Cytisus striatus* + in 16; *Calluna vulgaris* +, *Frangula alnus* in 19; *Juglans regia* 1, *Adenocarpus anisochilus* + in 20

Localities: 1. Cerezo de arriba (La Pinilla), 2. Riaza, 3. Villarejo (Sto. Tomé del puerto), 4. Cerezo de Arriba (Segovia), 5. Embalse de Becerril de la Sierra, 6. Miraflores de la Sierra (Madrid), 7. Navamorcuende (Toledo), 8. Barranco "Casa Forestal Las Juntas", 9. Muñotelo (Ávila), 10. Mengamuñoz (Ávila), 11. Nava del Barco (Ávila), 12. Tremedal (Ávila), 13. Navacepedilla de Corneja (Ávila), 14. Villafranca de la Sierra (Ávila), 15. Piedrahita de la Sierra (Ávila), 16. Serranillos (Ávila), 17. Zapardiel de la Ribera (Ávila), 18. Navacepeda de Tormes (Ávila), 19. Navamojada (Ávila), 20. Navalonguilla (Ávila), 21. Navamures (Ávila), 22. Gil Garcia (Ávila), 23. La Lastra del Cano (Ávila), 24. Becedas (Ávila), 25. Bejar (Salamanca)

Holco mollis-Quercetum pyrenaicae and *Pulmonario longifoliae-Quercetum pyrenaicae*, together with *Genisto falcateae-Quercetum pyrenaicae* (Table 3), occur in areas transitional between the temperate and Mediterranean regions, thus still receiving an adequate water supply (mainly *Holco-Quercetum*). Replacement communities include brooms (mainly *Genista*) and heaths (*Cytiso striati-Genistetum polygaliphyllae*, *Cytiso scoparii-Genistetum polygaliphyllae*, *Arctostaphylo crassifoliae-Daboecietum cantabricae*).

Genisto falcatae-Quercetum pyrenaicae and *Pyro bourgaeanae-Quercetum pyrenaicae* correspond to the northern plateau and surrounding forests, with different degrees of precipitation and continentality. In general, *Genisto-Quercetum* occurs in the most humid situations (connecting with *Holco mollis-Quercetum pyrenaicae* at higher altitudes or wetter locations) and includes shrub heaths as a replacement community (*Pterosparto lasianthi-Ericetum cinereae*). Both share *Genista hystrix* in their replacement communities (*Genisto hystricis-Cytisetum multiflori*, Table 3).

Arbuto unedonis-Quercetum pyrenaicae and *Sorbo torminalis-Quercetum pyrenaicae* are the southernmost communities in this area, occurring where temperatures are higher and there is higher rainfall retention. Thus, the replacement scrub includes heathlands (*Halimio ocymoidis-Ericetum umbellatae* and *Cytisetum multifloro-eriocarpi*). The first of these occupies meso-Mediterranean sites (below 1000 m) and is therefore enriched with thermophilous species typical of moderately humid forests of *Quercus rotundifolia* Lam. and *Quercus suber* (*Quercetea ilicis*), such as *Ruscus aculeatus*, *Arbutus unedo*, *Phillyrea angustifolia*, *Carex distachya*, *Rubia peregrina* and *Asparagus acutifolius* (Table 4). *Sorbo-Quercetum* grows above 1000 m and includes species such as *Sorbus torminalis* and *Sorbus aria*, relinquishing the thermophilous character noted above for *Arbuto-Quercetum*.

Western Iberia also constitutes the potential area of seral communities included in the ***Citysetea scopario-striati*** class (Gavilán et al. 2011), and their alliances could serve as a discriminant factor within our forest. In general terms, the ***Ulici europaei-Genistion polygaliiphyllae*** and ***Genistion polygaliiphyllae*** alliances are northwestern forests (4a and Ta, see Table 1) (thus *Holco-* and *Pulmonario-* but also *Linario-Quercetum*). Central communities are usually accompanied by the ***Genistion floridae*** alliance (4a and 4b, Table 1) (*Luzulo-Quercetum*) and graminoid species from *Festucion merinoi* (*Festuco merinoi-Quercetum*). Finally, northern-plateau forests such as *Genisto-Quercetum*, *Pyro-Quercetum*, but also *Festuco merinoi-Quercetum* include species from ***Cytisenion multiflori*** as replacement shrubs.

As the main distribution area of these forests, western Iberia is closely linked (bioclimatically) to their needs. There are two general characteristics that describe this: a strong Atlantic influence and a dominance of siliceous substrates. The first is more complex. The Atlantic Ocean establishes the maximum rainfall in the winter period and increases humidity in the atmosphere of western forests. This latter factor, together with precipitation levels, appears in a decreasing gradient from coastal to inland localities. Thus the westernmost communities (*Genisto-Quercetum*, *Holco-Quercetum*, *Sorbo-Quercetum*, *Arbuto-Quercetum*) enjoy a

Table 3 Phytosociological associations of *Quercus pyrenaica* in the Sistema Central of the Iberian Peninsula. *Holco molli-Quercetum pyrenaicae* (1–5), *Genisto falcateae-Quercetum pyrenaicae* (5–18) (*Quercenion pyrenaicae*, *Quercion pyrenaicae*, *Quercetalia roboris*, *Querco-Fagetea*)

N. relevé	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Exposure	NW	–	N	NW	SW	NW	NE	N	N	NW	W	–	NE	NW	–	NW	NE	NE
Altitude (1 = 10 m asl)	90	90	103	98	97	97	68	70	71	100	71	68	91	81	88	77	98	83
Characteristics																		
Quercus pyrenaica	5	4	4	4	4	5	5	5	4	5	5	5	4	5	5	4	2	5
Holcus mollis	1	1	1	1	2	1	2	2	2	1	.	2	.	2	2	1	1	2
Arenaria montana	.	1	1	1	1	1	1	.	+	1	.	1	+	1	.	1	1	
Aristolochia paucinervis	1	+	+	1	1	.	1	.	1	.	+	+	.	.	+	.	.	1
Viola riviniana	1	1	+	1	.	.	.	.	.	.	.	.	1	1	+	.	+	
Castanea sativa	+	.	+	+	2	.	.	.	.	.	.	.	.	.	+	.	4	+
Poa nemoralis	1	1	.	+	.	.	.	.	.	.	1	.	.	1	2	1	.	1
Sedum forsterianum	.	1	.	.	1	+	.	.	.	.	.	.	+	.	.	+	1	+
Physospermum cornubiense	2	1	.	.	1	.	.	.	.	.	1	.	1	1	2	.	.	
Prunella grandiflora	.	1	+	.	+	.	.	.	.	+	.	.	+	1	.	.	.	
Hieracium sabaudum	+	.	.	.	+	.	.	.	.	+	.	+	.	.	.	.	1	
Hedera helix	.	.	.	.	1	.	.	.	1	.	.	1	.	.	.	.	.	1
Brachypodium sylvaticum	.	.	.	.	+	.	.	.	.	+	+	1	.	.	.	.	.	
Hyacinthoides non-scripta	.	.	.	.	.	.	.	+	.	.	.	+	.	.	.	.	.	1
Veronica officinalis	.	.	1	.	.	.	.	.	.	+	.	.	.	.	.	.	+	
Primula veris s.l.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1
Milium vernale	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	1	.	
Crepis lampsanoides	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	
Differentials																		
Erica australis subsp. *aragonensis*	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Luzula lactea	.	.	1	+	+	.	.	.	.	.	.	.	.	.	.	.	.	
Genista falcata	1	.	1	.	1	2	.	.	.	2	.	.	.	1	3	.	1	

Cytisus striatus	.	.	.	.	.	.	.	+	.	.	.	.	.	+	.	.	.	+
Cytisus multiflorus	.	.	.	.	.	.	+	1	+	.	.	1	.	1	.	2	.	
Cytisus scoparius	.	.	.	.	.	1	1	.	.	.	.	1	.	.	.	.	1	1
Genista hystrix	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	
Trifolio-Geranietea and *Rhamno-Prunetea* characteristics																		
Conopodium subcarneum	1	+	+	+	+	1	.	1	1	1	1	1	1	1	1	1	.	1
Silene nutans	1	1	1	1	1	1	+	1	+	.	.	.	1	1	1	1	1	1
Clinopodium vulgare	+	1	1	1	1	1	1	.	.	1	+	1	.	1	1	1	1	1
Carex muricata subsp. *pairae*	1	.	+	1	1	.	1	1	.	.	1	1	.	.	1	.	+	+
Teucrium scorodonia	2	+	+	.	1	.	.	+	1	.	.	1	1	.	+	.	1	1
Lonicera periclymenum subsp. *hispanica*	+	.	+	.	.	.	.	1	1	.	1	1	.	.	1	.	1	1
Cruciata glabra	1	.	+	1	1	1	.	.	.	1	1	.	.	1	.	.	1	1
Crataegus monogyna	+	1	.	.	.	.	+	1	.	+	1	1	.	.	1	1	.	
Silene latifolia	.	.	.	.	+	.	1	+	.	.	.	1	.	.	1	1	.	
Lapsana communis	+	.	.	.	.	.	1	.	.	.	1	.	.	.	1	+	.	
Prunus spinosa	+	.	.	.	+	.	.	.	.	.	.	.	.	.	+	.	.	+
Viola odorata	1	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	1
Origanum virens	.	.	1	+	+	.	.	.	.	.	.	.	.	.	.	.	.	1
Tamus communis	.	.	.	.	+	.	.	.	.	.	.	1	.	.	.	.	.	1
Linaria triornithophora	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	+
Ornithogalum pyrenaicum	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	1
Astragalus glycyphyllos	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	+	.
Conopodium pyrenaeum	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.
Polygonatum odoratum	.	.	+	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.
Shrub and forest companions																		
Pteridium aquilinum	2	2	2	2	3	.	.	.	.	.	.	.	4	3	.	2	2	1
Daphne gnidium	.	.	.	.	+	1	1	1	.	.	1	1	.	.	1	2	.	.

(continued)

Table 3 (continued)

N. relevé	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Exposure	NW	–	N	NW	SW	NW	NE	N	N	NW	W	–	NE	NW	–	NW	NE	NE
Altitude (1 = 10 m asl)	90	90	103	98	97	97	68	70	71	100	71	68	91	81	88	77	98	83
Paeonia broteri	.	.	.	.	.	.	2	.	.	.	.	+	.	.	.	.	.	1
Genista tournefortii	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	+	.
Cistus psilosepalus	.	.	.	.	.	.	.	.	+	.	.	.	.	r	.	.	1	.
Quercus rotundifolia	.	.	.	.	.	.	.	.	r	.	.	.	.	.	+	.	.	.
Companions																		
Dactylis glomerata	.	+	+	1	+	1	1	1	+	+	2	1	1	+	.	2	+	+
Erica arborea	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.
Pinus pinaster s.l.	+	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.
Bryonia dioica	.	.	.	.	.	.	1	1	+	+	+	.	.	.	+	+	1	+
Companions																		
Anthoxanthum odoratum	1	.	1	.	1	1	.	.	.	1	.	.	.	1	1	1	1	.
Helictochloa marginata	.	+	1	1	+	+	.	.	.	1	.	.	1	1	.	.	1	.
Holcus lanatus	1	.	.	.	+	+	.	+	.	1	1	.	.	.	+	.	.	+
Agrostis castellana	.	.	.	1	.	1	1	1		1	2	+	.	.	.	.	1	.
Galium mollugo	.	+	.	.	.	.	.	+	.	.	.	+	+	.	1	+	.	+
Acinos alpinus subsp. *meridionalis*	+	+	.	.	.	.	.	.	+	.	.	.	+	+	+	.	.	.
Campanula rapunculus	.	+	.	.	+	+	.	.	+	.	+	.	.	.	.	.	+	.
Rumex acetosa	.	.	.	.	+	.	.	.	.	.	.	1	.	.	1	1	.	1
Thapsia villosa	.	.	.	.	+	+	.	.	+	.	+	.	.	.	.	.	+	.
Simethis mattiazzii	.	1	.	.	.	.	.	.	.	.	1		1	1	1	.	.	.
Asphodelus albus	.	.	.	.	.	.	.	+	.	.	+	+		+	2	.	.	.
Euphorbia oxyphylla	.	.	.	.	.	.	2	.	1	.	.	.	.	.	.	1	.	+
Poa pratensis	.	.	.	.	.	.	+	.	.	+	2	.	.	.	.	.	+	
Geranium lucidum	.	.	.	.	.	.	1		+	.	+	.	.	.	+	.	.	.

Thapsia maxima	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	+	.	.
Calluna vulgaris	.	+	.	.	.	.	.	.	.	1	.	.	.	.	.	.	+	.
Halimium ocymoides	.	+	1	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.
Pentaglottis sempervirens	+	.	+	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.
Trachynia distachya	.	.	.	.	.	.	+	1	+	.	.	.	.	.	.	.	.	.
Arrhenatherum album	.	.	.	.	+	.	1	.	2	.	.	.	.	.	.	.	.	.
Stipa gigantea	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	+
Thesium humifusum	.	.	.	.	.	.	+	.	.	.	.	.	.	+	.	.	.	.
Torilis arvensis	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.
Briza maxima	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.
Trisetum flavescens	.	.	.	+	.	1	.	.	.	.	.	.	.	.	.	.	.	.

Other species—Characteristics: *Geum sylvaticum* 1 in 2; *Cephalanthera longifolia* 1 in 5; *Quercus broteroi* + in 15; *Festuca* aggr. *rubra* 1 in 16. Differentials: *Melampyrum pratense* 2, *Erica australis* 1 in 2; *Melica uniflora* 1 in 5. Companions: *Allium massaessylum* + in 4, *Euphorbia amygdaloides* + in 7, *Lactuca viminea* + in 9; *Lathyrus niger* 1, *Festuca rivas-martinezii* 1 in 10; *Prunella vulgaris* 1 in 11; *Festuca livida* 1 in 14; *Centaurea alba* + in 17 and *Prunella laciniata* + in 18

Localities: All of them from Salamanca, except four from Cáceres. 1. Navasfrías, 2. El Payo, 3. La Alberca, 4. Piornal, 5. Sequeros, 6. Casafranca, 7. Salto de Villarino, 8. El Milano, 9. Aldeavilla de la Ribera, 10. El Maillo, 11. Villasbuenas, 12. Barruecopardo, 13. El Payo, 14. Villasrrubias, 15. Casillas de flores, 16. Alberguería de Argañán, 17. Linares de Riofrío, 18. Cristóbal

Table 4 Phytosociological associations of *Quercus pyrenaica* in the Sistema Central of the Iberian Peninsula. *Arbuto unedonis-Quercetum pyrenaicae* Rivas Goday ex Rivas Martinez 1987 (*Quercenion pyrenaicae*, *Quercion pyrenaicae*, *Quercetalia roboris*, *Querco-Fagetea*)

N. relevé	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
Exposure	SW	W	N	S	–	SE	N	W	W	SW	NW	NE	NE	N	E	W	NW	NW	S	NW	SE	S	SE	NE	W	S	W	E
Altitude (1 = 10 m asl)	82	77	77	60	45	50	61	77	56	75	77	80	63	66	48	70	67	60	75	58	63	58	73	68	74	65	65	58
Characteristics																												
Quercus pyrenaica	3	3	2	2	4	5	5	4	5	5	5	5	4	5	2	4	4	4	5	3	5	5	5	4	+	+	1	+
Tamus communis	1	+	1	.	1	1	1	1	2	.	.	.	+	.	1	1	2	1	1	1	1	1	1	+	1	1	1	2
Arenaria montana	.	1	1	1	.	1	1	1	1	1	1	1	1	1	1	1	1	.	+	.	1	.	+	.	.	.	.	1
Aristolochia paucinervis	.	1	2	.	.	1	1	1	+	.	.	+	+	1	1	.	1	.	.	.	1	+	1	1	1	+	1	+
Brachypodium sylvaticum	+	1	2	+	2	.	.	.	+	+	.	.	+	+	1	+	1	1	1	.	.	+	+	.	+	+	.	.
Holcus mollis	.	1	1	1	1	1	3	2	2	1	.	.	1	2	1	+	1	.	.	1	2	1	1	.	.	.	.	.
Luzula forsteri	.	1	1	+	.	1	1	2	+	.	.	1	1	1	1	1	1	.	+	.	1	1	.	.	.	+	.	.
Silene latifolia	.	.	+	.	.	+	.	+	1	.	1	+	.	1	+	.	.	.	1	.	1	.	1	.	.	.	.	+
Castanea sativa	.	+	.	.	.	.	.	+	.	+	1	1	2	.	.	.	1	.	1	4	+	.	1	.	.	.	+	.
Melittis melissophyllum	.	1	.	.	.	.	+	+	.	.	.	.	+	.	.	.	1	.	.	.	.	.	1	.	.	.	.	+
Sedum forsterianum	.	1	+	.	1	.	.	1	.	.	.	1	+	+	.	.	1	1	.	.	.	.	.	.	.	.	.	.
Hyacinthoides non-scripta	.	.	+	.	.	.	1	1	.	.	.	+	.	+	.	+	.	.	.	.	+	.	.	.	.	.	.	.
Silene nutans	.	.	1	.	.	.	.	1	.	.	.	.	.	.	.	.	1	.	.	.	+	.	.	1	.	.	.	.
Quercus broteroi	3	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	1	+	.	.
Geum sylvaticum	.	1	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Melica uniflora	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	2
Quercus xneomairei	.	.	.	.	.	.	.	.	+	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
Primula veris s.l.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Trifolio-Geranietea and *Rhamno-Prunetea* characteristics																												
Origanum virens	+	1	1	1	1	1	+	1	1	.	.	.	.	.	1	1	1	1	1	.	.	1	.	2	1	+	.	+
Teucrium scorodonia	.	1	1	+	1	1	1	.	1	.	1	1	1	+	1	1	1	1	1	1	1	1	1	.	+	.	.	1
Clinopodium vulgare subsp. *arundanum*	.	1	1	1	.	+	1	1	1	.	.	.	.	.	.	.	1	1	1	1	.	1	1	.	+	+	.	.

Crataegus monogyna	.	.	.	+	1	+	.	.	+	.	.	.	.	+	1	+	+	1	.	1	.	1	.	.	1	.	.	+
Silene mellifera	.	1	.	.	.	+	.	.	.	.	1	1	+	1	.	+	.	.	1	.	.	.	+	.	.	.	.	+
Carex lamprocarpa	.	1	1	.	+	.	.	1	.	.	.	.	.	.	.	.	1	.	+	.	.	.	+	1	+	.	.	.
Hedera helix	.	.	+	.	+	.	.	.	2	.	1	+	1	1	+	.	2	.	.	.	+	.	.	.	+	.	.	.
Cruciata glabra	.	+	+	.	.	.	1	.	.	1	.	.	+	1	.	.	+	.	.	.	.	.	.	.	.	.	.	.
Lonicera periclymenum subsp. *hispanica*	.	.	1	.	1	2	+	+	2	.	1	.	1	1	1	+	+	.	+	1	+	.	1	+	.	.	.	.
Vicia cracca	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	+	+	+	1	.	.	.	.	.	.	.	.	.
Conopodium subcarneum	.	+	1	+	.	.	.	.	.	1	.	.	1	.	.	.	1	.	.	+	1	.	.	.	.	.	.	.
Physospermum cornubiense	.	.	.	.	.	.	.	.	.	1	.	.	1	1	.	2	1	.	.	.	.	.	.	.	.	.	.	.
Clinopodium vulgare	.	.	.	.	.	.	.	.	+	.	.	1	+	1	.	.	.	.	.	.	.	1	.	.	.	.	.	.
Tanacetum corymbosum	.	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Polygonatum odoratum	.	.	.	.	.	1	.	.	+	.	1	1	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.
Linaria triornithophora	.	.	.	.	.	.	.	.	.	.	1	+	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Biscutella valentina subsp. *pyrenaica*	+	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Rosa corymbifera	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.
Arabis stenocarpa	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Astragalus glycyphyllos	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.
Conopodium pyrenaeum	.	.	.	.	.	.	.	.	.	.	.	.	+	1	.	.	.	.	.	.	.	.	.	.	.	.	.	
Trifolium ochroleucon	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Quercetea ilicis characteristics																												
Carex distachya	2	2	2	+	2	2	.	1	.	1	+	1	+	+	.	+	2	1	1	.	1	2	1	1	1	2	2	.
Daphne gnidium	+	1	1	1	1	1	1	1	+	1	.	+	.	.	1	1	+	1	2	1	+	1	1	+	1	1	1	.
Rubia peregrina	2	2	.	1	1	1	.	+	2	1	.	.	.	.	1	1	+	1	1	.	1	1	1	2	1	1	1	.
Ruscus aculeatus	.	.	1	.	1	2	1	+	2	.	1	.	+	.	+	.	2	.	.	.	.	2	1	.	.	.	.	.
Arbutus unedo	.	.	.	2	2	.	.	.	.	+	1	1	+	1	+	2	.	.	.	2	.	.	.	.	.	.	.	.
Asplenium onopteris	.	.	+	+	+	+	.	.	.	.	1	1	.	.	1	.	.	.	+	.	+	1	.	.	.	.	.	.
Quercus rotundifolia	+	.	.	r	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	2	2	1	2	.
Phillyrea angustifolia	.	.	.	1	1	.	.	.	.	+	.	.	.	.	1	2	.	.	.	1	.	.	.	.	.	.	.	.

(continued)

Table 4 (continued)

N. relevé	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
Exposure	SW	W	N	S	–	SE	N	W	W	SW	NW	NE	NE	N	E	W	NW	NW	S	NW	SE	S	SE	NE	W	S	W	E
Altitude (1 = 10 m asl)	82	77	77	60	45	50	61	77	56	75	77	80	63	66	48	70	67	60	75	58	63	58	73	68	74	65	65	58
Asparagus acutifolius	.	.	.	.	+	2	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	.
Viburnum tinus	.	.	+	.	.	.	.	.	.	.	+	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.
Juniperus oxycedrus	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.
Quercus suber	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.
Doronicum plantagineum	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Shrub and forest companions																												
Pteridium aquilinum	1	2	2	1	.	2	4	2	1	2	+	2	2	3	1	+	+	1	4	2	.	2	1	.	+	1	1	.
Cytisus scoparius	1	.	.	.	.	1	.	1	.	.	.	1	1	+	.	+	+	.	.	+	1	1	1	.	+	+	.	+
Osyris alba	2	.	.	.	+	+	.	.	.	1	1	.	.	.	.	+	.	.	.	+	.	1	1	.	.	.	.	.
Pinus pinaster s.l.	.	4	4	5	.	.	.	.	.	+	.	+	+	.	4	1	.	.	.	.	.	.	.	.	4	5	4	.
Erica arborea	.	+	.	+	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Genista falcata	.	.	.	.	.	.	.	.	1	.	1	1	1	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.
Calluna vulgaris	.	.	.	.	.	.	.	.	.	.	.	.	1	+	.	+	+	.	.	.	.	.	.	.	.	.	.	.
Celtis australis	.	.	.	.	+	.	+	.	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pistacia terebinthus	1	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	1
Erica australis	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.
Acer monspessulanum	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	+
Cytisus multiflorus	.	.	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.
Cistus salviifolius	.	.	.	.	.	.	.	1	.	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.
Cytisus eriocarpus	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	+	.	.	.	.
Paeonia broteri	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+	.	.	.	.
Cistus psilosepalus	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.
Adenocarpus complicatus	.	.	.	.	.	.	.	.	.	+	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.
Genista florida	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Companions																												
Galium aparine	.	.	.	.	.	+	.	.	.	1	+	.	+	1	1	1	.	.	.	.	+	1	1	1	.	.	.	1
Dactylis glomerata subsp. *hispanica*	.	+	2	2	.	+	.	.	+	.	.	.	.	.	.	.	.	1	1	.	.	.	.	1	1	1	1	.

Urginea maritima	+	.	.	1	.	2	.	.	1	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	+	+	.
Bryonia dioica	.	.	.	.	.	.	+	.	.	.	.	.	+	.	.	.	.	.	.	.	+	+	1	+	.	.	.	+
Thapsia villosa	.	.	.	.	.	.	.	.	+	.	.	.	.	+	.	.	.	+	+	.	.	.	.	+	.	+	.	+
Anthoxanthum odoratum	.	.	.	.	.	.	.	.	.	.	1	1	1	1	1	.	.	1	.	.	.	.	.	.	.	.	+	.
Geranium robertianum	.	.	.	.	.	+	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	1	1	.	1	.	.	.
Lathyrus latifolius	.	.	.	+	+	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.
Asphodelus albus	.	.	.	.	.	.	2	+	.	.	1	.	.	.	.	1	.	.	.	.	.	.	+	.	.	.	.	.
Acinos alpinus subsp. *meridionalis*	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.	.	+	.	.	.	.	+	.	+	.	.	.
Torilis japonica	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.	.	.	.	.	+	+	.	.	.	.	.
Lactuca viminea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	+	.	.	.	.	+	.
Agrostis castellana	1	+	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	2	.	.	.	.	.	.	.	.	.	.
Allium massaessylum	.	.	+	.	.	.	1	.	+	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.
Helictochloa marginata	.	.	.	.	.	.	.	.	.	1	.	+	.	+	.	1	.	.	.	.	.	.	.	.	.	.	.	.
Sanguisorba verrucosa	1	.	.	.	+	+	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carlina hispanica	.	+	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	+	.
Glandora prostrata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+	+	.	.	.	.	.
Psoralea bituminosa	+	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.
Simethis mattiazzii	.	.	.	.	.	.	.	.	.	+	.	.	.	+	.	1	.	.	.	.	.	.	.	.	.	.	.	.
Stipa gigantea	.	.	+	+	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Vicia disperma	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	1
Rhagadiolus stellatus	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.
Ferula communis	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.
Vicia hirsuta	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.	.	.	.	.	.
Thapsia maxima	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.
Rumex acetosa	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
Saxifraga granulata	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Scrophularia scorodonia	.	.	.	.	.	.	.	+	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Dorycnopsis gerardi	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Galium scabrum	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Epipactis helleborine	.	+	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

(continued)

Table 4 (continued)

N. relevé	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
Exposure	SW	W	N	S	–	SE	N	W	W	SW	NW	NE	NE	N	E	W	NW	NW	S	NW	SE	S	SE	NE	W	S	W	E
Altitude (1 = 10 m asl)	82	77	77	60	45	50	61	77	56	75	77	80	63	66	48	70	67	60	75	58	63	58	73	68	74	65	65	58
Pimpinella villosa	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Vincetoxicum nigrum	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Festuca elegans subsp. *merinoi*	.	r	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Other species—Characteristics: *Viola riviniana* + in 2; *Prunus avium* + in 15; *Lilium martagon* +, *Ilex aquifolium* + in 28. *Trifolio-Geranietea* and *Rhamno-Prunetea* characteristics: *Lonicera implexa* 1, *Lonicera etrusca* 1, *Euphorbia oxyphylla* 1, *Rosa pouzinii* + in 1; *Ornithogalum pyrenaicum* + in 3; *Prunus spinosa* + in 28. Shrubs and forest companions: *Lavandula pedunculata* + in 3; *Lavandula stoechas* subsp. *luisieri* + in 17; *Olea europea* + in 20. Companions: *Bupleurum rigidum* 1, *Centaurea alba* +; *Luzula lactea* 1 in 3; *Stipa bromoides* 1, *Prunella laciniata* + in 4; *Cephalanthera longifolia* + in 7; *Carex divulsa* + in 8; *Taxus baccata* +, *Quercus robur* + in 13; *Ranunculuspaludosus* 1 in 14; *Festuca livida* 1, *Lathyrus niger* 1 in 17; *Coincya setigera* + in 18; *Galium mollugo* + in 19; *Stipa lagascae* + in 26; *Arrhenatherum album* 1, *Lilium martagon* +, *Prunus spinosa* +, *Ilex aquifolium* + in 28

Localities: 1. Real de San Vicente (Toledo), 2. El Hornillo (Ávila), 3. Guisando (Ávila), 4. Arenas de San Pedro (Ávila), 5. Candeleda (Ávila), 6. Villanueva de la Vera, 7. Jaraiz de la Vera (Cáceres), 8. Barrado (Cáceres), 9. Arroyomolinos de la Vera (Cáceres), 10. Garcibuey (Salamanca), 11. Mogarraz (Salamanca), 12. Villanueva del Conde (Salamanca), 13. Las Casas del Conde (Salamanca), 14. Miranda del Castañar (Salamanca), 15. Sotoserrano (Salamanca), 16. Herguijuelo de la Sierra (Salamanca), 17. Hervás (Cáceres), 18. Navaconejo (Cáceres), 19. El Torno (Cáceres), 20. Villanueva de la Sierra (Cáceres), 21. Hoyos (Cáceres), 22. San Martín de Trevejo (Cáceres), 23. Villamiel (Cáceres), 24. San Martín de Valdeiglesias (Madrid), 25. La Adrada (Ávila), 26. La Adrada (Ávila), 27. Casavieja (Ávila), 28. Valero de la Sierra (Salamanca) milder climate than more central ones (*Luzulo-Quercetum*, *Festuco merinoi-Quercetum*). In contrast, the Azorean anticyclone effect appears to be stronger in these westernmost communities (specifically in the south), creating its own gradient of decreasing summer drought from these areas to inland ones (Gavilán et al. 2007). Therefore *Arbuto-Quercetum* and *Sorbo-Quercetum* have drier summers than *Festuco merinoi-Quercetum* or *Luzulo forsteri-Quercetum*. It is also important to recall the latitudinal gradient that governs the peninsula, with increasing average temperatures from north to south, giving *Arbuto-Quercetum* and *Sorbo-Quercetum* the highest average temperature in the whole western series. The mainly east-west orientation of the mountain ranges allows the entry of Atlantic winds, which increase humidity and reduce thermal contrasts.

B. Eastern Mediterranean Iberia

These forests are located mainly on sites with a particular type of siliceous soil known as Triassic rodenas (*Buntsandstein* sandstones and argillites), although the flora reveals some influence of the surrounding calcareous soils. The climate is strongly Mediterranean. These two characteristics give the eastern forest a pronounced different character but also increased isolation. Rainfall is concentrated in the summer-autumn season and not in winter as in the rest of the Iberian Peninsula, allowing forests to survive in this drier zone.

The analysis of these forests as a whole, including forests in the interior (e.g. near Cuenca and Teruel), showed three major floristic distinctions within them: the connection to the Sistema Central through western siliceous species; to the northern Sistema Ibérico through nemoral-temperate species; and finally a strong Mediterranean connection through more xeric-thermophilous species such as those of *Quercetea ilicis* class (Vilches et al. 2013a). Eastern forests could generally be differentiated through these latter species but primarily through the inclusion of the calcicolous flora and, due to their isolation, a higher rate of endemism. Species of the ***Cistion laurifolii*** and ***Ericenion arboreae*** constitute the replacement communities (*Pteridio aquilini-Lavanduletum pedunculatae* and *Erico scopariae-Cistetum populifolii*). The association defined in this area for supra-mediterranean Pyrenean forests is *Cephalanthero rubrae-Quercetum*, although recently a new meso-mediterranean association has been described (*Minuartio valentinae-Quercetum* in Vilches et al. 2013b) for Castellón province.

C. Southernmost Iberia

Given its latitude, the overall temperature in this area is higher than in the rest of the peninsula, causing *Quercus pyrenaica* forests to seek humid, cooler sites in mountains or in areas reached by humid maritime air. In this area we found communities above 1600 m on the Sierra Nevada (*Adenocarpo-Quercetum*), at or above 1200 m in Jaén (*Berberido-Quercetum*) and below 1000 m near the coast at Cádiz (*Luzulo baeticae-Quercetum*), which has one of the highest annual rainfall averages on the peninsula. Again, these communities (*Berberido-Quercetum*) appear as islands of silicicolous vegetation on decarbonated soils in a predominantly calcareous substrate. The forest is enriched with “mostajo” (*Sorbus aria*), “encina” (*Quercus rotundifolia* Lam.) and “arce” (*Acer granatense* Boiss.). Species of the class

Cisto-lavanduletea stoechadis enter as replacement communities (*Cistion laurifolii: Cytiso reverchonii-Cistetum laurifolii*, *Halimio ocymoidis-Cistetum laurifolii*) with brooms, "codeseras" (*Adenocarpus decorticans*, ***Adenocarpion decorticantis*** alliance), and *Berberis hispanica* Boiss. & Reut. (*Lonicero arboreae-Berberidion hispanicae*). The most coastal community, *Luzulo baeticae-Quercetum*, also includes gorse (*Ulex borgiae*), together with species from the ***Stauracanthion boivinii*** heaths (*Genisto tridentis-Stauracanthetum boivinii* and *Calluno vulgaris-Ulicetea minoris*).

Temperate Macroclimate (Suballiance *Quercenion robori-pyrenaicae*)

Temperate climates occur only in northern Iberia. In this Euro-Siberian region (with negligible summer drought) and within its biogeographic boundaries, annual precipitation increases significantly but with a particularly marked decrease from west to east. Western associations (*Linario-Quercetum*), especially those located in transitional areas between bioclimatic regions in Galicia and even León (*Holco-Quercetum* and *Genisto-Quercetum*), show the highest levels of precipitation in this northern sector. Although included as Mediterranean associations, *Holco-Quercetum* and *Genisto-Quercetum* receive higher precipitation amounts even in summer, than does the Eurosiberian association *Melampyro-Quercetum*. The class ***Calluno vulgaris-Ulicetea minoris*** provides the main replacement communities (*Daboecio-Ulicetum cantabrici* and *Arctostaphylo crassifoliae-Daboecietum cantabricae*), together with the *Ulici europaei-Cytision striati* (*Cytisetum striati*) and *Cytision multiflori*. of the class ***Citysetea scopario-striati***.

The main influence on this northeastern community is not the Atlantic Ocean but rather humid winds from the Bay of Biscay, which lead to less rainfall, as is the case of *Lonicero-Quercetum* in valleys open to the bay (*Cytiso scoparii-Genistetum polygaliphyllae*). In general this is a highly oceanic area (higher atmospheric humidity and reduced temperature ranges), so variations in temperature, particularly in winter, are a major differential factor. The orocantabrian community *Linario-Quercetum* is characterized by lower winter temperatures (Gavilán et al. 2007) and includes ***Daboecion cantabricae*** replacement communities (*Pterosparto cantabrici-Ericetum aragonensis*, *Halimio alyssoidis-Ulicetum breoganii*).

In general (despite being favoured by forest fires), the presence in these forests of species from the genus *Ulex* (Leguminosae) highlights the oceanic character mentioned above (Vilches 2014). Specifically, *Ulex gallii* s.l. is found commonly along the coast of the Bay of Biscay: *Ulex gallii* ssp. *breoganii* in Cantabrian-Asturian valleys (linked to *Lonicero-Quercetum*), and *Ulex gallii* ssp. *gallii* in the Cantabrian-Basque (linked to *Melampyro-Quercetum*) biogeographical sectors. *Ulex europaeus* appears throughout the whole of the northwest until Portugal.

Orocantabrian forests (*Linario-Quercetum*), although closely related to both, could be distinguished through endemics such as *Linaria triornithophora* and *Glandora diffusa*, together with other species such as *Mercurialis perennis*.

Latest Syntaxonomical Review

Our latest syntaxonomical review (Vilches 2014) showed a well-established climatic differentiation of the whole forest, although certain associations presented a degree of overlap, specifically with regard to relevés assigned to *Luzulo* and *Sorbo-Quercetum*, but also to the *Linario-Quercetum*, *Holco-Quercetum* and *Genisto-Quercetum*. The maximum overlap appeared between *Genisto-* and *Holco-Quercetum*. Although overlapping and suggested as synonyms by other authors (Ladero et al. 2004), these two associations formed two different groups with different degrees of oceanic effect on their climates. This led us to consider that a change in their definition as a community would possibly be more appropriate than a synonimization. This could be the intention of Rivas-Martínez in his last review of 2011, which left *Genisto-Quercetum* as a Bercian-Sanabriensean series (supra-temperate and meso-supra-mediterranean) and *Holco-Quercetum* (meso-supra-temperate and meso-mediterranean) as a West Carpetan [near Madrid, named for a pre-Roman people] and Lusitanian-Duriensean series. This includes the plain area in León inside *Pulmonario-Quercetum* (*Festuco heterophyllae-Quercetum* in Rivas-Martínez et al. 2002). The classification of the transitional area between temperate and Mediterranean regions has been discussed in numerous papers intended to delineate more accurately the border between the two macroclimatic regions. It is worth noting here the work of Rodríguez Guitián and Ramil-Rego (2008), which contains a general summary of existing reviews and a new chorological proposal for the northwest. They join the discussion on the definition of temperate climate in this area and link it to the establishment of Pyrenean oaks. As mentioned above, this forest type has been used for the biogeographical demarcation of the peninsula on several occasions. We should recall the tendency towards continentality (in the hydric sense) acquired by *Quercus pyrenaica* forests in this humid environment, displaying contrary behaviour to the rest of the peninsula in seeking to reduce their exposure to moisture. This hydric component of continentality (Tuhkanen 1980) has already been reported by Gavilán and Fernández-González (1997) as one of the discriminant variables of west-Iberian Pyrenean forests, specifically in the Lusitanian-Duriensean sector. There is thus a gradient of decreasing moisture from the west to the interior of the peninsula in the whole range of the western associations (*Genisto-Quercetum*, *Holco-Quercetum*, *Pyro-Quercetum* and even *Arbuto-Quercetum* and *Sorbo-Quercetum*). Winter-spring precipitation distribution patterns become particularly relevant in discriminating communities in the southwest quadrant and summer patterns in the northwest quadrant (Moreno et al. 1990; del Río et al. 2007; Gavilán and Fernández-González 1997; Entrocassi et al. 2004).

It is this gradient, which combines temperature and humidity, that can reveal important differences within associations such as *Arbuto*-*Quercetum* and *Sorbo*-*Quercetum*. These southwest associations, specifically *Arbuto*-*Quercetum*, show an internal division between Plasencia and Sierra Madrona forests (with a high component of species from the *Quercetea ilicis* phytosociological class) related to *Luzulo baeticae*-*Quercetum*, versus relevés from Salamanca, Avila and Cáceres with a high component of Atlantic species such as *Holcus mollis* or *Genista falcata*, as highlighted previously by Entrocassi et al. (2004). *Sorbo*-*Quercetum* is similarly spread across a group that is rich in Atlantic species and in species from the *Agrostietalia castellanae* order, compared to another group that includes *Festucion merinoi* species in the herbaceous layer (*Festuca baetica*, *Festuca elegans* ssp. *elegans*). Atlantic groups in these two associations are represented by *Allium massaessylum*.

In fact, along this study we realised that western Mediterranean forests of *Quercus pyrenaica* in Iberia can be roughly differentiated based on their representative *Allium* specie: *Allium victorialis* (on the northern plateau), *Allium scorzonerifolium* (in the inland south-central area) and *Allium massaessylum* (in the southwest). Finally we attach phytosociological tables (Tables 2–4) from forests in the Sistema Central, showing the wide compositional variety established there.

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Mediterranean Ultramafic (Serpentine) Chaparrals of California (USA): A Geobotanical Overview

Daniel Sánchez-Mata and María Pilar Rodríguez-Rojo

Abstract Some original results are presented from almost a decade of intensive fieldwork throughout the vast California ultramafic (serpentine) area. Bioclimatic and biogeographic data were used to gain a general understanding of the specialized vegetation developed on these peculiar sites, and specifically the potential natural vegetation (considered as a xero-edaphic climax). A complete geobotanical overview is presented for one of the most typical ultramafic vegetation types, the 'serpentine chaparrals', as they are called, classically, in the literature.

Following standardized phytosociological methods, we assembled over a hundred selected relevés and studied them by numerical analyses. These studies, plus bioclimatic and biogeographical considerations, permitted recognition of five vegetation types, defined as 'ultramafic chaparrals' and considered as xero-edaphic climax vegetation. Four of these five types are proposed as new phytosociological associations. For each vegetation type we present its complete characterization, dynamics and distribution, its original phytosociological table, and the obligatory type relevé, in strict compliance with the current International Code of Phytosociological Nomenclature. All these phytosociological associations recognized are included in the alliance *Quercion duratae* (*Heteromelo arbutifoliae-Quercetea agrifoliae* class). The individual associations are *Ceanotho jepsonii-Quercetum duratae*, *Ceanotho albiflori-Quercetum duratae*, *Arctostaphylo glaucae-Quercetum duratae*, *Arctostaphylo viscidae-Quercetum duratae*, and *Hesperoyucco whipplei-Quercetum duratae*.

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Introduction

Ultramafic rocks are found worldwide, from Arctic to equatorial areas and extending into the southern hemisphere. Their peculiar chemical composition result in ultramafic (serpentine) soils. The geological features and peculiarity of these rocks give rise to the distinctive vegetation found on ultramafic soils and to the adaptation and evolution of the various plants that now thrive only in ultramafic habitats. The ecological restrictions and fragmentation of these habitats generate a large group of endemics called ultramafic or serpentine endemics.

Both the vegetation and floristic characterization of ultramafic habitats has been widely discussed worldwide in the specialized literature since the 1950s, with particular emphasis on western North America (e.g. Kruckeberg 1951, 1964, 1969, 1984, 1991, 2002; Kruckeberg and Rabinowitz 1985; Jaffré et al. 1987; Baker et al. 1992; Reeves et al. 1996, 2000; Harrison 1997, 1999; Coleman and Kruckeberg 1999; Rodríguez-Rojo et al. 2001a, b; Reeves and Adiguzel 2004; Safford et al. 2005; Alexander et al. 2007; Sánchez-Mata 2007; Rajakaruna and Boyd 2009; Ghaderian et al. 2009; Harrison and Rajakaruna 2011; Tzonev et al. 2013; among others). Recently, researchers have redoubled their interest in this kind of habitat and focused on several specific aspects, such as heavy-metal accumulation by plants growing on ultramafic soils, geoecology, biodiversity conservation, habitat conservation, sensitivity of these habitats to climate variability, and related scientific topics.

This interest by researchers has led recently to the creation of the *International Society for Serpentine Ecology* (ISES), formalized through periodic international conferences that began in 1992. The first international conference on Serpentine Ecology took place at the University of California-Davis (USA) in 1992; the second (1997) was held in Nouméa (New Caledonia); the third (1999) in Berg-en-Dal (Kruger National Park, South Africa); the fourth (2003) at Universidad de La Habana (National Botanical Garden, Havana, Cuba); the fifth (2006) at Università degli Studi di Siena (Italy); the sixth (2008) at the College of the Atlantic (Bar Harbor, Maine, USA); the seventh (2011) at the Universidade de Coimbra (Portugal); and the eighth at Malaysia (Sabah Parks) in 2014.

Background

Ultramafic areas are very well represented throughout the Pacific Northwest territories of North America. The ultramafic rocks in these areas are mainly derived from oceanic crust on the ocean floor. There is a great diversity of habitats found in ultramafic areas, and their soils support a highly valuable biodiversity. Within this broad area, California is a privileged territory. Its varied climate together with the proliferation of a massive local occurrence of ultramafics have created a hotspot of serpentine biodiversity. This natural patchiness calls for the characterization of the different vegetation types and vegetation series that are closely related to ultramafic soils and biogeographical areas. The main focus of our research is to identify mature stands of ultramafic vegetation, seral plant communities, and dynamic patterns.

The first attempt to systematize the potential natural vegetation of the Pacific Northwest territories of North America, from the point of view of modern phytosociology, and to propose a consistent biogeographical delimitation of its geographic extension was published in the late 1990s (Rivas-Martínez 1997). The monograph on the potential natural (forest) vegetation in boreal North America and in western territories with a temperate bioclimate, appeared in 1999, is a classic work on North American geobotany (Rivas-Martínez et al. 1999).

The first compilation (Rivas-Martínez 1997) consists of an in-depth systematization and the proposal for the first phytosociological vegetation classes for California. Prior work and the habitual methodology used in phytosociology and in geobotanic science enabled the monograph to provide the first publication of the classes *Heteromelo arbutifoliae-Quercetea agrifoliae* Rivas-Martínez 1997 (mediterranean sclerophyllous and marcescent forest vegetation); *Calocedro decurrentis-Pinetea jeffreyi* Rivas-Martínez & Sánchez-Mata [in Rivas-Martínez] 1997 (mediterranean-temperate conifer forest vegetation); *Artemisio tridentatae-Juniperetea osteospermae* Rivas-Martínez & Costa [in Rivas-Martínez] 1997 (xeric mediterranean-temperate forest vegetation); and *Prosopido torreyanae-Fouquierietea splendentis* Rivas-Martínez 1997 (desert and semi-desert tropical shrub vegetation).

Two large orders are recognized in the class *Heteromelo arbutifoliae-Quercetea agrifoliae*, namely a) *Quercetalia agrifolio-wislizenii* Rivas-Martínez 1997 to group the potential forest vegetation structured by *Quercus* species; and b) *Adenostomo fasciculati-Rhamnetalia croceae* Rivas-Martínez 1997, which includes seral, climatic-climax or potential scrubland and shrub vegetation of potential *Quercus* formations (climatic-climax or xero-edaphic climax).

The alliance *Quercion duratae* Sánchez-Mata, Barbour & Rodríguez-Rojo [in Rivas-Martínez] was described within the *Adenostomo fasciculati-Rhamnetalia croceae* in 1997, in order to group the climax—or sometimes seral—scrub communities (xero-edaphic climax) growing on all kinds of undisturbed ultramafic soils. The nomenclatural type of this new proposed alliance was fixed in the association *Ceanotho albiflori-Quercetum duratae* Sánchez-Mata, Barbour & Rodríguez-Rojo [in Rivas-Martínez] 1997, which included the xero-edaphic climax vegetation (ultramafic chaparrals) occurring widely throughout the northern territories on the west side of the California Great Valley. On that occasion only the type relevé was published to legitimize the new association, in addition to the alliance *Quercion duratae*. Moreover, some general comments on California ultramafic vegetation, chaparral and ultramafics have been published by Sánchez-Mata et al. (2002a, b, 2004).

In the third edition of the classic book *Terrestrial Vegetation of California* (Barbour et al. 2007) a special new chapter was devoted to California ultramafic vegetation by Sánchez-Mata (2007); California ultramafic chaparrals were under study at that time, and some considerations on their diversity and their distribution were presented.

Material and Methods

Study Area

The study area included all of California state, focusing on its ultramafic outcrops. The main sources for the selection of sampling sites were the geological map of the US Geological Survey at scale 1:2,500,000 (Anon. 1959) and detailed maps compiled in Kruckeberg's monograph on California serpentines (1984). The territories studied (Fig. 2) cover the ultramafic areas in northern, central and southern California (from Trinity to Santa Barbara counties), the San Franscico Bay area, and the Sierra Nevada foothills (from Plumas to Tulare counties). The Klamath-Siskiyou mountains were also visited, but no ultramafic (serpentine) chaparrals (*Quercion duratae*) were found.

Bioclimatic Framework

In our study we follow the bioclimatic proposals of Rivas-Martínez et al. (2007), which have been compiled and updated recently (Rivas-Martínez et al. 2011).

Generally speaking, all the California territories in the study have a Mediterranean-type climate, with upper thermo-mediterranean to upper meso-mediterranean thermotypes and upper arid to lower humid ombrotypes (see Fig. 2). The Rivas-Martínez continentality index (Ic) shows a very close correlation to ultramafic vegetation types recognized in California at the level of potential natural vegetation, including ultramafic chaparrals. Pacific coastal areas, under the influence of permanent seasonal cloud and fog cover and with a very marked oceanic character, ($Ic = 0.0–8.0$) are seen as hypoeroceanic. In this system, $Ic = 8.0–14.0$ indicates moderately hyperoceanic areas; $Ic = 14.0–17.0$ indicates oceanic areas (euoceanic); and $Ic = 17.0–28.0$ indicates moderately continental areas. Table 1 shows some selected weather stations (supporting ultramafic vegetation throughout their territory) with their bioclimatic indices as mentioned. Figure 1 includes four selected climatic ombroclimograms.

Biogeographical Remarks

The first biogeographical proposals for the characterization of the great California landscapes were published in the late 1990s (Rivas-Martínez 1997). Since this first approach, studies are underway to pinpoint and delimit the territories according to

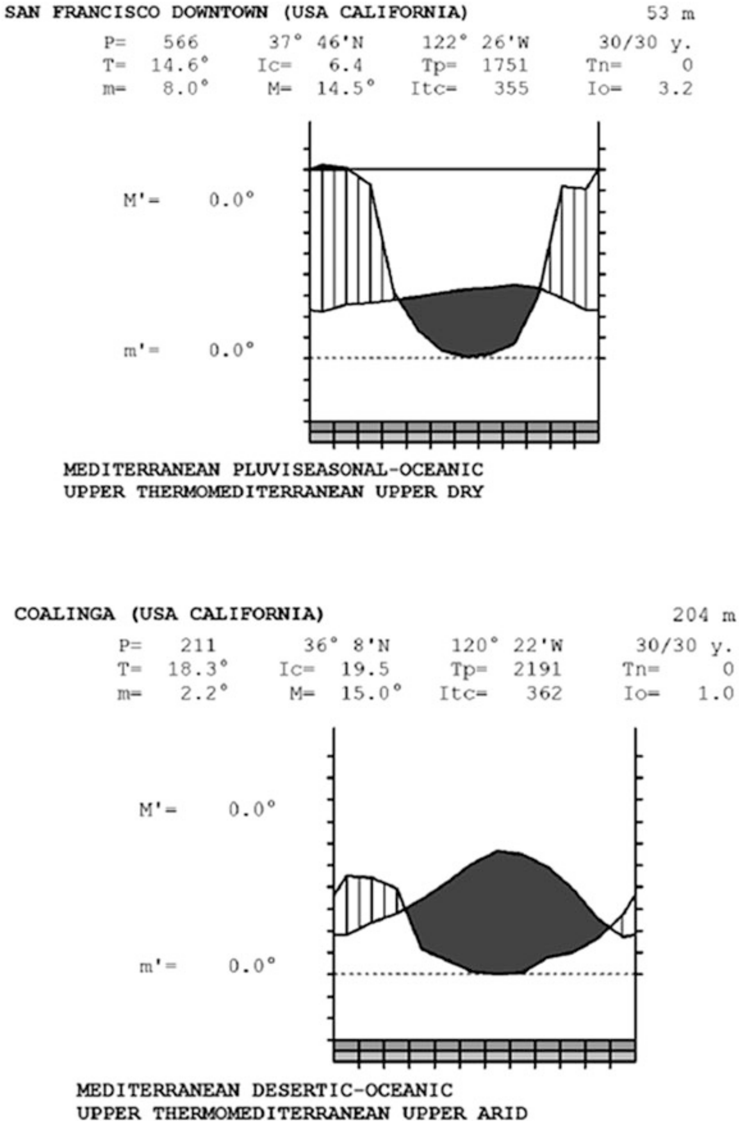


Fig. 1 (continued)

their peculiar vegetation series (involving vegetation dynamics, flora, bioclimatology, etc.). A version of the biogeographical approach to California is included in Fig. 2. The limits of the biogeographical units (still under study, in progr.) overlap the distribution of ultramafic outcrops, thereby facilitating the understanding of the geobotanical framework of our study.

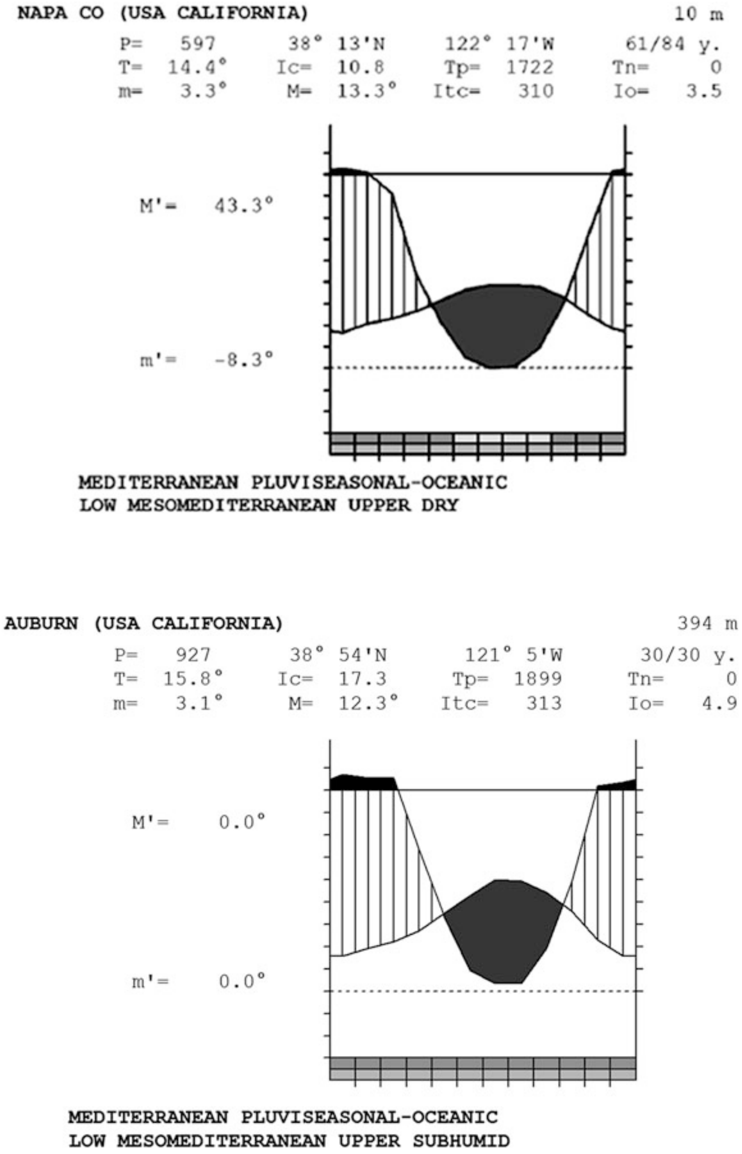


Fig. 1 Climatic diagrams (ombroclimograms) of four selected weather stations of California supporting ultramafic vegetation in their territory: San Francisco, Coalinga, Napa Co. and Auburn. *Source*: Centro de Investigaciones Fitosociologicas (CIF), www.globalbioclimatics.org

Data Sampling

We followed the phytosociological methods for vegetation sampling that use the Braun-Blanquet scale for species cover-abundances (Mueller-Dombois and Ellenberg 1974; Westhoff and van der Maarel 1978). Plot size ranged from

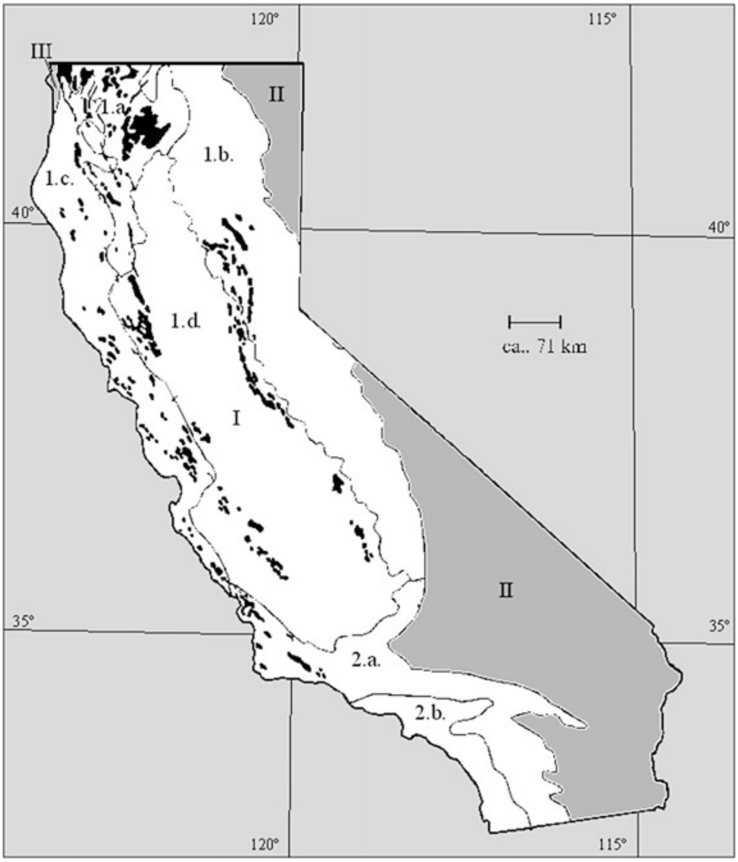


Fig. 2 Biogeographical map of the California Region (I) with the distribution of the main ultramafic (serpentine) outcrops. The biogeographical limits and unit names are adapted from Rivas-Martínez et al. (1999), and Sánchez-Mata (2007); geological information is based on Kruckeberg's map (1984) (II. Great Basin Region; III. Rocky Mountain Region) North California Province: I.1.a. Klamath-Mountains Sector; I.1.b. Sierra Nevada Sector; I.1.c. North Californian Coast Sector; I.1.d. California Great Valley Sector. South California Province: I.2.a. South Californian Ranges Sector; I.2.b. South California Coast and Channel Islands Sector

100 m^2 to 200 m^2. Environmental data collected for each site included altitude, slope, slope orientation (aspect), and geological substrate. Geographical coordinates were determined with detailed and specialized maps. The field sampling was carried out throughout the summer over 10 years.

Plant specimens were identified in consultation with the second edition of the *Jepson Manual* (Baldwin et al. 2012) and were confirmed with the collections in the Herbaria of the University of California at Davis (DAV, Center for Plant Diversity.). The taxonomic nomenclature and ranks follow the aforementioned compilation, except for a few taxa included in the Taxonomic Appendix of this paper.

Table 1 Bioclimatic indices and bioclimatic diagnosis—thermotypes and ombrotypes (Rivas-Martínez et al. 2007, 2011)

Weather station	Geographic situation	Latitude	Longitude	Altitude (m asl)	Ic	Io	Bioclimatic diagnosis
San Francisco	San Francisco Bay	37°46′ N	122°26′ W	53	6.4	3.23	Utm, Udry
Gilroy	Inner Central Coastal Ranges	37°00′ N	121°34′ W	59	12.7	2.68	Utm, Ldry
Coalinga	Inner Southern Coastal Ranges	36°08′ N	120°22′ W	204	19.5	0.96	Utm, Uarid
Napa Co.	Inner Northern Coastal Ranges	38°13′ N	122°17′ W	10	10.8	3.47	Lmm, Udry
Auburn	Sierra Nevada foothills	38°57′ N	121°05′ W	464	18.1	4.53	Lmm, Usubh
Placerville	Sierra Nevada foothills	38°43′ N	120°45′ W	789	17.5	6.72	Umm, Lhum

Ic = Tmax − Tmin; Io = Pp/Tp

Ic Continentality Index (simple), *Io* Ombrothermic Index, Thermotypes: *Lmm* lower meso-mediterranean, *Umm* upper mesomediterranean, *Utm* upper thermomediterranean; Ombrotypes: *Uarid* upper arid, *Ldry* lower dry, *Udry* upper dry, *Lsubh* lower subhumid, *Lhum* lower humid

Numerical Analyses

The total data-set of 134 relevés and 178 species was submitted to cluster analysis applying the beta-flexible linkage method (beta = −0.25) with Sorensen distance. Percentage cover values were log-transformed in order to reduce the importance of dominant species (van der Maarel 1979). The entire final data-set was subjected to detrended correspondence analysis (DCA) without down-weighting rare species. Canonical correspondence analysis (CCA) was used to test relationships of climate variables and altitude to the species composition of the vegetation data. Climate variables included annual precipitation (P); mean annual temperature (T); mean minimum temperature of the coldest month (Tmin); mean thermic amplitude (Ic, Continentality Index); and a precipitation/temperature ratio (Io, the so-called Ombrothermic Index). Climate values were obtained from the 'WorldClim model' (Hijmans et al. 2005). The explanatory power of each variable was tested with a Monte Carlo permutation test (reduced model, 999 permutations). A manual forward-selection procedure was used to select the two most important variables. Previously, all these environmental variables were projected passively onto the DCA diagram. Numerical analyses were performed with JUICE 7.0 software (Tichý 2002) combined with PC-ORD version 5 (McCune and Mefford 1999) for Cluster Analysis and CANOCO 4.5 package (ter Braak and Šmilauer 2002) for DCA and CCA.

Results

Vegetation Classification and Diversity Patterns

A partition level of five groups was chosen due to their particular floristic composition and geographic characteristics (Figs. 3 and 4, Table 2). The first partition level separates chaparrals along the east side of the California Great Valley, in the Sierra Nevada foothills (group 5), from the rest and is characterized by a 100 % presence of *Arctostaphylos viscida* (Plate 2c). At a lower partition level, chaparrals from around the Bay Area and surrounding territories (group 1 and 2) are separated from the west side (north-south) of the Great Valley ultramafic landscapes (group 3 and 4). Two groups are differentiated in the San Francisco Bay Area chaparrals: group 1 (CjQd), characterized by *Ceanothus jepsonii* (Plate 2a) from the northern Bay Area; and group 2 (AgQd), with a 100 % presence of *Arcostaphylos glauca* from the southeastern Bay Area. Differences in the floristic composition between ultramafic chaparrals from the Great Valley areas also separate the northern Great Valley (group 3, CaQd) from the southern Great Valley sites (group 4, HwQd), characterized by *Ceanothus jepsonii* subsp. *albiflorus* (Plate 2b) and *Hesperoyucca whipplei*, respectively. Constant species with a high frequency in all groups are *Quercus durata* (Plate 1d), *Ceanothus cuneatus*, *Adenostoma fasciculatum*, *Melica torreyana* and *Heteromeles arbutifolia*.

The DCA diagram in Fig. 5 shows the floristic relationships between these five groups or communities, as well as the correlation of climate and altitude variables with the ordination axes. Climate data and the geographic distribution of these five communities are also shown in Fig. 4 and Table 3 for some selected samples. As the gradient length of the first DCA axis was 2.6 s.d. (standard deviation) units, the use of unimodal ordination is quite appropriate. The first DCA axis was negatively

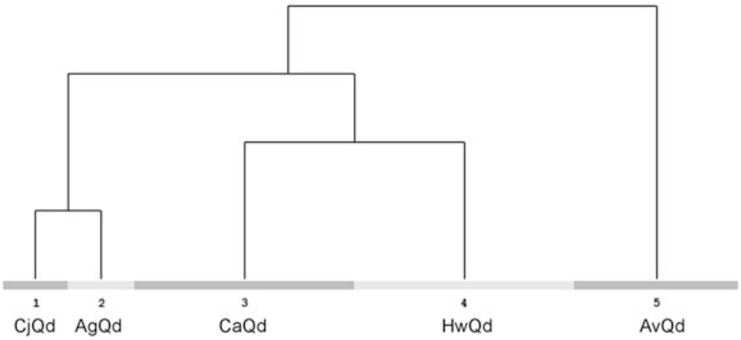


Fig. 3 Dendrogram of the flexible beta clustering ($\beta = -0.25$). Cluster abbreviations correspond to the five associations for serpentine chaparrals: AgQd, *Arctostaphylo glaucae-Quercetum duratae*; AvQd, *Arctostaphylo viscidae-Quercetum duratae*; CaQd, *Ceanotho albiflori-Quercetum duratae*; CjQd, *Ceanotho jepsonii-Quercetum duratae*; HwQd, *Hesperoyucco whipplei-Quercetum duratae*

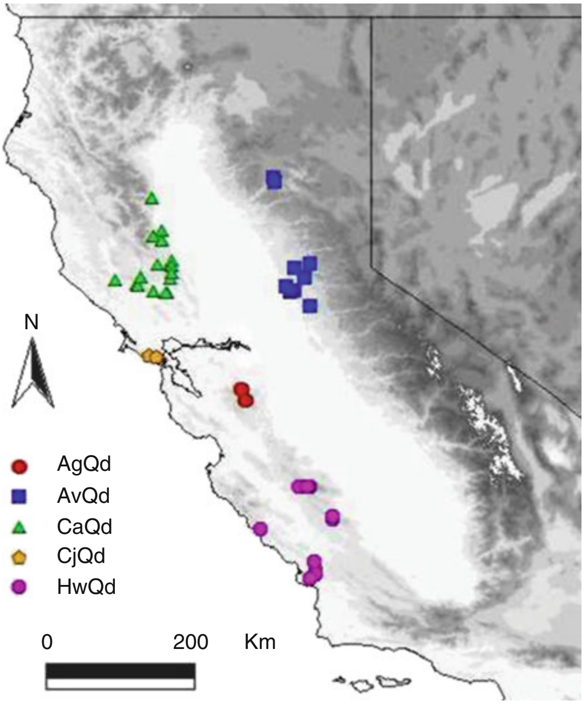


Fig. 4 Distribution map of the five recognized associations of ultramafic (serpentine) chaparrals in California. The abbreviations are those used in the Fig. 3

correlated with mean annual temperature (T) and precipitation (P), and ultramafic chaparrals of the Sierra Nevada foothills are positioned at the negative extreme of this axis. These sample sites are also located in the opposite direction to the altitude environmental arrow, which is also negatively correlated with T. The second DCA axis is positively correlated with the mean minimum temperature of the coldest month (Tmin) and negatively correlated with the continentality index (Ic). Most oceanic chaparrals from the northern Bay Area are positioned at the positive extreme of this second axis.

According to the Monte Carlo permutation test, all climate variables and altitude were also significant in CCA as explanatory variables of the variation in species composition. Variables Ic and Tmin had the strongest relationships with species composition. The lowest continentality indices are related to the northern Bay Area chaparrals (CjQd), which are closer to the coastal zone. The rest of the communities show higher values than Ic = 9, increasing as they move towards the interior of the continent; thus, the highest continentality values belong to sites located on the west side of the Great Valley (CaQd) and on the east side, in the Sierra Nevada foothills (AvQd). Differences in Tmin are also related to the differences between the mild temperatures in winter in the northern Bay Area and the lowest minimum temperatures around the Great Valley territories.

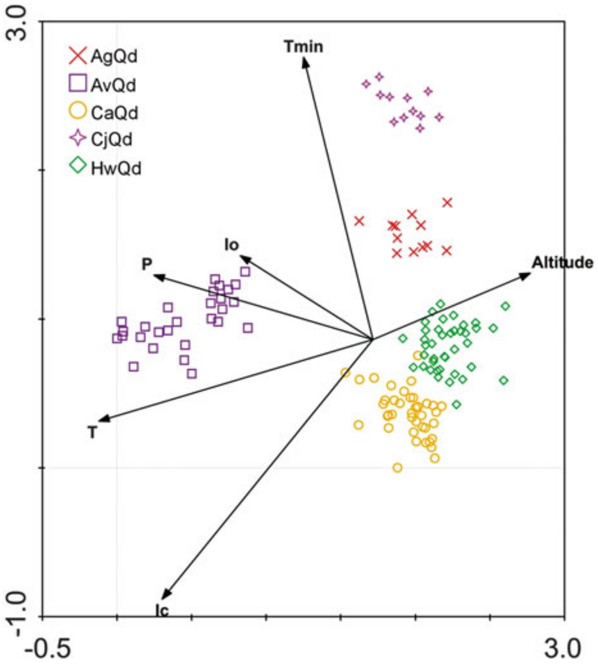


Fig. 5 DCA ordination plots (first and second axis) obtained from the vegetation data. Axis 1 and axis 2 explain 7 % and 4.8 % of the total species variability respectively. The legend shows the respective group of each sample. Environmental variables are altitude, annual mean temperature (T), mean minimum temperature of the coldest month (Tmin), annual precipitation (P), mean thermic amplitude (Ic, Continentality Index), and precipitation/temperature quotient (Io, Ombrothermic Index). The abbreviations are those used in the Fig. 3

Syntaxonomical Results: Vegetation Overview

Following the International Code of Phytosociological Nomenclature (Weber et al. 2000), we distinguished and characterized the following vegetation types as ultramafic (serpentine) chaparrals (abbreviations: s = seedling; p = parasitic plant; S2 = second stratum).

Group 1 (CjQd): ***Ceanotho jepsonii-Quercetum duratae*** ass. nova hoc loco (Table 4; *holotypus*, relevé 11*)

Hyperoceanic (subhyperoceanic) ultramafic (serpentine) chaparrals occurring throughout the northern Bay Area (Fig. 4, Table 3). *Ceanothus jepsonii*, *Arctostaphylos glandulosa*, and *Arctostaphylos montana* are indicator species of these chaparrals with hyperoceanic character. Frequent species are also *Arctostaphylos manzanita, Iris macrosiphon, Galium andrewsii* subsp. *gatense*, and *Polygala californica,* but with a wider geographic distribution towards the interior of the continent or towards the north and south. The presence of non-mature individuals of *Hesperocyparis sargentii* indicates that the potential vegetation in these areas corresponds to forests of Sargent cypress (*Hesperocyparis sargentii*) and that

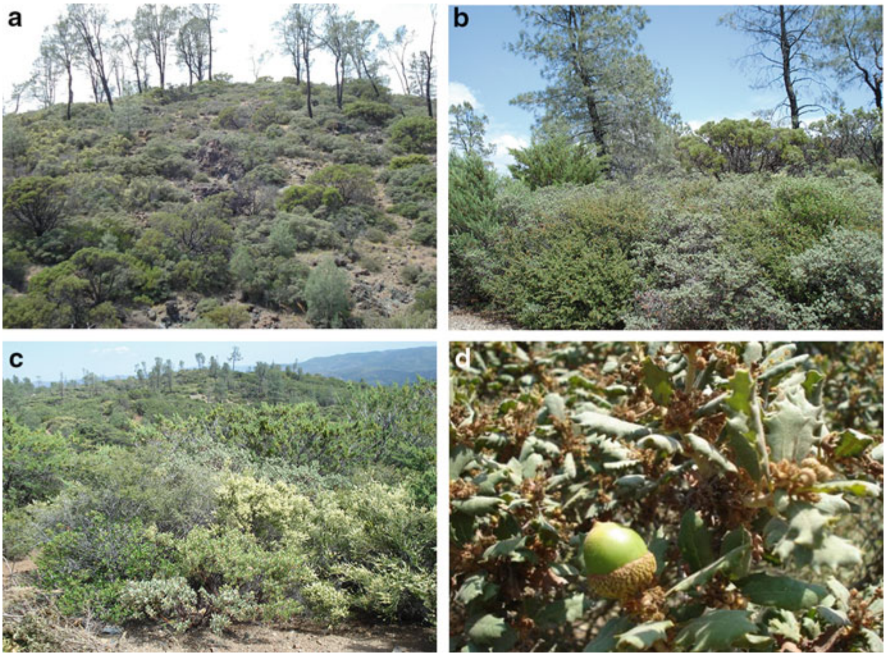


Plate 1 (*left* to *right*, *above* to *below*): (**a**) and (**b**) Structure and detail of ultramafic (serpentine) chaparrals characteristic of the west side of the California northern Great Valley (*Ceanotho albiflori-Quercetum duratae*); leather oak (*Quercus durata*) structures the shrub formation with scattered gray pines (*Pinus sabiniana*). (**c**) Shrub dynamic formation after fire as seral vegetation from *Ceanotho albiflori-Quercetum duratae*; dominant shrubs are *Adenostoma fasciculatum* (white bloom in front), *Ceanothus cuneatus*, *Arctostaphylos viscida* subsp. *pulchella*, and *Hesperocyparis macnabiana*, among others. (**d**) Detailed picture of leather oak (*Quercus durata*) with male catkins, female flowers and acorns. All the pictures from the great ultramafic areas throughout Pope Valley, Napa County

Quercus durata chaparral represents a seral stage. The total absence of *Pinus sabiniana*, as compared with its high frequency in the other communities, reveals its negative diagnostic value for hyperoceanic chaparrals. Seral ultramafic chaparrals.

Holotypus: California, Marin Co.: Mount Tamalpais State Park, 680 m, 37°55′ N and 122°25′ W; 80 % cover, 10 % slope, 100 m^2 area.

Characteristics: 4 *Quercus durata*, 2 *Heteromeles arbutifolia*, 1 *Adenostoma fasciculatum*, + *Arctostaphylos montana*, 3 *Ceanothus jepsonii*, + *Quercus wislizenii* subsp. *frutescens*, 1 *Hesperocyparis sargentii* (S2), + *Umbellularia californica* (S2), + *Pseudotsuga menziesii* (S2), + *Garrya congdonii*, + *Ceanothus cuneatus*, 2 *Melica torreyana*, 1 *Polygala californica*, + *Lomatium dasycarpum*, and + *Castilleja foliolosa*; others: 1 *Galium porrigens*, 1 *Sanicula pinnatifida*, + *Monardella purpurea*, + *Iris macrosiphon*, + *Zigadenus fremontii*, and + *Nassella pulchra*.

Group 2 (AgQd): ***Arctostaphylo glaucae-Quercetum duratae*** ass. nova hoc loco (Table 5; *holotypus*, relevé 7*)

Table 2 Synoptic table of the *Quercion duratae* chaparrals in California

Association	**CjQd**	**AgQd**	**CaQd**	**HwQd**	**AvQd**
No. of relevés	12	12	40	40	30
Diagnostic species					
Ceanothus jepsonii	100	.	.	.	.
Hesperocyparis sargentii (S2)	83	.	10	.	.
Polygala californica	83	25	20	.	.
Arctostaphylos glandulosa	67	.	.	.	.
Arctostaphylos montana	67	.	.	.	.
Iris macrosiphon	33	.	.	.	.
Umbellularia californica	67	.	20	2	43
Arctostaphylos manzanita	25	.	.	.	.
Galium andrewsii subsp. *gatense*	25	.	.	.	.
Arctostaphylos glauca	.	100	.	.	.
Ericameria arborescens	17	100	.	.	3
Juniperus californica	.	100	2	50	.
Garrya congdonii	17	100	65	32	.
Zigadenus fremontii	17	83	.	.	.
Pedicularis densiflora	17	50	5	.	.
Rhamnus crocea	.	42	5	.	.
Marah fabaceus	.	33	.	.	.
Arceuthobium campylopodum	.	25	.	.	.
Ceanothus jepsonii subsp. *albiflorus*	.	.	100	.	.
Arctostaphylos viscida subsp. *pulchella*	.	.	88	.	.
Lomatium marginatum var. *purpureum*	.	.	60	.	.
Festuca californica	.	.	58	.	.
Pickeringia montana	.	.	48	.	7
Hypericum concinnum	.	.	35	.	.
Bromus anomalus	.	.	30	.	.
Toxicodendron diversilobum	.	75	85	40	77
Eriophyllum lanatum s.l.	.	.	82	40	73
Frangula californica	.	8	38	22	.
Triteleia laxa	.	.	30	15	.
Clematis lasiantha	.	.	28	2	13
Perideridia kelloggii	.	.	25	5	.
Adiantum jordanii	.	.	22	.	.
Elymus glaucus	.	.	15	.	.
Hesperoyucca whipplei	.	.	.	100	.
Pentagramma triangularis	.	.	25	55	.
Arctostaphylos obispoensis	.	.	.	48	.
Trichostema lanatum	.	.	.	42	.
Eriodyction tomentosum	.	.	.	40	.
Ericameria nauseosa var. *mohavensis*	.	.	.	40	.
Eriophyllum confertiflorum	.	.	.	40	.
Baccharis pilularis subsp. *consanguinea*	.	.	.	35	3
Lupinus albifrons	.	.	.	30	.
Quercus berberidifolia	.	.	48	50	.
Lonicera hispidula	.	75	20	68	37
Fraxinus dipetala	.	.	18	42	.
Phoradendron villosum	.	50	.	45	13
Monardella villosa	.	.	22	38	7
Poa secunda	.	.	.	35	20
Calystegia collina s.l.	.	.	15	35	7
Mimulus aurantiacus	.	25	2	32	7
Cordylanthus tenuis var. *capillaris*	.	.	.	30	.
Pinus coulteri	.	.	.	25	.
Ceanothus oliganthus subsp. *sorediatus*	.	.	2	18	.
Chorizanthe staticoides	.	.	.	15	.

(continued)

Table 2 (continued)

Arctostaphylos viscida	.	.	.	.	100
Rhamnus ilicifolia	.	.	38	45	80
Polygala cornuta	.	.	.	.	57
Ceanothus lemmonii	.	.	.	.	40
Galium californicum subsp. *sierrae*	.	.	.	.	40
Salvia sonomensis	.	.	2	.	40
Chlorogalum grandiflorum	.	.	.	.	37
Ceanothus prostratus	.	.	.	.	37
Pinus ponderosa subsp. *pacifica*	.	.	.	.	33
Rhus tripartita	.	.	.	.	30
Lomatium dasycarpum subsp. *tomentosum*	.	.	.	.	30
Hordeum jubatum	.	.	.	.	30
Frangula californica subsp. *tomentella*	.	.	30	10	53
Eriogonum nudum s.l.	17	42	15	.	53
Quercus wislizenii subsp. *frutescens*	17	33	.	12	50
Lepechinia calycina	.	.	.	.	27
Calocedrus decurrens	.	.	.	.	23
Quercus chrysolepis	.	.	2	.	20
Wyethia reticulata	.	.	.	.	17
Constant species					
Quercus durata	100	100	100	100	100
Ceanothus cuneatus	100	100	85	85	47
Adenostoma fasciculatum	67	92	80	70	47
Melica torreyana	100	92	90	48	60
Heteromeles arbutifolia	92	75	95	95	70
Eriodyction californicum	17	50	30	48	47
Pinus sabiniana	.	100	100	80	80
Lomatium dasycarpum	42	42	15	35	.
Chlorogalum pomeridianum	.	25	30	30	.
Galium andrewsii	.	75	65	68	.
Galium porrigens	17	.	72	62	83
Melica californica	.	.	45	45	53

Columns correspond to the five clusters obtained in the beta-flexible classification. Frequency values of species in each group are shown. Only constant species with a frequency more than 40 % in at least one cluster are included. Dark grey shaded values indicate diagnostic species with $\Phi \geq 0.5$ and light grey shaded values indicate diagnostic species with $0.5 > \Phi \geq 0.25$

Oceanic (euoceanic) ultramafic (serpentine) chaparrals occurring along the southeastern San Francisco Bay Area (Diablo Ranges), characterized by *Arctostaphylos glauca*, in the central part of California (Fig. 4, Table 3). *Ericameria arborescens* and *Juniperus californica* are frequent species in these chaparrals, but they have their optimum distribution in southern California. Xero-edaphic climax ultramafic chaparrals.

Holotypus: California, Santa Clara Co.: San Antonio Valley Road, Red Mountain, 890 m, 37°23′ N and 121°30′ W; S face, 90 % cover, 5 % slope, 200 m^2 area.

Characteristics: 4 *Quercus durata*, 1 *Arctostaphylos glauca*, 1 *Ceanothus cuneatus*, + *Heteromeles arbutifolia*, 1 *Pinus sabiniana*, 1 *Garrya congdonii*, + *Juniperus californica*, 1 *Adenostoma fasciculatum*, + *Pinus sabiniana* (s), 1 *Quercus durata* (s), 2 *Melica torreyana*, 1 *Galium andrewsii*, *Phoradendron villosum* (p), + *Lomatium dasycarpum*, 1 *Castilleja foliolosa*, and + *Polygala californica*; others: + *Toxicodendron diversilobum*, + *Eriodyction californicum*, 1 *Lonicera hispidula*, + *Ericameria arborescens*, and + *Zigadenus fremontii*.

Plate 2 (*left* to *right*, *above* to *below*): Some selected shrubs frequent and characteristic of the California ultramafic (serpentine) chaparrals: (**a**) *Ceanothus jepsonii* in bloom, from the Carson Ridge ultramafic outcrops, Marin County. (**b**) Detailed branch with fruits of *Ceanothus jepsonii* subsp. *albiflorus*, from the Knoxville ultramafic area, Lake County. (**c**) *Arctostaphylos viscida* in bloom, from the ultramafic areas of Georgetown, El Dorado County. (**d**) *Fremontodendron californicum* in bloom, from the Knoxville ultramafic area, Lake County

Table 3 Geographic coordinates and climate values of ten samples with their corresponding association

Association	Deg_lon	Deg_lat	Alt (m asl)	Alt-WCM (m asl)	T (°C)	Tmin (°C)	P (mm)	Ic	Io
CjQd	−122.65	37.93	370	343	12.89	4.2	1055	8.6	6.82
CjQd	−122.58	37.91	660	527	12.61	4.1	1066	9	7.05
AgQd	−121.56	37.53	780	758	14.21	2.3	581	15.8	3.41
AgQd	−121.5	37.38	840	673	14.33	2.0	562	15.7	3.27
CaQd	−122.4	38.85	700	692	13.31	0.6	895	16.4	5.60
CaQd	−122.38	38.91	300	351	14.57	0.2	682	17.5	3.9
AvQd	−120.73	38.53	680	676	14.33	0.9	965	17.4	5.61
AvQd	−120.91	38.98	600	607	14.43	1.1	1105	17.2	6.38
HwQd	−120.76	36.35	840	834	12.99	−1.3	545	16	3.50
HwQd	−120.66	35.36	690	706	12.61	−1.4	657	10.8	4.34

Climate values were obtained from the WorldClim model (Hijmans et al. 2005)

Abbreviations: *Alt* altitude of the sampled relevé, *Alt-WCM* altitude from the WorldClim Model, *T* annual mean temperature, *Tmin* mean minimum temperature of the coldest month, *P* annual precipitation, *Ic* Continentality Index, *Io* Ombrothermic Index

Table 4 *Ceanotho jepsonii-Quercetum duratae* ass. nova *(Quercion duratae*, *Adenostomo fasciculatae-Rhamnetalia croceae*, *Heteromelo arbutifoliae-Quercetea agrifoliae)*

Altitude (1=10 m)	68	37	67	40	70	70	66	37	37	39	68	66
Number of taxa	10	11	11	11	12	12	13	13	14	20	21	24
Ordinal number	1	2	3	4	5	6	7	8	9	10	11*	12
Characteristics												
Quercus durata	4	3	4	4	4	3	4	3	4	3	4	4
Ceanothus jepsonii	1	2	1	2	1	1	1	2	1	1	3	2
Ceanothus cuneatus	+	1	1	1	+	+	+	1	1	1	+	+
Melica torreyana	+	1	2	1	2	2	2	1	+	1	2	1
Heteromeles arbutifolia	+	1	+	1	+	+	+	+	.	1	2	2
Hesperocyparis sargentii (s)	1	+	+	+	+	+	.	+	.	+	1	+
Polygala californica	1	.	.	+	1	+	+	+	1	+	1	1
Adenostoma fasciculatum	+	.	+	+	.	+	+	1	.	.	1	1
Arctostaphylos glandulosa	1	.	1	+	+	1	1	.	.	+	.	+
Arctostaphylos montana	.	+	.	.	1	+	+	+	.	+	+	1
Umbellularia californica (s)	.	+	.	.	.	+	+	+	+	+	+	+
Lomatium dasycarpum	.	+	+	.	.	+	.	+	.	.	+	.
Pseudotsuga menziesii (s)	.	.	.	.	.	.	.	+	+	+	+	+
Dendromecon rigida	.	+	.	.	.	.	+	+	.	.	.	+
Galium andrewsii subsp. *gatense*	1	.	1	.	+	.	.	.	.	.	.	.
Quercus durata (s)	.	.	+	1	.	.	1	.	.	.	.	.
Arctostaphylos manzanita	.	.	.	.	.	.	.	.	+	1	.	+
Castilleja foliolosa	.	.	.	+	.	.	.	.	.	.	+	+
Garrya congdonii	.	.	.	.	+	.	.	.	.	.	+	.
Garrya fremontii	.	.	.	.	.	.	.	.	1	1	.	.
Quercus wislizenii subsp. *frutescens*	.	.	.	.	.	.	.	.	.	.	+	1
Others												
Iris macrosiphon	.	.	.	.	.	.	.	.	1	+	+	+
Calochortus amabilis	.	1	.	.	.	.	+	.	+	.	.	.
Eriodyction californicum	.	.	.	.	.	.	.	.	1	+	.	.
Pedicularis densiflora	.	.	.	.	+	.	.	.	.	.	.	+
Ericameria arborescens	.	.	.	.	.	.	.	.	+	+	.	.
Calamagrostis ophitidis	.	.	.	.	.	.	.	.	+	+	.	.
Eriogonum nudum s.l.	.	.	.	.	.	.	.	.	.	+	.	+
Aspidotis densa	.	.	.	.	.	.	.	.	.	+	.	+
Zigadenus fremontii	.	.	.	.	.	.	.	.	.	+	+	.
Galium porrigens	.	.	.	.	.	.	.	.	.	.	1	1
Sanicula pinnatifida	.	.	.	.	.	.	.	.	.	.	1	+
Monardella purpurea	.	.	.	.	.	.	.	.	.	.	+	+
Nassella pulcra	.	.	.	.	.	.	.	.	.	.	+	+

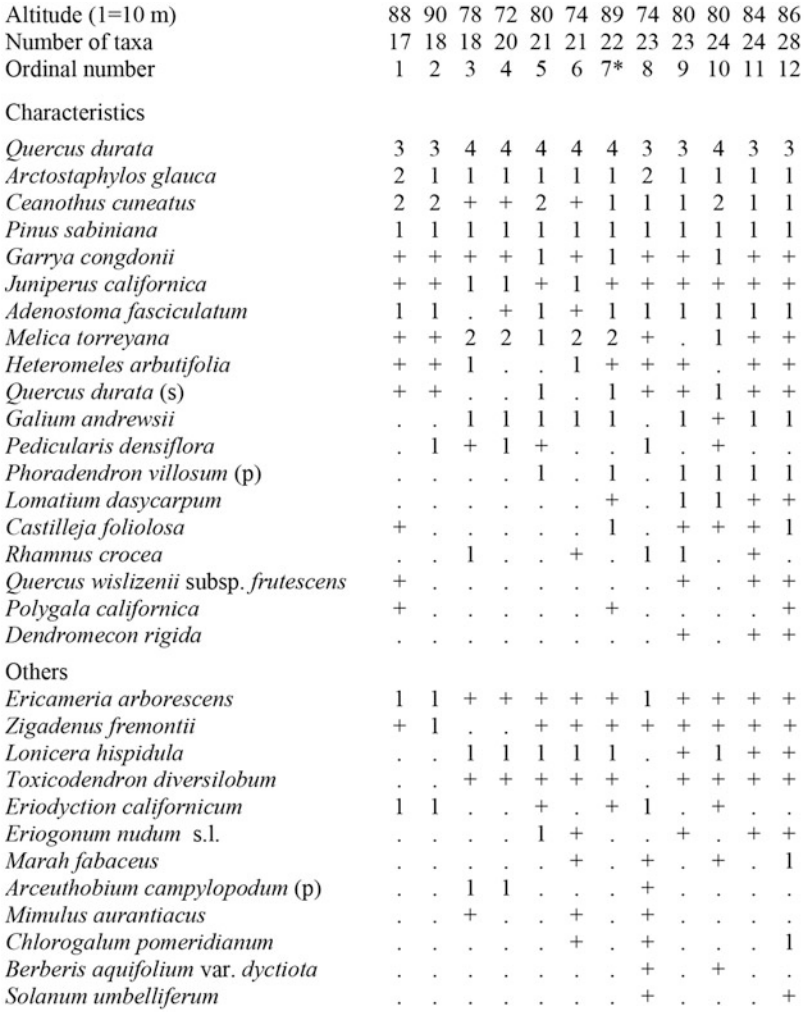
Localities (CA):

1, 3, 5–7, 11*, and 12. Marin Co.: Mount Tamalpais State Park, N37°55′–W122°25′–, 80 % cover, 10 % slope, 100 m^2 area (**holotypus associatio*: relevé 11)

2, 4, 8, 9, and 10. Marin Co.: Bolinas Road between Fairfax and Bolinas, Bolinas Ridge, N37°56′–W122°39′, W and SW faces, 90 % cover, 15 % slope, 100 m^2 area, chaparral on ultramafic soils from serpentinized bedrocks

Abbreviations: *s* seedling

Table 5 *Arctostaphylo glaucae-Quercetum duratae* ass. nova (*Quercion duratae*, *Adenostomo fasciculatae-Rhamnetalia croceae*, *Heteromelo arbutifoliae-Quercetea agrifoliae*)



Altitude (1=10 m)	88	90	78	72	80	74	89	74	80	80	84	86
Number of taxa	17	18	18	20	21	21	22	23	23	24	24	28
Ordinal number	1	2	3	4	5	6	7*	8	9	10	11	12
Characteristics												
Quercus durata	3	3	4	4	4	4	4	3	3	4	3	3
Arctostaphylos glauca	2	1	1	1	1	1	1	2	1	1	1	1
Ceanothus cuneatus	2	2	+	+	2	+	1	1	1	2	1	1
Pinus sabiniana	1	1	1	1	1	1	1	1	1	1	1	1
Garrya congdonii	+	+	+	+	1	+	1	+	+	1	+	+
Juniperus californica	+	+	1	1	+	1	+	+	+	+	+	+
Adenostoma fasciculatum	1	1	.	+	1	+	1	1	1	1	1	1
Melica torreyana	+	+	2	2	1	2	2	+	.	1	+	+
Heteromeles arbutifolia	+	+	1	.	.	1	+	+	+	.	+	+
Quercus durata (s)	+	+	.	.	1	.	1	+	+	1	+	+
Galium andrewsii	.	.	1	1	1	1	1	.	1	+	1	1
Pedicularis densiflora	.	1	+	1	+	.	.	1	.	+	.	.
Phoradendron villosum (p)	.	.	.	.	1	.	1	.	1	1	1	1
Lomatium dasycarpum	.	.	.	.	.	.	+	.	1	1	+	+
Castilleja foliolosa	+	.	.	.	.	.	1	.	+	+	+	1
Rhamnus crocea	.	.	1	.	.	+	.	1	1	.	+	.
Quercus wislizenii subsp. *frutescens*	+	.	.	.	.	.	.	.	+	.	+	+
Polygala californica	+	.	.	.	.	.	+	.	.	.	.	+
Dendromecon rigida	.	.	.	.	.	.	.	.	+	.	+	+
Others												
Ericameria arborescens	1	1	+	+	+	+	+	1	+	+	+	+
Zigadenus fremontii	+	1	.	.	+	+	+	+	+	+	+	+
Lonicera hispidula	.	.	1	1	1	1	1	.	+	1	+	+
Toxicodendron diversilobum	.	.	+	+	+	+	+	.	+	+	+	+
Eriodyction californicum	1	1	.	.	+	.	+	1	.	+	.	.
Eriogonum nudum s.l.	.	.	.	.	1	+	.	.	+	.	+	+
Marah fabaceus	.	.	.	.	.	+	.	+	.	+	.	1
Arceuthobium campylopodum (p)	.	.	1	1	.	.	.	+	.	.	.	.
Mimulus aurantiacus	.	.	+	.	.	+	.	+	.	.	.	.
Chlorogalum pomeridianum	.	.	.	.	.	+	.	+	.	.	.	1
Berberis aquifolium var. *dyctiota*	.	.	.	.	.	.	.	+	.	+	.	.
Solanum umbelliferum	.	.	.	.	.	.	.	+	.	.	.	+

Others: *Ericameria nauseosa* s.l. + in 1; *Ceanothus leucodermis* 1, *Frangula californica* 1, *Viola pedunculata* + and *Achillea millefolium* s.l. + in 2

1, 2, 7*, 11 and 12. Santa Clara Co.: S. Antonio Valley Road, Red Mountain, N37°23′–W121°30′, S, S, and SW faces, 90 %, 90 %, and 100 % cover, 5 % slope, 200 m^2 area (**holotypus associatio*: relevé 7)

3–6, 8–10. Alameda Co.: Mines Road, N37°32′–W121°34′, NE face, 80 % cover, 5 % slope, 200 m^2 area, chaparral on ultramafic soils from serpentinized bedrocks

Abbreviations: *s* seedling, *p* parasitic plant

Group 3 (CaQd): ***Ceanotho albiflori-Quercetum duratae*** Sánchez-Mata, Barbour & Rodríguez-Rojo [in Rivas-Martínez] 1997 in Itinera Geobotanica 10:40 (Table 6; *holotypus,* relevé 14*)

Oceanic (semi-hyperoceanic to semi-continental) ultramafic (serpentine) chaparrals characterized by *Ceanothus jepsonii* subsp. *albiflorus*, *Arctostaphylos viscida* subsp. *pulchella*, and *Lomatium marginatum* var. *purpureum*, with a distribution restricted to the northern Great Valley territories (Fig. 4, Table 3). These have a wide range of continentality, from Ic = 13–18, resulting from their distribution. Other frequent species in these chaparrals are *Fremontodendron californicum* (Plate 2d), *Pickeringia montana, Festuca californica, Hypericum concinnum, Eriophyllum lanatum* s.l., *Adiantum jordanii*, and *Perideridia kelloggii*. The dynamic of these chaparrals are characteristic being replaced by ultramafic (serpentine) chemise chaparrals (*Adenostomion fasciculatae*) by fire (Plate 1c). Xeroedaphic climax ultramafic chaparrals (Plate 1a, b).

Holotypus: California, Colusa Co.: 15 miles west of Williams, Blue Ridge near Bear Creek, 350 m, 39°04′ N and 122°23 W; SE face, 80 % cover, 5 % slope, 200 m^2 area.

Characteristics: 4 *Quercus durata*, 1 *Fraxinus dipetala*, 3 *Pinus sabiniana*, 2 *Ceanothus jepsonii* subsp. *albiflorus*, + *Rhamnus ilicifolia*, + *Rhus aromatica*, 1 *Arctostaphylos viscida* subsp. *pulchella*, 2 *Styrax redivivus*, 2 *Heteromeles arbutifolia*, 1 *Ceanothus cuneatus*, 1 *Garrya congdonii*, 1 *Perideridia kelloggii*, 1 *Melica torreyana*, 1 *Lomatium marginatum* var. *purpureum*, and 1 *Adiantum jordanii*; others: 2 *Toxicodendron diversilobum*, 1 *Frangula californica* subsp. *tomentella*, + *Eriodyction californicum*, 1 *Eriophyllum lanatum* s. l., + *Calamagrostis ophitidis*, 1 *Galium porrigens*, 2 *Bromus anomalus*, + *Festuca californica*, + *Elymus elymoides*, 1 *Melica californica*, and + *Elymus glaucus*.

Group 4 (HwQd): ***Hesperoyucco whipplei-Quercetum duratae*** ass. nova hoc loco (Table 7; *holotypus*, relevé 13*)

Hyperoceanic (subhyperoceanic) and oceanic (euoceanic) ultramafic (serpentine) oceanic chaparrals occurring throughout the southern Great Valley territories (Temblor Ranges) (Fig. 4, Table 3). Diagnostic species are *Hesperoyucca whipplei, Arctostaphylos obispoensis, Trichostema lanatum, Eriodyction tomentosum, Ericameria nauseosa* var. *mohavensis*, and *Eriophyllum confertiflorum*. Frequent species are *Fraxinus dipetala, Quercus berberidifolia, Ceanothus oliganthus* subsp. *sorediatus,* and *Poa secunda*. *Pinus coulterii* has a distribution restricted to west-central and southwestern California, where its presence in the ultramafic chaparrals indicates this southern character.

Holotypus: California, S. Luis Obispo Co.: Stenner Creek Road, 420 m, 35° 19′ N and 120°40′ W; N face, 90 % cover, 10 % slope, 200 m^2 area.

Characteristics: 3 *Quercus durata*, 1 *Heteromeles arbutifolia*, 3 *Ceanothus cuneatus*, 1 *Rhus aromatica*, + *Quercus berberidifolia*, + *Trichostema lanatum*, 1 *Hesperoyucca whipple*i, + *Calystegia collina* s. l., and + *Lomatium dasycarpum*; others: + *Umbellularia californica* (S2), 1 *Ceanothus leucodermis*, 1 *Toxicodendron diversilobum*, + *Frangula californica*, 1 *Artemisia californica*, + *Mimulus aurantiacus*, + *Eriodyction californicum*, + *Lotus scoparius*, 1 *Eriophyllum*

Table 6 *Ceanotho albiflori-Quercetum duratae* Sánchez-Mata, Barbour & Rodríguez-Rojo [in Rivas-Martínez] 1997 *(Quercion duratae, Adenostomo fasciculatae-Rhamnetalia croceae, Heteromelo arbutifoliae-Quercetea agrifoliae*)

Altitude (1=10 m)	52	83	78	17	64	34	38	78	27	69	32	71	69	35	73	70	45	38	72	45
Number of taxa	14	14	17	18	18	19	19	21	23	23	23	24	27	27	27	28	28	29	30	30
Ordinal number	1	2	3	4	5	6	7	8	9	10	11	12	13	14*	15	16	17	18	19	20
Characteristics																				
Quercus durata	4	3	3	4	4	4	4	4	4	5	3	4	4	4	4	4	5	5	3	4
Ceanothus jepsonii subsp. *albiflorus*	1	+	+	1	2	1	1	3	1	2	2	1	1	2	1	2	2	1	+	2
Pinus sabiniana	1	+	1	1	1	1	1	1	2	1	+	1	1	3	1	1	2	1	+	2
Arctostaphylos viscida subsp. *pulchella*	+	+	1	+	1	+	1	+	2	+	+	1	+	1	1	+	1	+	+	1
Heteromeles arbutifolia	+	2	1	1	1	+	+	.	1	1	+	1	1	2	2	+	2	2	+	3
Melica torreyana	1	.	.	+	1	1	2	1	1	1	2	+	.	1	.	2	2	3	1	2
Ceanothus cuneatus	.	.	1	.	1	+	.	1	1	2	+	2	+	1	1	+	1	+	+	+
Garrya congdonii	.	.	.	.	+	+	1	.	.	1	.	2	+	1	1	1	1	2	+	.
Adenostoma fasciculatum	+	1	.	.	1	1	+	+	1	+	.	+	1	.	1	+	.	.	.	.
Galium andrewsii	.	.	.	+	+	.	.	1	.	1	1	.	+	.	1	1	1	1	.	1
Lomatium marginatum var. *purpureum*	.	.	.	1	.	.	.	.	1	+	1	1	.	1	.	1	.	1	+	1
Pickeringia montana	.	+	.	.	.	.	.	1	+	+	.	.	1	.	+	+	.	.	.	.
Fraxinus dipetala	.	.	.	.	.	.	2	.	.	.	.	.	.	1	1	.	1	2	1	1
Calystegia collina s.l.	+	+	1	.	.	.	.	.	.	.	1	.	.	.	.	1	.	+	.	.
Lomatium dasycarpum	.	+	.	.	.	.	1	.	.	.	.	.	.	.	.	+	+	+	.	1
Rhamnus ilicifolia	.	.	.	.	.	.	1	+	.	.	+	.	.	+	.	+	.	1	.	.
Quercus berberidifolia	.	.	.	.	.	.	.	+	+	.	+	+	+	.	.	.	.	+	+	.
Polygala californica	.	.	.	1	.	.	1	.	1	.	.	.	.	.	.	.	1	.	.	.
Adiantum jordanii	.	.	.	.	.	.	1	.	.	.	.	.	.	1	.	.	.	2	.	+
Styrax redivivus	.	.	.	.	.	.	.	.	.	.	.	1	.	2	.	.	.	1	.	2
Rhus aromatica	.	.	.	.	.	+	.	+	.	.	.	.	.	+	.	.	.	.	.	.
Quercus durata x *Q. berberidifolia*	.	.	.	.	.	.	.	.	1	.	.	.	1	.	.	1	.	.	.	.
Hesperocyparis macnabiana	.	.	.	.	.	.	.	.	.	.	.	.	1	.	+	1	.	.	.	.
Fremontodendron californicum	.	.	.	.	.	.	.	.	.	.	.	.	1	.	+	+	.	.	.	.
Perideridia kelloggii	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	.	1	.
Others																				
Eriophyllum lanatum s.l.	.	+	1	.	+	+	.	+	.	+	+	1	+	1	1	1	+	+	1	+
Toxicodendron diversilobum	1	1	1	+	.	.	1	.	1	1	1	.	1	2	1	.	2	3	.	2
Galium porrigens	.	1	.	+	+	.	1	.	.	1	1	1	+	1	1	.	1	2	1	1
Bromus anomalus	+	.	1	.	+	.	1	+	.	1	.	1	.	2	.	.	1	+	1	1
Eriodyction californicum	+	1	+	.	.	+	.	+	+	+	.	1	+	+	.	+	.	+	.	.
Frangula californica subsp. *tomentella*	.	.	.	+	+	.	.	+	+	+	+	.	1	1	.	+	1	.	+	+
Festuca californica	+	.	1	1	.	.	.	1	1	.	1	.	+	+	1	+	+	.	.	.
Elymus elymoides	.	.	1	.	.	.	.	+	.	+	.	+	+	+	+	1	.	+	+	.
Cercocarpus montanus s.l.	.	+	.	.	.	+	.	.	.	1	.	1	1	.	1	.	1	1	1	.
Melica californica	.	.	.	.	+	.	1	.	1	+	.	1	.	1	.	+	.	1	.	1
Umbellularia californica (s)	+	.	+	+	.	.	.	.	1	+	1	.	.	.	.	.	1	.	1	.
Triteleia laxa	.	.	.	.	.	.	.	.	+	.	.	.	+	.	+	+	1	1	.	.
Eriogonum nudum s.l.	.	.	1	+	.	+	.	.	.	.	.	+	.	.	.	+	1	.	.	.
Chlorogalum pomeridianum	.	.	.	.	.	+	.	.	+	.	.	.	+	.	1	.	+	.	.	1
Elymus glaucus	.	.	.	.	.	.	1	+	.	.	.	.	.	+	+	.	.	1	.	+
Pentagramma triangularis	.	.	.	.	.	+	.	.	.	.	1	+	.	.	.	.	.	+	+	.
Monardella villosa	.	.	.	.	+	.	.	.	.	+	.	.	.	.	.	.	1	.	.	+
Iris douglasiana	.	.	.	1	.	.	.	.	.	.	1	.	.	+	.	.	.	.	.	.
Lonicera hispidula	.	.	.	.	.	.	+	.	.	.	.	.	.	.	+	.	1	.	.	2

Characteristics: *Frangula californica* + in 1, 1 in 3; *Clematis lasiantha* + in 4 and 19; *Castilleja foliolosa* + in 5 and 13; *Rhamnus crocea* + in 15, 1 in 20; *Aesculus californica* + in 17, 1 in 19; *Juniperus californica* 1 in 6; *Quercus agrifolia* (s) + in 19; *Quercus wislizeni* (s) + in 20; *Salvia sonomensis* + in 20. **Others:** *Hypericum concinnum* 1 in 3 and 13; *Aspidotis densa* + in 4 and 12; *Phacelia corymbosa* 1 in 5; *Stipa lemmonii* + in 6, 1 in 8; *Mimulus aurantiacus* + in 6; *Cirsium occidentale* s.l. + in 8 and 20; *Ceanothus oliganthus* subsp. *sorediatus* + in 9; *Silene californica* + in 9, 1 in 12; *Dichelostemma capitatum* 1 in 11; *Calycanthus occidentalis* 1 in 11, + in 19; *Pseudotsuga menziesii* (s) + in 11 and 19; *Keckiella lemmonii* + in 12, 1 in 19; *Calamagrostis ophitidis* + in 14; *Arceuthobium occidentale* (p) 1 and *Cercis occidentalis* (s) + in 15 and 17; *Allium falcifolium* + and *Calochortus amabilis* 1 in 16; *Hesperocyparis sargentii* (s) + in 13 and 15; *Achillea millefolium* s.l. 1 in 18 and 20; *Ribes amarum*, *Vitis californica*, *Quercus chrysolepis*, and *Dichelostemma volubile* + in 19; *Eschscholzia californica* + and *Pedicularis densiflora* 1 in 20

(continued)

Table 6 (continued)

Localities (CA):

1. Lake Co.: Middletown, Western Mine Road, N38°42′–W122°37′, E face, 80 % cover, 5 % slope, 200 m^2 area, patchy serpentinized outcrops, red soils

2. Sonoma Co.: Mercuryville-Geyserville, The Geysers Road, N38°46′–W122°48′, S face, 90 % cover, 10 % slope, 200 m^2 area, serpentinized andesite outcrops

3. Sonoma Co.: Mercuryville-Geyserville, The Geysers Road, N38°47′–W122°49′, SW face, 90 % cover, 5 % slope, 200 m^2 area, serpentinized andesite outcrops

4. Napa Co.: Middletown-Aetna Springs, Butts Canyon Road, N38°41′–W122°27′, E face, 90 % cover, 15 % slope, 200 m^2 area

5. Colusa Co.: Stonyford-Fouts Springs, Fouts Springs Road, N39°21′–W122°37′, W face, 90 % cover, 10 % slope, % slope, 200 m^2 area

6. Glenn Co.: Stonyford-Elk Creek, Stony Creek Road, N39°26′–W122°30′, SE face, 60 % cover, 5 % slope, 400 m^2 area

7. Colusa Co.: Rumsey-Bear Valley, Bear Creek, N39°00′–W122°23′, SE face, 80 % cover, 5 % slope, 200 m^2 area, masive serpentinized outcrops

8. Lake Co.: Kelseyville-Cobb, Bottle Rock Road, N38°52′–W122°46′, SW face, 80 % cover, 5 % slope, 200 m^2 area

9. Napa Co.: Moskowite Corners-Pope Valley, Chiles Pope Valley Road, N38°55′–W122°23′, E face, 90 % cover, 10 % slope, 200 m^2 area, masive serpentinized outcrops

10. Colusa Co.: Walker Ridge, Wilburg Springs-Wintun Camp, Wilbur Springs Road, N39°01′–W122°25′, E face, 80 % cover, 10 % slope, 200 m^2 area, masive serpentinized outcrops

11. Sonoma Co.: Alderglen Springs, Oat Valley, N38°50′–W122°04′, SE face, 80 % cover, 10 % slope, 200 m^2 area, masive serpentinized outcrops

12. Tehama Co.: Paskenta-Covelo, Round Valley Road, N39°49′–W122°38′, N face, 80 % cover, 15 % slope, 200 m^2 area, strongly serpentinized andesites

13. Napa Co.: Moskowite Corners-Pope Valley, Chiles Pope Valley Road, N38°55′–W122°23′, NE face, 90 % cover, 10 % slope, 200 m^2 area, masive serpentinized outcrops

14*. Colusa Co.: 15 miles West of Williams, Blue Ridge near Bear Creek, N39°04′–W122°23′, SE face, 80 % cover, 5 % slope, 200 m^2 area [reg. 59b/9-96] [**holoypus associatio*: relevé 14, cf. Rivas-Martínez 1997: 41]

15. Lake Co.: Rieff Road, Donald and Sylvia McLaughlin University of California Natural Reserve, N38°41′–W122°26′, 80 % cover, 200 m^2 area, gabbro soils

16. Lake Co.: Knoxville-Lower Lake, Morgan Valley Road near to Hunting Creek, Donald and Sylvia McLaughlin University of California Natural Reserve, N38°51′–W122°24′, 80 % cover, 5 % slope, 200 m^2 area, gabbro soils

17. Colusa Co.: Lodoga, Frenzel Creek, Mendocino National Forest, N39°18′–W122°31′, W face, 80 % cover, 10 % slope, 200 m^2 area, masive serpentinized outcrops

18. Colusa Co.: Rumsey-Bear Valley, Bear Creek, N39°00′–W122°23′, E face, 80 % cover, 5 % slope, 200 m^2 area, masive serpentinized outcrops

19. Tehama Co.: Paskenta-Covelo, Round Valley Road, N39°49′–W122°38′, E face, 60 % cover, 20 % slope, 400 m^2 area, strongly serpentinized andesites

20. Colusa Co.: Bear Valley, Bear Valley Creek, Bear Valley Road, N39°01′–W122°34′, W face, 60 % cover, 15 % slope, 400 m^2 area

Abbreviations: *s* seedling, *p* parasitic plant

confertiflorum, 1 *Galium porrigens*, + *Eschscholzia californica*, 1 *Pentagramma triangularis*, and + *Selaginella bigelovii*.

Group 5 (AvQd): ***Arctostaphylo viscidae-Quercetum duratae*** ass. nova hoc loco (Table 8; *holotypus*, relevé 7*)

Oceanic (semi-continental) ultramafic (serpentine) chaparrals from the east side of the Great Valley territories—Sierra Nevada foothills—(Fig. 4, Table 3), which

Table 7 *Hesperoyucco whipplei-Quercetum duratae* ass. nova (*Quercion duratae*, *Adenostomo fasciculatae-Rhamnetalia croceae*, *Heteromelo arbutifoliae-Quercetea agrifoliae*)

Altitude (1=10 m)	80	82	84	80	41	69	76	40	83	92	93	95	42	66	69	80	80	85	83	90
Number of taxa	13	14	15	15	16	17	17	20	20	20	21	21	22	23	26	26	26	27	27	27
Ordinal number	1	2	3	4	5	6	7	8	9	10	11	12	13*	14	15	16	17	18	19	20
Characteristics																				
Quercus durata	4	4	4	3	3	4	4	3	5	4	4	4	3	3	3	4	4	3	5	5
Hesperoyucca whipplei	1	+	1	1	+	+	1	+	+	+	+	1	1	+	+	1	+	1	1	+
Heteromeles arbutifolia	.	.	+	+	+	+	+	1	2	1	1	1	1	1	1	1	1	1	1	1
Pinus sabiniana	1	2	1	1	.	1	1	.	1	1	1	.	.	+	+	1	1	+	2	1
Ceanothus cuneatus	.	.	.	+	3	.	2	3	1	3	1	1	3	3	2	+	1	+	1	+
Adenostoma fasciculatum	.	.	.	1	.	.	1	.	+	.	.	+	.	+	+	1	1	1	1	+
Juniperus californica	1	1	1	1	.	.	1	.	.	1	1	.	.	.	.	+	.	.	1	+
Galium andrewsii	.	1	+	.	.	1	.	.	+	1	1	.	.	1	1	.	1	1	.	.
Quercus berberidifolia	.	.	+	.	+	+	+	1	.	.	.	.	+	+	1	.	+	+	.	.
Rhamnus ilicifolia	.	.	+	+	.	.	.	.	.	1	+	.	.	1	+	.	+	.	+	+
Melica torreyana	.	1	1	.	.	.	2	.	.	.	.	.	.	.	.	1	2	.	1	1
Calystegia collina s.l.	.	+	.	.	.	1	.	.	.	+	+	.	+	.	.	.	.	1	.	.
Monardella villosa	.	.	+	.	.	.	1	.	.	.	.	+	.	1	+	.	1	.	.	.
Lomatium dasycarpum	.	.	+	.	1	+	.	1	.	.	1	.	+	.	.	.	.	.	.	.
Garrya congdonii	.	.	.	+	+	.	2	.	2	.	.	.	.	.	.	.	1	1	.	.
Phoradendron villosum (p)	.	.	+	+	.	.	+	.	.	1	1	.	.	.	.	.	+	.	.	.
Arctostaphylos obispoensis	+	.	+	+	.	.	.	.	.	.	.	1	.	+	1	1	.	.	.	.
Trichostema lanatum	+	.	.	.	.	+	+	.	.	.	.	+	+	.	.	1	1	.	.	.
Fraxinus dipetala	.	+	.	+	.	+	.	.	.	.	.	+	.	.	.	1	.	.	+	1
Quercus durata x *Q. berberidifolia*	.	.	+	+	.	.	.	1	+	.	.	.	.	.	.	.	.	+	.	.
Rhus aromatica	.	.	.	+	.	.	.	.	.	.	.	+	1	.	+	+	.	.	.	.
Quercus wislizenii subsp. *frutescens*	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	+	.	.	+	+
Others																				
Lonicera hispidula	+	.	.	.	1	.	+	.	.	1	+	+	.	.	.	2	1	+	2	2
Galium porrigens	1	.	.	.	1	+	.	1	.	.	1	+	1	+	1	.	1	.	.	.
Pentagramma triangularis	+	+	.	.	+	+	.	1	.	+	1	+	1	.	+	.	.	.	.	.
Melica californica	.	+	.	.	.	.	.	.	2	1	1	1	.	.	.	1	.	2	+	1
Eriodyction californicum	.	.	.	.	.	+	+	.	+	.	.	.	+	.	.	+	+	+	+	+
Ericameria nauseosa var. *mohavensis*	+	+	1	+	.	.	.	+	+	.	.	.	.	.	.	.	+	1	.	.
Toxicodendron diversilobum	+	+	.	.	.	.	.	1	.	.	.	.	1	1	.	2	.	.	1	2
Eriophyllum confertiflorum	.	+	.	.	+	.	.	+	.	+	+	.	1	+	+	.	.	.	.	.
Eriophyllum lanatum s.l.	.	.	.	.	.	.	.	.	+	.	.	+	.	.	+	1	+	1	1	1
Baccharis pilularis subsp. *consanguinea*	.	+	.	.	.	.	.	+	.	.	.	.	.	+	+	+	.	.	+	+
Chlorogalum pomeridianum	1	.	.	.	+	+	.	.	.	1	1	+	.	.	.	.	.	.	.	.
Elymus elymoides	+	.	.	.	1	.	.	+	+	.	.	.	.	.	.	.	+	+	.	.
Cordylanthus tenuis subsp. *capillaris*	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	1	+	1	1	1
Eriodyction tomentosum	.	.	.	.	.	.	.	.	+	+	+	.	.	.	.	+	+	+	+	+
Cercocarpus montanus s.l.	.	.	.	.	.	+	+	.	+	+	.	.	.	+	.	.	+	.	.	.
Poa secunda	.	.	.	.	.	.	+	1	+	1	1	.	.	.	.	.	+	+	.	.
Mimulus aurantiacus	.	.	.	.	.	.	.	+	+	.	.	+	+	.	+	.	.	+	.	+
Lupinus albifrons	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.	+	+	+	+
Pinus coulteri	.	.	.	.	.	.	.	+	.	.	.	+	.	.	.	+	.	.	+	+
Frangula californica	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	.	.	+	.	.
Ceanothus oliganthus var. *sorediatus*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	1
Triteleia laxa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	1	1
Chorizanthe staticoides	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	1	+

Characteristics: *Quercus agrifolia* (s) + in 8 and 15; *Clematis lasiantha* 1 in 11; *Dendromecon rigida* + and *Ceanothus papillosus* 1 in 12; *Garrya elliptica* + in 15 and 1 in 14; *Dryopteris arguta* + in 15 and 14; *Monardella villosa* subsp. *obispoensis* and *Arctostaphylos pungens* 1 in 18 and 19; *Perideridia kelloggii* 1 in 19 and + in 20. **Others:** *Fritillaria viridea* + in 5 and 8; *Viola pedunculata* 1 in 5 and + in 8; *Stachys bullata* + in 5 and 14; *Iris douglasiana* and *Sanicula crassicaulis* 1 in 6; *Marah macrocarpus* 1 in 10 and + in 6; *Ceanothus integerrimus* + in 12; *Umbellularia californica* (s) +, *Artemisia californica* 1, *Eschscholzia californica* + and *Selaginella bigelovii* + in 13; *Lotus scoparius* + in 13 and 1 in 14; *Ceanothus leucodermis* 1 in 13 and 15; *Salvia mellifera* 1 in 14; *Ribes malvaceum* + in 14 and 15; *Symphoricarpos mollis* + in 15; *Argemone corymbosa* + in 16 and 19; *Frangula californica* subsp. *tomentella* + in 17 and 18;

(continued)

Table 7 (continued)

Cirsium occidentale s.l. + in 18; *Achillea millefolium* s.l. 1 in 18 and + in 9; *Sambucus mexicana* + in 20

Localities (CA):

1, 2, 3, 4, 7 and 17. S. Benito Co.: Hernandez, Clear Creak Road to S. Benito Mountain, N36°21′–W120°46′, SW face, 80 % cover, 10 % slope, 200 m^2 area, chaparrals on ultramafic soils fron masive serpentinized rocks

5. and 8. S. Luis Obispo Co.: S. Luis Obispo to Irish Hills, Prefumo Canyon Road, N35°15′–W120°44′, NW, N faces, 100 %, 90 % cover, 10 % slope, 200 m^2 area

6. S. Benito Co.: Between Bitterwater and Hernandez, Coalinga Road, Lorenzo Vasquez Canyon, N36°21′–W120°52′, N face, 70 %, 10 % slope, 200 m^2 area

9. S. Benito Co.: Hernandez, Clear Creak Road to S. Carlos Peak, North Quicksilver Trail, N36°22′–W120°44′, SW face, 80 % cover, 10 % slope, 200 m^2 area, chaparrals on ultramafic soils from masive serpentinized rocks

10. and 11. Fresno Co.: Parkfield Grade to Coalinga, Gavilan Ridge, N36°00′–W120°28′, N, E faces, 90 %, 80 % cover, 10 %, 5 % slope, 200 m^2 area, chaparrals on rocky slopes

12. Monterey Co.: Santa Lucia Range, Los Padres National Forest, Los Burros Road between Alder Peak and Lion Peak Camp, Head of Point Salmon Creek Trail, N35°51′–W121°19′, SW face, 90 % cover, 10 % slope, 200 m^2 area

13*. S. Luis Obispo Co.: S. Luis Obispo, Stenner Creek Road, N35°19′–W120°40′, N face, 90 %, 100 % cover, 10 % slope, 200 m^2 area (**holotypus associatio*: relevé 13)

14. S. Luis Obispo Co.: S. Luis Obispo, Los Padres National Forest, Cuesta Ridge Botanical Area, N35°28′–W120°41′, W face, 90 % cover, 5 % slope, 200 m^2 area

15. S. Luis Obispo Co.: S. Luis Obispo, Los Padres National Forest, Cuesta Ridge Botanical Area, N35°22′–W120°40′, W face, 80 % cover, 5 % slope, 200 m^2 area

16. Monterey Co.: Parkfield Coalinga Road to Parkfield close to Cholame Creek, N35°58′–W120°27′, SW face, 80 % cover, 10 % slope, 200 m^2 area

18. S. Benito Co.: Hernandez, Clear Creak Road to S. Carlos Peak, Cinnabar Hill, N36°22′–W120°44′, SW face, 80 % cover, 10 % slope, 200 m^2 area, chaparrals on ultramafic soils from masive serpentinized rocks

19. and 20. Fresno Co.: Parkfield Coalinga Road to Coalinga, N35°59′–W120°28′, SW face, 80 % cover, 10 % slope, 200 m^2 area

Abbreviations: *s* seedling, *p* parasitic plant

are the most inland communities of *Quercus durata* and have a semi-continental character within a narrow range of the Ic index (Ic = 17–18.5). The diagnostic species of these chaparrals are *Arctostaphylos viscida, Ceanothus lemmonii, Rhus aromatica, Ceanothus prostratus, Polygala cornuta, Galium californicum* subsp. *sierrae, Chlorogalum grandiflorum, Lomatium dasycarpum* subsp. *tomentosum*, and *Wyethia reticulata*. Above altitudes of (600)–700 m, their floristic composition is enriched by the conifer trees that are characteristic of the nearby forest vegetation on ultramafic soils: pine forests dominated by *Pinus ponderosa* subsp. *pacifica*, with *Calocedrus decurrens* and *Pseudotsuga menziesii*. All these, together with *Quercus chrysolepis*, also present in these chaparrals, are characteristic tree species of the *Calocedro-Pinetea jeffreyi* class (conifer and mixed conifer and evergreen forests of the Californian biogeographical region).

Holotypus: California, Placer Co.: Forest Hill Road to Moshiron Drive, Shady Oak Drive, 600 m, 38°59′N and 120°55′W; N face, 80 % cover, 5 % slope, 200 m^2 area.

Table 8 *Arctostaphylo viscidae-Quercetum duratae* ass. nova (*Quercion duratae*, *Adenostomo fasciculatae-Rhamnetalia croceae*, *Heteromelo arbutifoliae-Quercetea agrifoliae*)

Altitude (1=10m)	82	82	28	61	20	64	60	68	48	51	65	45	45	105	21
Number of taxa	11	12	14	17	22	22	23	23	24	25	25	25	25	26	26
Ordinal number	1	2	3	4	5	6	7*	8	9	10	11	12	13	14	15
Characteristics															
Quercus durata	3	3	4	5	4	4	4	4	3	3	4	3	4	3	3
Arctostaphylos viscida	1	1	1	1	2	1	1	2	2	2	2	2	2	2	2
Rhamnus ilicifolia	.	.	1	1	1	1	+	.	1	1	1	1	+	1	1
Pinus sabiniana	.	.	.	1	1	2	1	2	1	1	1	1	1	+	1
Heteromeles arbutifolia	.	.	.	2	1	.	2	1	1	1	2	1	1	.	1
Melica torreyana	.	1	1	2	.	1	2	.	.	.	1	1	+	.	.
Pinus sabiniana (s)	.	.	.	.	1	1	.	1	1	+	.	.	.	.	1
Chlorogalum grandiflorum	.	.	1	.	1	.	.	+	1	+	.	1	.	.	+
Quercus wislizenii subsp. *frutescens*	.	.	1	.	1	.	.	.	1	1	.	+	+	.	1
Ceanothus cuneatus	.	.	2	2	.	2	2	1	.	.	1	.	.	.	.
Polygala cornuta	.	+	.	.	.	.	.	.	+	+	.	1	1	1	.
Salvia sonomensis	.	.	.	.	2	.	.	.	1	1	.	1	1	.	2
Adenostoma fasciculatum	.	.	.	.	.	+	.	.	1	2	+	+	1	.	.
Galium californicum subsp. *sierrae*	.	.	.	.	1	.	.	1	+	1	.	.	.	.	1
Wyethia reticulata	.	.	.	.	+	.	.	1	+	1	.	1	.	.	.
Fremontodendron decumbens	.	.	.	.	.	.	.	.	1	1	.	+	1	.	.
Ceanothus roderickii	.	.	.	.	.	.	.	.	1	+	.	1	2	.	.
Rhus aromatica	.	.	.	.	+	.	.	+	.	+	.	.	.	.	1
Senecio laynae	.	.	.	.	+	.	.	.	+	.	.	.	+	.	.
Others															
Galium porrigens	.	+	.	1	1	+	1	1	+	+	1	.	+	1	1
Eriophyllum lanatum s.l.	+	+	.	.	+	+	.	1	1	+	+	.	+	1	+
Toxicodendron diversilobum	.	.	+	.	+	.	1	2	1	1	+	+	1	1	1
Eriogonum nudum s.l.	+	.	1	1	.	.	+	1	1	+	.	.	.	+	.
Melica californica	.	+	2	1	.	2	1	.	.	.	1	1	+	.	.
Frangula californica subsp. *tomentella*	.	.	+	.	.	1	.	+	.	.	1	1	1	1	+
Eriodyction californicum	.	.	.	.	+	.	.	+	+	+	.	.	+	+	+
Umbellularia californica	+	+	.	.	.	+	+	.	.	.	+	.	.	+	.
Ceanothus lemmonii	.	.	1	.	1	.	.	1	1	2	.	.	.	.	1
Pinus ponderosa subsp. *pacifica*	+	.	+	.	.	+	.	.	.	.	+	.	.	1	.
Lonicera hispidula	.	1	.	.	.	+	+	.	.	.	1	.	.	+	.
Calocedrus decurrens	.	+	.	.	.	+	.	.	.	.	+	.	.	+	.
Lomatium dasycarpum subsp. *tomentosum*	.	.	.	1	.	.	+	.	1	.	.	.	.	.	1
Lepechinia calycina	.	.	.	.	1	.	.	.	.	1	.	.	1	.	+
Hordeum jubatum	.	.	.	.	.	1	.	.	.	.	1	+	+	.	.
Quercus chrysolepis	1	1	.	.	.	.	.	.	.	.	.	.	.	1	.
Aspidotus densa	1	.	.	.	.	1	.	.	.	.	1	.	.	.	.
Pseudotsuga menziesii	.	1	.	.	.	.	.	.	.	.	+	.	.	1	.

Characteristics: *Garrya fremontii* + in 2; *Quercus douglasii* (s) + in 3; *Brodiaea minor*, *Calochortus monophyllus*, and *Helianthemum scoparium* + in 4 and 7; *Ceanothus tomentosus* 1 in 5 and + in 6; *Castilleja foliolosa* 1 in 5 and + in 6; *Calystegia collina* s.l. + in 6 and 1 in 9; *Phoradendron villosum* (p) + in 6 and 5; *Calystegia stebbinsii* + in 6; *Quercus douglasii* + in 7; *Pickeringia montana* + and *Hesperocyparis macnabiana* 1 in 8; *Clematis lasiantha* + in 8 and 15. **Others:** *Monardella stebbinsii* 1 and *Penstemon newberryi* + in 1; *Ericameria nauseosa* s.l. 1 in 1 and + in 15; *Pteridium aquilinum* subsp. *pubescens* 1, *Quercus breweri* 1, *Trientalis latifolia* 1, *Carex multicaulis* 1, *Amelanchier alnifolia* var. *semiintegrifolia* +, *Monardella villosa* s.l. + and *Polystichum imbricans* + in 2; *Ceanothus velutinus* + in 2 and 1 in 15; *Cordylanthus tenuis* var. *brunneus* + in 2 and 1 in 7; *Elymus multisetus* + in 4 and 1 in 7; *Poa secunda* and *Ceanothus prostratus* + in 4 and 7; *Allium fimbriatum* s.l. 1 in 4 and + in 7; *Selaginella hansenii* 1 in 4; *Carex brainerdii* 1 and *Cercis occidentalis* (s) + in 5 and 6; *Monardella sheltonii* + in 5 and 15; *Lotus scoparius* + in 5 and 15; *Streptanthus polygaloides* and *Allium sanbornii* 1 in 6 and 9; *Triteleia bridgesii* +, *Bromus laevipes* +, and *Luzula comosa* + in 7; *Pinus ponderosa* subsp. *pacifica* (s) + in 8; *Eschscholzia caespitosa* + in 9; *Pinus attenuata* +, *Ceanothus integerrimus* 1, *Iris douglasiana*

(continued)

Table 8 (continued)

+, *Madia elegans* 1, *Vicia americana* +, *Grindelia camporum* +, *Baccharis pilularis* subsp. *consanguinea* +, *Mimulus aurantiacus* +, and *Ericameria arborescens* + in 15

Localities (CA):

1. Plumas Co.: Plumas National Forest, between Little Caribou and Caribou, N40°04′–W121°10′, S face, 70 % cover, 20 % slope, 200 m^2 area, chaparrals on rocky slopes

2. Plumas Co.: Plumas National Forest, between Virgilia and Rich Bar, Serpentine Canyon, N40°01′–W121°09′, W face, 70 % cover, 20 % slope, 200 m^2 area, chaparrals on rocky slopes

3. El Dorado Co.: Between Rescue and Coloma, Lotus Road, N38°43′–W120°55′, NE face, 60 % cover, 5 % slope, 200 m^2 area

4. and 7*. Placer Co.: Forest Hill Road to Moshiron Drive, Shady Oak Drive, N38°59′–W120°55′, S, N faces, 80 % cover, 5 % slope, 200 m^2 area (**holotypus associatio*: relevé 7)

5. and 15. El Dorado Co.: Salmon Falls Road, N38°46′–W121°01′, S faces, 100 % cover, 5 % slope, 200 m^2 area

6. and 11. El Dorado Co.: Between Georgetown and Meadow Brook, Meadow Brook Road, Head of Traverse Creek, N38°52′–W120°48′, SW, W faces, 80 %, 60 % cover, 10 %, 5 % slope, 200 m^2 area

8. Amador Co.: Shenandoah Road to Shenandoah Valley, River Pines, N39°02′–W120°44′, E face, 100 % cover, 10 % slope, 200 m^2 area

9. and 10. El Dorado Co.: Rescue, Pine Hill, Pineoakyo Road-Sunny Hill Road, N38°43′–W120°58′, SW face, 100 % cover, 5 % slope, 200 m^2 area, dense chaparrals on ultramafic soils from gabbro rocks

12. and 13. El Dorado Co.: Rescue, Pine Hill, Pineoakyo Road, N38°42′–W120°58′, S, SE faces, 90 % cover, 10 % slope, 200 m^2 area, dense chaparrals on ultramafic soils from gabbro rocks

14. Placer Co.: Tahoe National Forest Michigan Bluff Road to Michigan Bluff, N39°02′–W120°44′, SE face, 80 % cover, 20 % slope, 200 m^2 area

Abbreviations: *s* seedling, *p* parasitic plant

Characteristics: 4 *Quercus durata*, 2 *Heteromeles arbutifolia*, 2 *Ceanothus cuneatus*, 1 *Pinus sabiniana*, + *Quercus douglasi*, 1 *Arctostaphylos viscida*, + *Rhamnus ilicifolia*, + *Helianthemum scoparium*, 2 *Melica torreyana*, + *Brodiaea minor*, and + *Calochortus monophyllus*; others: 1 *Toxicodendron diversilobum*, + *Umbellularia californica*, + *Lonicera hispidula*, + *Ceanothus prostratus*, 1 *Galium porrigens*, 1 *Elymus multisetus*, 1 *Melica californica*, + *Eriogonum nudum* s.l., + *Lomatium dasycarpum* subsp. *tomentosum*, + *Cordylanthus tenuis* var. *brunneus*, + *Poa secunda*, + *Allium fimbriatum* s.l., + *Triteleia bridgesii*, + *Bromus laevipes*, and + *Luzula comosa*.

Discussion

California ultramafic (serpentine) chaparrals support the potential vegetation on subhyperoceanic to oceanic ultramafic areas (Ic = 10–21) with (thermo)-meso-mediterranean thermotypes and with (arid) to lower humid ombrotypes. The floristic structure of this potential vegetation is composed by the leather oak (*Quercus* *durata*), the dominant character species, and by companion evergreen sclerophyllous shrubs, of which the next most frequent species are from the genera *Arctostaphylos* and *Ceanothus*. These two genera are the most diverse in California and contain many narrowly endemic taxa (Keeley and Davis 2007); they play an important role in differentiating community diversity.

Throughout California ultramafic supra-mediterranean, oro-mediterranean and oro-submediterranean (oro-temperate submediterranean) thermotype areas (mountain-high mountain areas and Klamath-Siskiyou territories), the potential ultramafic (serpentine) chaparrals are replaced by conifer forests such as: ponderosa pine (*Pinus ponderosa* subsp. *pacifica*) forests in mountain areas; Jeffrey pine (*Pinus jeffreyi*) forests at higher altitudes; northern foxtail pine (*Pinus balfouriana*) woodlands and Shasta red fir (*Abies shastensis*) in high-mountain landscapes of Shasta-Klamath-Siskiyou territories; and southern foxtail pine (*Pinus austrina*) woodlands and Critchfield red fir (*Abies critchfieldii*) woodlands in high mountains of southern Sierra Nevada.

According to our results, continentality is an important environmental factor driving the community diversity of ultramafic chaparrals. In hyperoceanic (ultrahyperoceanic, sub-hyperoceanic and euhyperoceanic) meso-mediterranean areas ($Ic < 10$) along the Pacific coast (from Mendocino to San Luis Obispo counties) and in the San Francisco Bay area, ultramafic chaparrals constitute the seral vegetation, where the potential natural vegetation is conifer forest dominated by Sargent cypress (*Hesperocyparis sargentii*). Permanent and seasonal fog, high air humidity, and the maritime oceanic realm strongly support the existence of this endemic California vegetation type, and disturbed stands of this peculiar forest vegetation allow the development of ultramafic chaparral on sunny slopes and in clearings. These climatic features are revealed (in terms of floristic composition) by the absence of *Pinus sabiniana* in the *Ceanotho jepsonii-Quercetum duratae*, the most oceanic ultramafic chaparral association, which is replaced by another conifer tree, *Hesperocyparis sargentii*, forming potential forest communities. However, differences in continentality are not so marked towards the interior of the continent (along similar altitudinal ranges), as occurs throughout the inner Coast Ranges and the Sierra Nevada foothills (Great Valley territories, west to east sides). Thus the differentiation of ultramafic chaparral communities may be explained mostly by biogeography.

In the present study, our syntaxonomical approach has considered all the leather-oak communities in California within the *Quercion duratae* alliance. The successful completion of the whole alliance will lead us to further studies on other ultramafic woody (forest) vegetation types, such as Sargent cypress forests and woodlands (*Hesperocyparis sargentii*).

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Taxonomic Appendix

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Phytosociological Appendix

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\+ *Adenostomo fasciculati-Rhamnetalia croceae* Rivas-Martínez 1997

* *Quercion duratae* Sánchez-Mata, Barbour & Rodríguez-Rojo [in Rivas-Martínez] 1997

- *Ceanotho jepsonii-Quercetum duratae* ass. nova hoc loco
- *Ceanotho albiflori-Quercetum duratae* Sánchez-Mata, Barbour & Rodríguez-Rojo [in Rivas-Martínez] 1997
- *Arctostaphylo glaucae-Quercetum duratae* ass. nova hoc loco
- *Arctostaphylo viscidae-Quercetum duratae* ass. nova hoc loco
- *Hesperoyucco whipplei-Quercetum duratae* ass. nova hoc loco

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Part III
Local Vegetation Description and Analysis

Amphibious Vegetation in the Afro-Alpine Belt and the Role of Cryoturbation in Creating Regeneration Niches

Ulrich Deil, Miguel Alvarez, and Andreas Hemp

Dedicated to Prof. Dr. Kazue Fujiwara on the occasion of her 70th birthday.

Abstract The wetland vegetation of the Afro-(sub)alpine belt, which is dominated by tussock grassland, has embedded in it ericaceous shrubs, *Helichrysum* cushions and *Carex* bogs, which constitute small microhabitats with annuals. A synopsis of these annual turfs is presented in a constancy table, based upon the available plot data (168 relevés), sampled on the tops of the high volcanoes of East Africa (3500–4500 m altitude). The results are compared with similar vegetation types in the Ethiopian Highlands, Drakensberg Mts. and Marion Island (South Africa).

Subularia monticola and *Crassula granvikii* characterize this vegetation type, together with vicarious species from the genera *Limosella*, *Crassula*, *Sagina*, *Isolepis* and *Ranunculus*. These short-living herbs regenerate and establish on open patches, created in the perennial turf by cryo- and bioturbation, by needle ice and frost-heaving, and they colonize the shores of oligotrophic lakes with fluctuating water levels, germinating under water (tenagophytes). Geocarpy is an important adaptation to soil movement in the cryoro-tropical thermoclimate.

The Afro-tropical *Subularia* communities share some floristic and ecological characteristics with boreal and subarctic littoral vegetation (Littorellion with *Subularia aquatica*) and with the Crassuletalia peduncularis-venezuelensis in the oro-tropical belt of the Andes.

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Introduction

Under climatic conditions that allow the existence of a perennial herb layer, short-living and low-growing annuals can occur only when the closed plant canopy is opened from time to time by physical or biotic disturbance. Bare ground, offering a regeneration niche for plants with low competitive ability and r-strategies, can result from lateral movements (e.g. mass movement of screes and boulders, solifluction processes, erosion or depositions of fresh sediment) or vertical movements (e.g. bio- and cryoturbation, topsoil lifting by needle ice) of the substrate. This contribution will focus on the role of cryoturbation and needle ice for creating a niche for short-living annuals.

Cryoturbation is a common phenomenon in high latitudes. The periglacial processes and the resulting relief features (stone circles, pingos, etc.) are well known, and the spatial vegetation patterns created by freezing and melting cycles have been studied intensively in many arctic and subarctic areas (see for example Kade et al. 2005; Vonlanthen et al. 2008). But cryoturbation also occurs at high altitudes, above treeline in both temperate and tropical climates. Therefore, Rivas-Martínez (1981) and Rivas-Martínez et al. (2007) distinguishes cryoro-tropical, cryoro-mediterranean and cryoro-temperate bioclimatic thermotypes. Especially in the alpine and subalpine belts of the inner Tropics, where diurnal temperature variation is greater than the seasonal variation (creating a so-called "daytime climate"), frost can occur every night.

Seasonal wetlands and amphibious environments, in the oro-tropical belt, are habitats in which annuals can compete with perennial sedges, grasses and dwarf shrubs because cryoturbation and needle-ice formation in wet or water-saturated soils can open regeneration niches for small annuals. Several seasonal wetland types can be distinguished, according to relief features and hydrology (Deil 2005; Deil et al. 2011): 1) lakeshores and small water runnels with fluctuating water level; 2) micro-pools embedded in fens, bogs and moorland; and 3) ephemeral ponds in depressions, flooded during the snow-melting period.

In the alpine belt of the Andean Cordillera, vegetation studies in seasonal wetlands are quite common. A synopsis of the plant communities growing there was recently presented by Deil et al. (2011). Some characteristic taxa among the annuals are species of the genera *Limosella* (Scrophulariaceae), *Isolepis* (Cyperaceae) and *Crassula* (Crassulaceae), which characterize the South American order Crassuletalia peduncularis-venezuelensis (Limoselletea australis). In his study about the Páramo vegetation of the Columbian Cordillera, Cleef (1981) was the first to point out the remarkable floristic similarity between the oro-tropical wetlands of South America and the Afro-alpine vegetation, where other vicariant *Crassula*, *Limosella* and *Ranunculus* species occur in such habitats.

Vegetation studies in wetlands of the Afro-alpine belt are rare. One reason might be that the area is much smaller than in South America, because the cryoro- and oro-tropical bioclimatic belt is restricted to the top of a few isolated mountains

(Mt. Elgon, Mt. Kenya, the Aberdares, Mt. Kilimanjaro, and the Ruwenzori Mts.). Only in the Ethiopian Highlands (Bale Mts. and Simian Mts.) and in the Drakensberg Mts. in South Africa are there larger areas above the treeline that are as easily accessible for research as the Altiplano of the Andes.

Early plant ecological studies of the Afro-alpine belt by Hedberg (1964) and Coe (1967) showed that, beside annuals from the genera *Crassula*, *Limosella*, *Isolepis*, *Sagina*, *Cardamine* and *Montia*, *Subularia monticola* is a characteristic element of open patches in alpine wetlands. This is confirmed by a detailed analysis of the horizontal and vertical structure of *Carex* fens on Mt. Elgon and Ruwenzori by Rejmánková and Rejmánek (1995).

Subularia (Brassicaceae) is a genus with two species (Mulligan and Calder 1964): *S. aquatica* L. is a circum-polar taxon with a centre of distribution in the boreo-atlantic Scandinavian region and with southern outliers in the Pyrenees, in Central Asia and in the Sierra Nevada of California; and *S. monticola* A. Br. ex Schweinf. is restricted to the Abyssinian Highland (the Simian and Bale Mountains in Ethiopia) and to the alpine belt of the high mountains of Kenya, Tanzania, Uganda and Democratic Republic of the Congo. Like the other annuals from the above-mentioned genera, these taxa belong to the life form 'tenagophytes' *sensu* Hejný (1957) or "hydrotherophytes" *sensu* Rivas-Martínez et al. (2007). These species germinate under water or when the topsoil is waterlogged; then they either finish their life cycle submerged permanently in shallow water or they reproduce after emergence in an amphibious environment.

The aims of this contribution are the following:

1) To present a synopsis of those plant communities of Afro-alpine wetlands that are characterized by the annual life form. A question is whether the isolated mountains differ in their floristic composition or whether there are common characteristic species, supporting the proposal of the class Limoselletea africanae derived by Knapp (1966) in a deductive way.

2) To examine special adaptations of the species to cryoturbation, needle ice formation and inundation. For example, geocarpy (lowering the ripe inflorescence back to the soil and deposition of seeds directly into the topsoil) is mentioned by Agnew and Hedberg (1969) as an adaptation to solifluction processes in the Afro-alpine environment.

Study Area and Available Data Set

Solifluction and topsoil lifting by needle ice both occur in the high mountains of East Africa, mainly at altitudes above 4000 m (Spönemann 1977). Vegetation studies in this Afro-alpine belt have been checked for plot-related vegetation data (phytosociological relevés), but no study focussing on seasonal wetland vegetation and plant communities in shallow water was found. Existing observations are scattered and included in studies dealing with high-altitude vegetation in general. The main focus in these studies is description of the more widespread plant communities, such as shrublands with Ericaceae, *Alchemilla* and *Helichrysum*, *Dendrosenecio* and *Lobelia* communities, *Carex* bogs and *Festuca* tussock grasslands. Sample size was adapted to these communities and included the inundated micro-habitats embedded in these vegetation types. Only exceptionally was amphibious vegetation along the shorelines of shallow lakes or in runnels sampled separately.

In general, only few data were available. The vegetation types in the publications were defined by small numbers of relevés. Most data were from E. Beck (Bayreuth, Germany) and his working group (Beck et al. 1983, 1987; Rehder et al. 1988; Schmitt 1991; Schmitt and Beck 1992; Hemp 2008). They document the vegetation on Mt. Kilimanjaro (Tanzania), Mt. Elgon (Kenya), Mt. Kenya (Kenya), the Aberdares (Kenya) and the Ruwenzori Mts. (Uganda) (see Fig. 1 and Annex to Table 1). Further observations come from the Ugandan part of Mt. Elgon (Wesche 2002). van Zinderen Bakker and Werger (1974) record a *Crassula natans* community from the high altitudes of the Drakensberg (Lesotho, South Africa). For comparison and to link this synopsis in Africa to that from South America (Deil et al. 2011), a phytosociological table was included that has a *Crassula moschata* community from subantarctic Marion Island (South Africa), from the vegetation monograph of Gremmen (1981). The data from these studies are presented in a constancy table. Column numbers give the absolute frequency except in two studies, where the constancy is based on more than five relevés and has been transformed into five equal constancy classes (I = 1–20 %, etc.). The data from Rehder et al. (1988) were not included in this table because their study used very broadly defined mapping units.

Data from lower altitudes (2200–2400 m) were excluded from the table but will be discussed. This concerns the vegetation monograph about the Kahnzi-Biéga National Park in former Zaire (Fischer 1996) and a study of weed vegetation from the Bale Mountains in Ethiopia (Succow 1989) with seasonal wetland species in a secondary habitat. Further valuable observations come from Rejmánková and Rejmánek (1995), who compared vertical structure, nitrogen content and redox potential of *Carex runssoroensis* fens on Ruwenzori and Mt. Elgon.

Nomenclature for vascular plants follows the African Plants Database (2013) except for *Limosella*., the taxonomic treatment of which is outdated and unclear according to Cook (2004). *L. macrantha*, *L. grandiflora* and *L. africana* are unresolved names according to the African Plants Database (2013). Lichens were not considered because they were not sampled or noted by all authors.

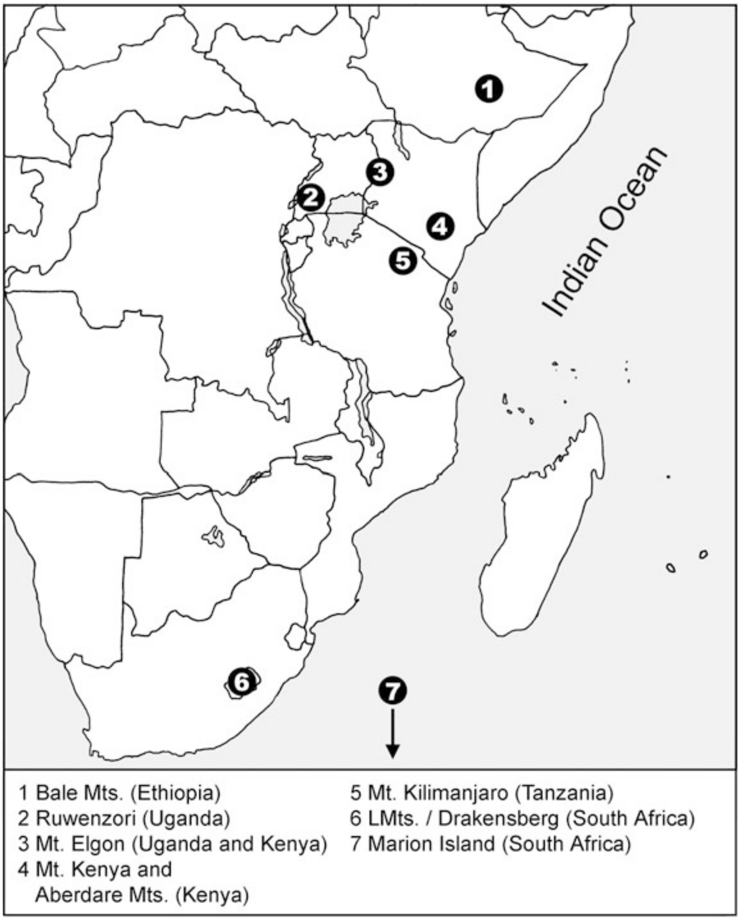

Fig. 1 Locations of field studies

Results

Open patches in *Carex runssoroensis-Deschampsia caespitosa-Agrostis gracilifolia* tussock grassland, *Carex monostachya* bogs on Mt. Kilimanjaro and the Aberdares, and the fringes of small lakes and water runnels in the Afro-alpine belt of the East African high mountains (3000–4500 m) are colonized by a number of annuals, which characterize the *Crassula granvikii-Subularia monticola* community group (see Table 1, col. 1–12).

The most constant, characteristic element is *Subularia monticola*, a mat-forming annual with subulate (therefore *Subularia*!) fleshy leaves, that grows on wet ground, emergent shorelines or permanently submerged in shallow oligotrophic water. It is distributed in the East African high mountains from the Simian and Bale Mountains

Table 1 Afro-alpine ephemeral wetland vegetation

Column no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14
State	UG	UG	UG	UG	UG	UG	TZ	TZ	TZ	KE	TZ	KE	ZA	ZA
Number of relevés	3	4	7	3	5	2	2	3	2	2	3	119	8	5
CS of *Crassula granvikii-Subularia monticola*-communities														
Crassula granvikii	**1**	**3**	**IV**	**2**	.	.	.	**1**	.	**1**	.	**I**	.	.
Subularia monticola	**1**	**3**	**IV**	.	**1**	**2**	**1**	**3**	.	.	.	**I**	.	.
Sagina afroalpina	**1**	**3**	**IV**	**2**	.	.	**1**	.	.	.	.	.	.	.
Limosella africana	**1**	**2**	**IV**	.	.	.	.	.	.	.	.	.	.	.
Limosella macrantha	**1**	.	**I**	.	.	.	.	.	**2**	.	.	.	.	.
Isolepis graminoides	**1**	**2**	**I**	.	.	.	.	.	.	.	.	.	.	.
Isolepis setacea	.	**3**	**III**	**2**	.	.	.	.	.	.	.	**I**	.	.
Isolepis fluitans	**1**	.	**II**	**2**	.	.	.	**3**	.	.	.	**III**	.	.
Ranunculus volkensii	.	.	**II**	**3**	.	.	.	.	.	**1**	**1**	.	.	.
Cardamine obliqua	**1**	**3**	**I**	**1**	.	.	.	.	.	.	.	**I**	.	.
Sibthorpia europaea	**2**	**2**	**V**	**1**	.	.	.	.	.	.	.	**I**	.	.
Cotula abyssinica	.	.	**II**	**1**	.	.	.	.	.	.	.	.	.	.
Eriocaulon volkensii	.	.	.	.	.	.	.	.	.	1	1	II	.	.
Colpodium hedbergii	.	.	.	1	.	.	.	.	.	.	.	.	II	.
Sagina abyssinica	.	.	.	.	.	.	2	.	.	.	.	.	.	.
Cerastium octandrum	.	.	.	.	5	.	1	.	.	.	.	.	.	.
Ranunculus oreophytus	.	.	.	.	5	.	.	2	.	.	3	I	.	.
Haplocarpha rueppellii	.	.	.	.	.	.	.	.	.	.	2	I	.	.
Limosella longiflora	.	.	.	.	.	2	.	.	.	.	1	.	.	.
CS of *Limosella capensis-Crassula natans*-community												.		
Crassula natans	.	.	.	.	.	.	.	.	.	.	.	.	**V**	.
Limosella grandiflora	.	.	.	.	.	.	.	.	.	.	.	.	**V**	.
Lagarosiphon muscoides	.	.	.	.	.	.	.	.	.	.	.	.	**V**	.

CS of *Crassulo moschatae-Clasmatocoleetum vermicularis*												.		
Crassula moschata	.	.	.	.	.	.	.	.	.	.	.	.	.	**5**
Clasmatocolea vermicularis	.	.	.	.	.	.	.	.	.	.	.	.	.	**5**
Callitriche antarctica	.	.	.	.	.	.	.	.	.	.	.	.	.	**5**
CS of spring vegetation												.		
Montia fontana	.	.	II	.	.	.	.	1	.	1	.	.	.	.
Callitriche stagnalis	.	.	I	3	.	.	.	.	.	.	.	.	.	.
Ranunculus stagnalis	.	.	IV	1	.	.	.	.	.	.	1	.	.	.
Myosotis vestergrenii	.	.	I	.	.	.	.	.	.	.	.	.	.	.
CS of afro-alpine *Carex*-bogs												.		
Tufted monocots												.		
Carex runssoroensis	3	4	V	3	.	2	.	.	.	2	.	.	.	.
Deschampsia caespitosa	.	4	.	3	.	.	.	.	.	.	3	I	.	.
Agrostis gracilifolia	2	3	V	1	.	2	.	.	.	2	.	I	.	.
Festuca abyssinica	.	2	III	1	5	.	.	.	.	.	2	I	.	.
Festuca pilgeri	.	2	II	.	.	.	.	.	.	.	.	IV	.	.
Colpodium chionogeiton	.	.	.	.	.	.	2	.	.	.	.	.	.	.
Carex monostachya	.	.	.	.	.	.	.	.	.	.	3	V	.	.
Poa leptoclada	.	3	II	.	5	.	1	.	.	.	.	I	.	.
Luzula abyssinica	.	.	III	.	.	.	.	.	.	.	2	I	.	.
Perennial herbs												.		
Lobelia deckenii (incl. ssp. *elgonensis*)	2	3	III	1	.	.	.	.	.	2	2	II	.	.
Swertia crassiuscula	2	2	III	.	.	.	.	.	.	1	.	I	.	.
Conyza subscaposa	2	2	V	1	.	.	.	.	.	.	.	I	.	.
Dendrosenecio elgonensis s.str.	.	2	V	1	5	.	.	.	.	.	.	.	.	.
Lycopodium saururus	2	2	.	.	.	.	.	.	.	1	.	I	.	.
Afrosciadium kerstenii	.	2	III	.	5	.	.	.	.	.	1	.	.	.

(continued)

Table 1 (continued)

Column no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14
State	UG	UG	UG	UG	UG	UG	TZ	TZ	TZ	KE	TZ	KE	ZA	ZA
Number of relevés	3	4	7	3	5	2	2	3	2	2	3	119	8	5
Carduus keniensis	.	.	III	2	.	.	.	.	.	.	1	I	.	.
Lysimachia serpens	.	.	II	1	.	.	.	1	.	.	.	III	.	.
Alchemilla microbetula	.	.	V	2	.	1	.	.	.	.	.	.	.	.
Dwarf shrubs												.		
Alchemilla johnstonii	1	3	II	1	1	.	.	.	.	2	1	IV	.	.
Alchemilla elgonensis	2	4	V	1	.	.	.	.	.	.	.	.	.	.
Helichrysum amblyphyllum	.	2	I	.	.	.	.	.	.	.	.	.	.	.
Helichrysum formosissimum	.	.	II	.	4	.	.	.	.	.	.	I	.	.

Diagnostic species of the communities in bold in Ethiopia, via Kenya, Uganda and Democratic Republic of the Congo, to Tanzania. In the relevés it is documented for the Ugandan part of Mt. Elgon, for Mt. Kilimanjaro, the Aberdares and the Ruwenzori Mountains (Wesche 2002; Schmitt 1991; Schmitt and Beck 1992; Beck et al. 1983; Hemp 2008); it is also included in the species lists of Hedberg (1964) and Coe (1967). *S. monticola* can germinate very effectively under water and on water-saturated soil, opened by cryoturbation, but also on mud polygons created by rock hyrax (*Procavia capensis*) and the Afroalpine vlei rat (*Otomys orestes*) (Mahaney and Boyer 1988). On Mt. Kenya, *S. monticola* occurs sporadically in *Philippia keniensis*-*Dendrosenecio brassica* wetlands and in some shrub communities of the Afro-alpine belt (Rehder et al. 1988). Coe (1967) recorded it from the shores of Lake Michaelson, Lake Höhnel and Teleki Tarn (Mt. Kenya).

Other taxa are represented by habitat-equivalent, vicarious species: *Crassula granvikii*, *C. natans* and *C. moschata*; *Limosella africana*, *L. macrantha*, *L. longiflora* and *L. grandiflora*; *Sagina afroalpina* and *S. abyssinica*; *Ranunculus volkensii*, *R. oreophytus* and *R. stagnalis*; and coexisting *Isolepis* spp. (*I. graminoides*, *I. setacea*, *I. fluitans*).

The *Carex* bogs on the Kenyan slope of Mt. Elgon (col. 10) and the *Carex*-*Deschampsia* bogs on Mt. Kilimanjaro (col. 11) are floristically impoverished and without *Subularia monticola*.

On Mt. Kilimanjaro, mono-dominant turfs of *Limosella macrantha* occur on muddy lake shores with fluctuating water level (col. 9, Fig. 2).

The vegetation mosaic of Afro-alpine tussock bogs in the Drakensberg (Lesotho) and Basutoland (Oranje) includes small patches with stagnant water and muddy soil, opened by cryoturbation and needle ice and colonized by the *Limosella capensis*-*Crassula natans* community (Table 1, col. 13) (van Zinderen Bakker 1965; van Zinderen Bakker and Werger 1974).

The Crassulo moschatae-Clasmatocoleetum vermicularis (Table 1, col. 14), recorded by Gremmen (1981) from the Marion and Prince Edward Islands, is quite different floristically from the Afro-alpine annual wetland turfs. It can be interpreted as an extremely impoverished outlier of the South American class Limoselletea australis (see vegetation group G in Deil et al. 2011).

In the high-altitude parts of the Kahnzi-Biéga National Park in eastern [former] Zaire, there are no species from the *Crassula*-*Subularia* communities. Fischer (1996) does mention, from open patches between 2200 and 2400 m, dwarf annuals such as *Coelachne africana, Anagallis angustiloba, Isolepis setacea* and *I. costata*. Similarly, such aquatic annuals (*Coelachne africana, Isolepis fluitans, I. costata* and *Panicum hymeniochilum)* occur as well in swamps of the lower montane areas below 2000 m on Mt. Kilimanjaro, North and South Pare and the West Usambara Mountains in Tanzania (Hemp 2008, unpub. data).

In the Afro-alpine belt of the Simian and Bale Mountains in Ethiopia, *Subularia monticola* communities can be expected but no phytosociological records from primary habitats were available to us. Succow (1989) however, documents a species group from 2200 to 2400 m, within weed vegetation, that has *Limosella africana*, *Crassula granvikii*, *Juncus bufonius* and other annuals. These colonize vertisols

Fig. 2 Muddy lakeshores at Mawenzi (Mt. Kilimanjaro) with *Limosella macrantha* (Photo: A. Hemp)

with gilgai micro-relief. Gilgai soils resemble soils resulting from solifluction and cryoturbation: they are mobile substrates kept open by waterlogging and by peloturbation due to shrinking and swelling processes (Knight 1980).

Discussion

Syntaxonomy

The synopsis shows that the amphibious habitats in the Afro-alpine belt of the East African Mountains are characterized by a number of common species, such as *Subularia monticola*, *Carex runssoroensis* and *Agrostis gracilifolia*. The latter two tussock species form the matrix around patches, which are opened by cryoturbation and frost heaving. Another result is that geographical vicariance plays a major role in several genera (*Limosella*, *Sagina*, *Isolepis* and *Ranunculus*). This vicariance can be the result of allopatric speciation without adaptive radiation, i.e. the vicarious species remained in the same ecological and coenological context. These phenomena of vicariance and parallel evolution are common patterns within seasonal wetland vegetation (Deil 2005): Evolution lines have entered the amphibious environment and speciated within this habitat. Examples seen worldwide include *Isoetes*, *Limosella* and *Crassula* of Section Helophyton (= *Tillaea*). For the Afro-alpine *Ranunculus* species the situation is different: Gehrke and Linder (2009) showed by molecular methods that *Ranunculus volkensii*, *R. oreophytus* and *R. stagnalis* originated from multiple recruitments from the Holarctic kingdom into the African mountains, followed by *in situ* differentiation.

According to Smith and Cleef (1988), the flora above the tree line in tropical mountains is mostly of extra-tropical origin. *Subularia* and *Sagina* are of holarctic origin (northern temperate geoelements *sensu* Hedberg 1986). The phylogeography of *Subularia* has not yet been studied by molecular methods, but for another taxon of northern origin (*Arabis alpina*), Koch et al. (2006) could prove two successive immigration events from Asia Minor, probably by mountain hopping via Arabia, during the Pleistocene. Even so, recent long-distance dispersal by birds cannot be excluded for *Subularia*.

The data are too preliminary to establish a syntaxonomic system of higher rank. With more data available, and with relevés sampled on smaller plots and selected by stronger criteria for abiotic homogeneity, one might describe the *Subularia monticola* community group in the future as an Afro-alpine alliance of annual vegetation on open soil, subjected to cryoturbation, frost heaving and needle-ice formation. Whether such a syntaxon can be included in the class Limoselletea africanae, outlined by Knapp (1966) in a deductive way, must remain an open question. One pre-condition is a better taxonomic treatment of the genus *Limosella*. Such a "Subularion monticolae" would be the oro-tropical equivalent of the alliance Littorellion (class Isoeto-Litorelletea), an alliance of submerged vegetation with *Subularia aquatica* in oligotrophic freshwater lakes in the boreal and temperate zones and in the subalpine belt of the Pyrenees (Dierssen 1975; Schaminée et al. 1992; Molina et al. 1999).

Adaptations, Functional Traits and the Role of Cryoturbation as Ecological Factor

In their review of tropical alpine ecology, Smith and Young (1987) draw the conclusion that many aspects of the morphology and ecophysiology of Afro-alpine plants are adaptations to extreme diurnal climate fluctuations. This is correct for the evolution of the giant rosette form (*Dendrosenecio*, *Lobelia*, *Espeletia*). For annuals in the oro-tropical climate, though, the situation is totally different: The severe, harsh environmental conditions (frost heaving, solifluction, needle-ice formation) are a pre-condition for creating a niche in the plant cover dominated by perennials. These annual plants show a number of functional and other adaptations, as follow.

Ecophysiology and Carbon Gain To survive with the low levels of inorganic carbon in oligotrophic water, *Subularia*, *Crassula* and *Limosella* employ Crassulacean Acid Metabolism, like many other aquatic taxa (Keeley 1998). *Subularia* has large aerenchyma in its leaves and roots. These "leaves" are in fact bifacial phyllodes, and the taxon has an isoetoid growth form (Nowak et al. 2010). Seeds of many taxa are able to germinate under water and to mobilize energy by a fermentation pathway.

Pollination The pollination of *Subularia monticola* has not been studied, but its close relative *S. aquatica* is cleistogamous when submerged (Woodhead 1951).

Dispersal The species have developed mechanisms to disperse their seeds close to the short-living mother plants, where open soil and little competition by perennials can be expected. One adaptation to achory is the non-floating seeds in *Subularia* (Woodhead 1951); another strategy is geocarpy, i.e. active burial of the ripe seeds by dropping the inflorescence into the soil. This strategy is known from ephemeral wetland species such as *Hydrocotyle cyptocarpa* in South America (Pérez-Moreau 1938; Alvarez et al. 2012). For Afro-alpine plants, geocarpy is recorded for *Limosella africana*, *L. macrantha*, *Ranunculus oreophytus*, *R. stagnalis*, *Haplosciadium abyssinicum* and *Halocarpha rueppelii* (Agnew and Hedberg 1969). Others species disperse their seeds on the soil surface. To fix the seeds in the muddy, moving substrate, the radicle of *Subularia aquatica* has a crown of hairs to keep the seedling in position. This has to be verified for *S. monticola*. The abundant seedlings observed by Mahaney and Boyer (1988) on mud polygons on Mt. Kenya make a similar behaviour probable.

Life on Moving Ground When established, *Subularia monticola* can survive frost heaving by remaining intact in small cavities in the ice. It avoids further the perils of solifluction—like *Limosella africana*—when growing below the water surface (Hedberg 1964). Individuals of *Subularia monticola* and *Crassula granvikii* can also root again after being uprooted by frost heaving. This strategy of "solifluction floating" is more common in cryptogams. An example of such an ambulatory behaviour is the lichen *Catapyrenium lachneum* in the high Andean Páramo (Pérez 1997). Some mosses remain unattached to the substrate when uprooted by needle ice and form globular mosses, blown around by wind or shifted by solifluction. A representative of this strategy in the Afro-alpine region is *Grimmia ovalis* (Beck et al. 1986).

Cryoturbation and soil movement by needle ice can create niches for short-living annuals in a plant cover dominated by perennials. One example is *Koenigia islandica* (Polygonaceae), the only annual vascular plant of the high Arctic; another is *Phippsia algida*. Both species have southern outliers on cryoturbated sites in the Rocky Mountains of North America (Johnson and Billings 1962; Reynolds 1984). Soil freezing also enables the highly disjunct occurrence of *Phippsia algida* in the

Central Andes near Mendoza (Argentina) (Roig et al. 2007). And even in dry grasslands (Festucetalia valesiacae) of the continental inner valleys of the European Alps, needle ice can create a niche for small annuals like *Clypeola jonthlaspi* by raising and opening the topsoil (Schwabe and Kratochwil 2004).

Annex to Table 1

Rare Species In col. 3: Agrostis quinqueseta II, Helichrysum argyranthemum I, H. odoratissimum I, Helictotrichon umbrosum I. In col. 4: Epilobium salignum 1, Hypericum scioanum 1, Juncus dregeanus 1. In col. 5: Senecio mattirolii 5, Helichrysum stuhlmannii 5, Alchemilla subnivalis 5, Galium ruwemzoriense 1. In col. 6: Alchemilla roccatii 2. In col. 7: Crepis dianthoseris 1, Senecio purtschelleri 1, S. telekii 1. In col. 8: Poa muhavurensis 1, Cardamine spec. aff. pratensis 2, Peucedanum kerstenii 1, Marchantia sp. 2, Tortella spec. 2, Ditrichum spec. 1, Mnium sp. 1. In col. 11: Alchemilla argyrophylla 1, Euryops dacrydioides 1, Haplosciadium abyssinicum 3, Rostraria cristata 1, Pentaschistis borussica 1, Senecio meyeri-johannis 1, Swertia volkensii 2. In col. 12: Cyperus nigricans III, Helichrysum ellipticifolium III, Hydrocotyle sibthorpioides III, Agrostis kilimandscharica II, Anthoxanthum nivale II, Hypericum peplidifolium II, Hypericum scioanum II, Phyllanthus boehmii humilis II and further non-diagnostic companions see Schmitt (1991). In col. 13: Agrostis magellanica 3, Azorella selago 3, Calyptrochaeta apiculata 2, Fossombronia australis 3, Hygroamblystegium filum 3, Juncus scheuchzerioides 2, Lophocolea randii 1, Poa cookii 1, Ranunculus biternatus 4.

Bibliographic Sources and Study Areas for Columns in Table 1

Wesche (2002) Mt. Elgon, Uganda
col. 1: *Carex runssoroensis-Subularia monticola*-comm. typical subcomm.
col. 2: *Carex runssoroensis-Subularia monticola*-comm. *Deschampsia caespitosa*-subcomm.
col. 3: *Carex runssoroensis-Subularia monticola*-comm. *Ranunculus stagnalis*-subcomm.
col. 4: *Callitriche stagnalis-Deschampsia caespitosa*-comm.

Schmitt and Beck (1992) Ruwenzori (Uganda)
col. 5: *Festuca abyssinica-Senecio mattirolii* grassland, *Ranunculus oreophytus* subcomm.
col. 6: *Limosella aquatica-Subularia monticola*-comm.

Beck et al. (1983) Mt. Kilimanjaro, Tanzania
col. 7: community with *Colpodium chionogeiton*
col. 11: *Deschampsia caespitosa*-*Carex monostachya*-comm

Hemp (2008) Mt. Kilimanjaro, Tanzania
col. 8: *Subularia monticola*-comm.

Hemp (ined.) Mt. Kilimanjaro, Tanzania
col. 9: *Limosella macrantha*-comm.

Beck et al. (1987) Mt. Elgon, Kenya.
col. 10: *Carex*-bog

Schmitt (1991) Aberdares (Kenya)
col. 12: *Carex monostachya*-comm. group

van Zinderen-Bakker & Werger (1974) Lesotho-Mountains, South Africa
col. 13: Crassuletum natantis

Gremmen (1981) Marion Islands, South Africa
col. 14: Crassulo moschatae-Clasmatocoleetum vermicularis

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Large Habitat Range But Low Floristic Variation: The Case of *Festuco rubrae-Agrostietum capillaris* Grasslands

Dan Gafta and Sorana Muncaciu

Abstract We attempted to classify 414 grassland stands dominated by *Festuca rubra* and *Agrostis capillaris* in the southeastern Carpathian region and to infer the main ecological factors underlying the observed floristic variation. Several internal criteria were employed to select the optimal number of clusters resulting from applying the fuzzy C-medians algorithm to the Bray-Curtis distance matrix. Species fidelity, non-metric multidimensional scaling and relative importance of four plant functional groups were subsequently used to validate floristically and ecologically the clusters of relevés distinguished.

Sixty-five relevés were excluded from the final classification as being boundary or outlying communities with respect to cluster medoids. The remaining 349 relevés were assigned to five facies: *potentillosum aureae* (*PA*), *loliosum perennis* (*LP*), *violosum caninae* (*VC*), *typicum* (*T*) and *succisosum pratensis* (*SP*). The strongest gradient detected runs from acidophilous grasslands (*PA* and *LP*) to those formed on base-rich substrates (*VC* and *SP*). A much weaker eco-floristic differentiation is induced by elevation and the predominant management type, i.e. colline-submontane meadows (*LP* and *SP*) *versus* montane-subalpine pastures (*PA* and *VC*). Unlike mega-forbs, the proportion of tall herbs, graminoids and legumes differs significantly between certain facies but also tends to discriminate between mown and grazed grasslands.

The facies distinguished herein are fuzzier and differ more or less from the five subassociations recently acknowledged in the literature through an empirical phytosociological classification. Although we did not consider relevés in which third-party species were dominant, our data set contained some noise due to inconsistencies in the occurrence patterns of grazing-tolerant and ruderal species. The fuzzy clustering output is less useful as a typological reference but provides a good basis for unravelling successional pathways under different environmental conditions and grassland use modes.

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Introduction

Semi-natural grasslands dominated by *Festuca rubra* and *Agrostis capillaris* cover large areas in the northwestern Balkan Peninsula and southeastern Carpathian region. Based on floristic relevés collected in former Yugoslavia, these grasslands were assigned originally to *Festuco rubrae-Agrostietum* Horvát 1951 (Horvát et al. 1974). The occurrence of this plant association has been reported subsequently from Slovakia (Jurko 1969), Romania (Pop 1976; Coldea 1991), Hungary (Borhidi and Sánta 1999) and northern Bulgaria (Apostolova and Meshinev 2006; Velev et al. 2010). Whereas most Croatian and Serbian authors (e.g. Horvát et al. 1974; Petković 1985; Jovanović-Dunjć and Jovanović 1989; Kojić et al. 1998; Šegulja 2005; Trinajstić 2008) have considered this plant association as part of the *Arrhenatherion* alliance, authors from other countries have assigned it to the *Cynosurion* alliance. Some distinct higher syntaxa were even proposed, such as *Agrostio-Festucion rubrae* (Puşcaru et al. 1956) and *Festuco-Agrostion capillaris* (Redžić 2007), but at least the former has no support in terms of character (good diagnostic) species. Such different coeno-taxonomic interpretations are probably related to particularities of the regional climate and plant species distributions within the area between the eastern Carpathians and western Balkans.

According to Palearctic and EUNIS habitat classification, these two anthropogenic grassland types were assigned, respectively, to the 'Eastern Carpathian yellow oatgrass meadows' (type 38.2323) and 'Nemoral *Agrostis-Festuca* grasslands' (type E1.721) (Doniţă et al. 2005). These grasslands have developed on moderately acidic to neutral soils (pH = 4.4–6.4) which are rather rich in humus and total nitrogen (0.4–0.6 %) and well provisioned with water (Coldea 2012). In the southeastern Carpathian region they cover a wide altitudinal range, from the lower colline to upper montane belt, a range that overlaps with the distributions of forests of sessile oak (*Quercus petraea*) and beech (*Fagus sylvatica*). Depending on site conditions, soil fertility, floristic composition and management type, these meadows can reach levels of net green-phytomass production between 3.5 and 21.8 ton/ha (Puşcaru-Soroceanu 1963).

The maintenance of these swards depends on periodic organic fertilisation and traditional use through grazing, mowing or both. As in other anthropogenic grasslands (cf. Baur et al. 2006; Maurer et al. 2006; Kleijn et al. 2009), local declines in species richness and shifts in the floristic composition of *Festuco rubrae-Agrostietum* communities have often been reported (e.g. Puşcaru-Soroceanu 1963; Coldea et al. 2008) because of their abandonment or changes in their management (mostly overgrazing and the cessation of mowing). Therefore, their rich biodiversity and economic value call for appropriate conservation by continuing the traditional practices of grassland use.

The large ecological range over which these grasslands occur in Romania has determined many phytosociologists to distinguish quite a number of subassociations and facies of *Festuco-Agrostietum capillaris* or its synonym *Agrostio-Festucetum rubrae* (Sanda et al. 1980; Coldea 1991, 2012; Oroian 1998;

Bărbos 2006; Chifu et al. 2006). So far, the few synthetic analyses performed on relatively large sets of relevés have not questioned the statistical and ecological validation of these lower syntaxa (Coldea 1991, 2012; Sanda 2002). The latest revision, based on 347 relevés gathered throughout Romania, has empirically acknowledged five subassociations (Coldea 2012): *typicum, genistetosum sagittalis, nardetosum, caricetosum montanae* and *trifolietosum patens*.

The aim of this study was to classify the *Festuco rubrae-Agrostietum capillaris* grasslands by numerical means and to infer the main ecological factors responsible for the observed floristic variation. Because our data set did not include relevés attributed originally to the subassociations *caricetosum montanae* and *trifolietosum patens*, we could not enter the ecological and statistical differentiation of these subunits into the discussion.

Material and Methods

Data Collection

A set of 414 relevés of *Festuco rubrae-Agrostietum capillaris* (hereafter referred to as F-A), representing the Romanian Carpathian region, was collected from published literature and dissertations. The relevés were selected on the basis of the following criteria: (a) the two co-dominant species (*Festuca rubra* and *Agrostis capillaris*) must each have a cover of at least two on the Braun-Blanquet scale; and (b) none of the other vascular plant taxa can reach more than two on this cover scale. Bryophytes and lichens were excluded from the species list because they were not recorded in all relevés. The names of vascular plant taxa used herein are consistent with the current online version of the Flora Europaea (http://rbg-web2.rbge.org.uk/FE/fe.html).

By using species trait descriptors available in the LEDA trait base (Kleyer et al. 2008) and the Ecological Flora of the British Isles (Fitter and Peat 1994), four plant functional groups were distinguished: graminoids (*Poaceae* and *Cyperaceae*), legumes (*Fabaceae*), tall herbs (potentially growing over 0.5 m high) and mega-forbs (conspicuously large-leaved). A few species had to be included in two functional groups, and about half the species did not fit in any group.

Based on the locality name of each relevé, occurrence patterns were inferred roughly and represented on a UTM 50 km × 50 km-grid map (Fig. 1).

Fig. 1 Presence of F-A grasslands (marked with a dot at cell level) on a UTM 50 × 50 km grid-map of Romania as inferred from the approximate locations of the 414 relevés collected

Numerical Analyses

Species cover classes were converted to percentages by reducing them to the class midpoint. Bray-Curtis distance was employed to calculate the pairwise resemblance between relevés. The classification of relevés was conducted by the fuzzy C-medians algorithm (FCMed), which attempts to distinguish prototypes as vectors of medians (medoids) and to assign degrees of cluster membership to each object (De Cáceres Ainsa 2012). A low value (1.2) of the fuzziness coefficient was employed because of the large amount of noise usually present in ecological community data. The minimum fuzzy-set cardinality, i.e. the fewest relevés that a fuzzy cluster must have in order to be retained by the procedure, was set to 10. FCMed was run successively, specifying different numbers of groups as input, from two to ten. The optimal number of clusters was selected based on three internal criteria: maximum normalised Dunn coefficient, minimum normalised partition entropy (Dunn 1976) and minimum group-average silhouette (Rousseuw 1987). Once the optimal solution was chosen, the partitions were "defuzzied" by discarding all relevés with low group membership weights (0.5 or less). The remaining relevés were assigned uniquely to the clusters determined, based on their largest membership weight. The resulting trimmed partitions were employed in the subsequent analyses. The internal validation of clusters was done by inspecting the departures of relevé silhouette values from zero. The significance of differences in location and scale between the distributions of relevé silhouettes across clusters was estimated by using the non-parametric Conover exact test.

The floristic distinctiveness of the relevé clusters was assessed through diagnostic species, which were assessed primarily by the Phi coefficient in association with the right-tailed, exact Fisher test (Chytrý et al. 2002). In addition, for those species with Phi values larger than 0.15, the indicator values (Dufrêne and Legendre 1997) were also calculated and their statistical significance estimated by a Monte Carlo test with 9999 permutations. The number and quality of diagnostic species in each cluster, relative to the average species richness of the stands, was evaluated by means of the Sharpness Index, calculated over all taxa with Phi larger than 0.05 (Chytrý and Tichý 2003). Cluster separation and variation were expressed, respectively, through the border isolation index and the relative contribution to total error sum-of-squares (De Cáceres Ainsa 2012).

The ecological differentiation of the relevé clusters was assessed by indirect ordination (configuration in low-dimensional space) and by between-cluster comparisons in terms of the relative importance of the plant functional groups. Several exploratory runs of the non-metric multi-dimensional scaling (NMDS) in 2–6 dimensions were conducted on the distance matrix of relevés. The three-dimensional solution was finally retained, based on the small change in stress with increasing dimensionality (Legendre and Legendre 1998). The relationships between NMDS axes and species cover were assessed by Spearman's coefficient of correlation.

The relative importance of plant functional groups in a community was estimated by the ratio of the cumulative cover of species in the target guild to the cover sum of all species present in that relevé. The significance of pair-wise differences between relevé clusters, in terms of the relative importance of tall herbs, graminoids and mega-forbs, was estimated by employing Mood's median exact test.

All statistical tests were considered significant at an alpha probability level of 5 %. No *p*-value adjustments were applied in *post-hoc* tests implying multiple comparisons. The numerical analyses were performed using Ginkgo (De Cáceres Ainsa 2012), except for NMDS and non-parametric, one-way between-group tests that were run in SAS/STAT 9.2 (SAS Institute 2008).

Results

Numerical Classification of Relevés and Cluster Validation

All three criteria used to evaluate the goodness of relevé partitioning agreed in reaching their maximum or minimum after running the FCMed analysis with

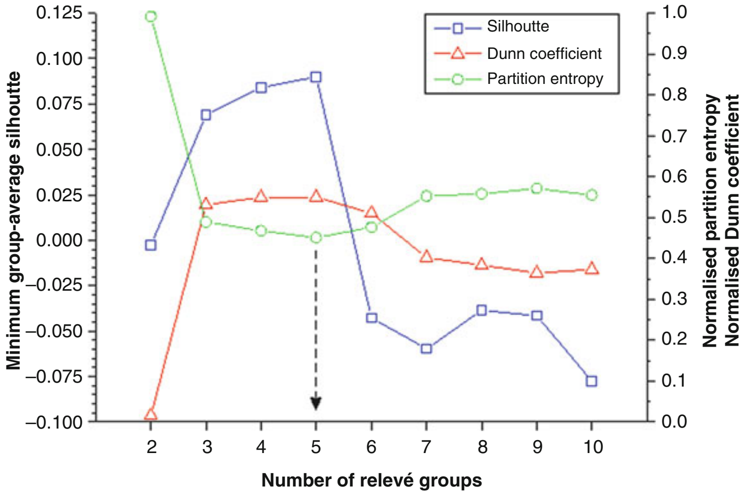


Fig. 2 Distribution of the minimum group-average silhouette, normalised partition entropy and normalised Dunn coefficient as functions of the input number of relevés groups. The *dashed arrow* corresponds to the optimal solution

different numbers of groups specified as input (Fig. 2). Consequently, the partitioning of relevés into five groups was retained as optimal.

After removing the boundary or outlying relevés, the remaining 349 with cluster membership weights over 0.5 were retained as presumably representative of the five groups. Their validation is supported by the location and extension of the distributions of silhouette values, which all lie above zero (Fig. 3). However, cluster distinctiveness differs significantly, as clusters C1, C3 and C4 appear to be resolved better than groups C2 and C5 (Fig. 3). A rather similar pattern is revealed by the border isolation index, which reaches its largest values in clusters C1 and C3, and the lowest value in group C5 (see Table 1).

Fifty taxa with Phi values of at least 0.15, and which are associated significantly with one relevé group (as ascertained by the Fisher test), were retained as diagnostic species for one cluster or another (Table 2). Most of these taxa also have significant indicator values, which means that their relative abundances are concordant with their fidelities to the relevé groups (Table 2). There are only two species (*Medicago lupulina* and *Trisetum flavescens*) that discriminate two clusters (C2 and C5) with respect to the others (Table 2).

The largest Sharpness Index was observed in cluster C2, which also had the most diagnostic species (Tables 1 and 2). The opposite held true for cluster C4, which had the highest floristic variation (Table 1).

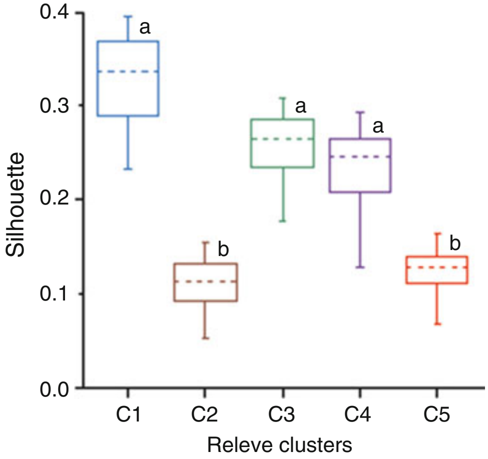


Fig. 3 Distribution of relevé silhouettes by cluster. Different/same lower-case letters indicate significant/non-significant pair-wise differences in location between the distributions

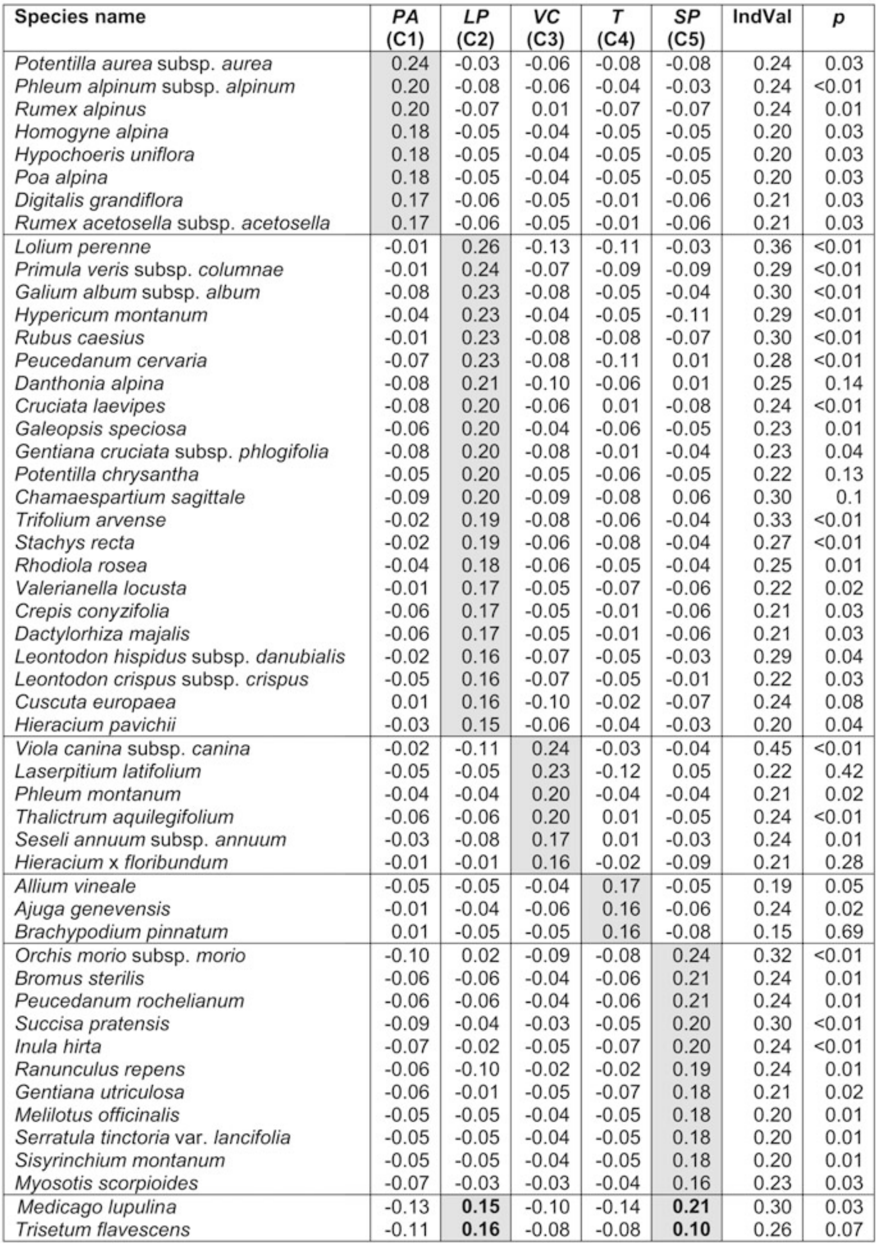
Table 1 Summary of cluster descriptors. Facies abbreviations: *PA* (cluster C1) = *potentillosum aureae*; *LP* (cluster C2) = *loliosum perennis*; *VC* (cluster C3) = *violosum caninae*; *T* (cluster C4) = *typicum*; *SP* (cluster C5) = *succisosum pratensis*

Relevé cluster (facies)	Number of relevés	Average species richness/relevé	Sharpness index	Contribution to total error sum-of-squares (%)	Border isolation
C1 (*PA*)	76	30.53	39.02	19.48	−0.33
C2 (*LP*)	76	38.80	57.01	21.26	−0.43
C3 (*VC*)	45	35.89	33.30	14.51	−0.31
C4 (*T*)	80	34.95	29.56	28.00	−0.44
C5 (*SP*)	72	39.46	46.63	16.74	−0.58

Ecological and Structural Differentiation of Relevé Clusters

The five clusters of relevés are distinguished clearly in the ordination space, although the separation is not crisp (Fig. 4). The NMDS axis 1 is best correlated with the relative cover of *Trifolium repens* ($r = +0.244$, $p < 0.0001$) and *Colchichum autumnale* ($r = -0.222$, $p < 0.0001$), which are well known, respectively, as nitrophilous and meso-basophilous species. The NMDS axis 2 is best correlated with the relative cover of *Bromus commutatus* (-0.200, $p = 0.0002$), which is a sub-thermophilous grass occurring mostly in colline meadows. The strongest ecological gradients, overlapping on axis 1, are related to soil fertility, i.e. base and nitrogen content. Along these edaphic gradients, the sharpest separation occurs between clusters C1 and C2 and between clusters C3 and C5. A weaker, thermal gradient is distinguishable along axis 2, with the grasslands in clusters C2 and C5 appearing more thermophilous than those in clusters C1 and C3 (Fig. 4). The core of cluster C4 is positioned almost in the center of the ordination space (Fig. 4), so its component relevés have ecological features that are intermediate

Table 2 Phi coefficients, indicator values (IndVal) and associated alpha-probability (p) of the diagnostic species of each facies (cluster of relevés). Only the last two species are diagnostic for two facies. Abbreviations are as in Table 1



Species name	*PA* (C1)	*LP* (C2)	*VC* (C3)	*T* (C4)	*SP* (C5)	IndVal	*p*
Potentilla aurea subsp. *aurea*	0.24	-0.03	-0.06	-0.08	-0.08	0.24	0.03
Phleum alpinum subsp. *alpinum*	0.20	-0.08	-0.06	-0.04	-0.03	0.24	<0.01
Rumex alpinus	0.20	-0.07	0.01	-0.07	-0.07	0.24	0.01
Homogyne alpina	0.18	-0.05	-0.04	-0.05	-0.05	0.20	0.03
Hypochoeris uniflora	0.18	-0.05	-0.04	-0.05	-0.05	0.20	0.03
Poa alpina	0.18	-0.05	-0.04	-0.05	-0.05	0.20	0.03
Digitalis grandiflora	0.17	-0.06	-0.05	-0.01	-0.06	0.21	0.03
Rumex acetosella subsp. *acetosella*	0.17	-0.06	-0.05	-0.01	-0.06	0.21	0.03
Lolium perenne	-0.01	0.26	-0.13	-0.11	-0.03	0.36	<0.01
Primula veris subsp. *columnae*	-0.01	0.24	-0.07	-0.09	-0.09	0.29	<0.01
Galium album subsp. *album*	-0.08	0.23	-0.08	-0.05	-0.04	0.30	<0.01
Hypericum montanum	-0.04	0.23	-0.04	-0.05	-0.11	0.29	<0.01
Rubus caesius	-0.01	0.23	-0.08	-0.08	-0.07	0.30	<0.01
Peucedanum cervaria	-0.07	0.23	-0.08	-0.11	0.01	0.28	<0.01
Danthonia alpina	-0.08	0.21	-0.10	-0.06	0.01	0.25	0.14
Cruciata laevipes	-0.08	0.20	-0.06	0.01	-0.08	0.24	<0.01
Galeopsis speciosa	-0.06	0.20	-0.04	-0.06	-0.05	0.23	0.01
Gentiana cruciata subsp. *phlogifolia*	-0.08	0.20	-0.08	-0.01	-0.04	0.23	0.04
Potentilla chrysantha	-0.05	0.20	-0.05	-0.06	-0.05	0.22	0.13
Chamaespartium sagittale	-0.09	0.20	-0.09	-0.08	0.06	0.30	0.1
Trifolium arvense	-0.02	0.19	-0.08	-0.06	-0.04	0.33	<0.01
Stachys recta	-0.02	0.19	-0.06	-0.08	-0.04	0.27	<0.01
Rhodiola rosea	-0.04	0.18	-0.06	-0.05	-0.04	0.25	0.01
Valerianella locusta	-0.01	0.17	-0.05	-0.07	-0.06	0.22	0.02
Crepis conyzifolia	-0.06	0.17	-0.05	-0.01	-0.06	0.21	0.03
Dactylorhiza majalis	-0.06	0.17	-0.05	-0.01	-0.06	0.21	0.03
Leontodon hispidus subsp. *danubialis*	-0.02	0.16	-0.07	-0.05	-0.03	0.29	0.04
Leontodon crispus subsp. *crispus*	-0.05	0.16	-0.07	-0.05	-0.01	0.22	0.03
Cuscuta europaea	0.01	0.16	-0.10	-0.02	-0.07	0.24	0.08
Hieracium pavichii	-0.03	0.15	-0.06	-0.04	-0.03	0.20	0.04
Viola canina subsp. *canina*	-0.02	-0.11	0.24	-0.03	-0.04	0.45	<0.01
Laserpitium latifolium	-0.05	-0.05	0.23	-0.12	0.05	0.22	0.42
Phleum montanum	-0.04	-0.04	0.20	-0.04	-0.04	0.21	0.02
Thalictrum aquilegifolium	-0.06	-0.06	0.20	0.01	-0.05	0.24	<0.01
Seseli annuum subsp. *annuum*	-0.03	-0.08	0.17	0.01	-0.03	0.24	0.01
Hieracium x *floribundum*	-0.01	-0.01	0.16	-0.02	-0.09	0.21	0.28
Allium vineale	-0.05	-0.05	-0.04	0.17	-0.05	0.19	0.05
Ajuga genevensis	-0.01	-0.04	-0.06	0.16	-0.06	0.24	0.02
Brachypodium pinnatum	0.01	-0.05	-0.05	0.16	-0.08	0.15	0.69
Orchis morio subsp. *morio*	-0.10	0.02	-0.09	-0.08	0.24	0.32	<0.01
Bromus sterilis	-0.06	-0.06	-0.04	-0.06	0.21	0.24	0.01
Peucedanum rochelianum	-0.06	-0.06	-0.04	-0.06	0.21	0.24	0.01
Succisa pratensis	-0.09	-0.04	-0.03	-0.05	0.20	0.30	<0.01
Inula hirta	-0.07	-0.02	-0.05	-0.07	0.20	0.24	<0.01
Ranunculus repens	-0.06	-0.10	-0.02	-0.02	0.19	0.24	0.01
Gentiana utriculosa	-0.06	-0.01	-0.05	-0.07	0.18	0.21	0.02
Melilotus officinalis	-0.05	-0.05	-0.04	-0.05	0.18	0.20	0.01
Serratula tinctoria var. *lancifolia*	-0.05	-0.05	-0.04	-0.05	0.18	0.20	0.01
Sisyrinchium montanum	-0.05	-0.05	-0.04	-0.05	0.18	0.20	0.01
Myosotis scorpioides	-0.07	-0.03	-0.03	-0.04	0.16	0.23	0.03
Medicago lupulina	-0.13	**0.15**	-0.10	-0.14	**0.21**	0.30	0.03
Trisetum flavescens	-0.11	**0.16**	-0.08	-0.08	**0.10**	0.26	0.07

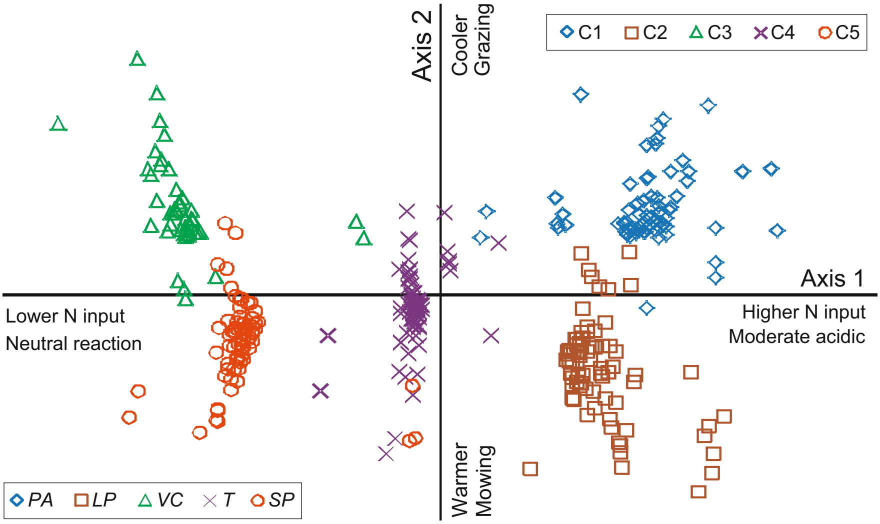


Fig. 4 Ordination of the 349 F-A relevés along the two most important NMDS axes extracted from the three-dimensional solution (stress criterion = 0.11; real versus scaling distance correlation = 0.971). Abbreviations are as in Table 1

relative to those of the other clusters. The minimum and maximum mean species richness per relevé are found, respectively, in cluster C1 and C5 (Table 1), which are located at the ends of the combined ecological gradients revealed along the two NMDS axes.

The proportion of tall herbs is significantly larger in the relevés of clusters C2 and C5 than in those from the other clusters (Fig. 5A). Also, legumes are relatively most abundant in the communities of clusters C2 and C5, contrasting in this respect with those in cluster C3 (Fig. 5B). On the other hand, the proportion of graminoids in the relevés of clusters C1 and C3 is higher than in their counterparts in clusters C2 and C5 (Fig. 5C). These patterns suggest that tall forbs and legumes respond differently than do graminoids to the ecological factors underlying the NMDS axis 2, along which the two groups of clusters (C2 and C5 *versus* C1 and C3) are set apart only fuzzily (Fig. 4). Finally, the proportion of mega-forbs is not significantly different among the five clusters of relevés (Fig. 5D).

Eco-floristic Description of the Facies

Each cluster of relevés was assigned to a lower syntaxon (facies) based on its diagnostic species, of which those displaying a narrower ecological tolerance (stenoecious or specialised species) were selected as differential for the given facies. The synoptic composition expressed by species constancies of all facies is presented in Table 3.

Table 3 Species constancy (%) by facies of *Festuco rubrae-Agrostietum capillaris*. Species with constancies lower than 4 % in every facies were omitted. Abbreviations are as in Table 1

Species name (alphabetic list)	*PA*	*LP*	*VC*	*T*	*SP*
Achillea distans subsp. *distans*	9	3	11	3	6
Achillea millefolium	55	63	56	66	81
Agrimonia eupatoria subsp. *eupatoria*	1	1	0	5	6
Agrostis capillaris	100	100	100	100	100
Agrostis stolonifera	0	3	4	1	1
Ajuga genevensis	5	4	2	13	3
Ajuga reptans	1	3	0	5	3
Alchemilla glaucescens	0	5	2	1	3
Alchemilla xanthochlora	24	34	18	21	21
Allium vineale	0	0	0	4	0
Alopecurus pratensis subsp. *pratensis*	3	8	2	4	4
Angelica sylvestris	1	3	0	1	4
Antennaria dioica	7	12	0	3	4
Anthericum ramosum	0	4	0	3	1
Anthoxanthum odoratum	74	64	87	85	78
Anthyllis vulneraria subsp. *vulneraria*	14	18	24	20	24
Arabis hirsuta	1	3	4	0	0
Arnica montana	12	18	4	9	6
Arrhenatherum elatius	1	4	0	1	8
Asperula cynanchica	7	12	7	8	10
Astrantia major	7	11	11	8	7
Avenula pratensis	0	1	0	0	4
Avenula pubescens subsp. *pubescens*	0	4	0	0	3
Bellis perennis	1	1	0	3	4
Betula pendula	1	3	0	4	1
Botrychium lunaria	1	1	0	4	0
Brachypodium pinnatum	5	3	2	11	1
Briza media	50	61	53	65	58
Bromus commutatus subsp. *commutatus*	0	4	0	5	6
Bromus hordeaceus subsp. *hordeaceus*	4	4	0	1	0
Bromus sterilis	0	0	0	0	6
Bunias orientalis	0	1	2	5	3
Bupleurum falcatum subsp. *falcatum*	0	3	2	4	0
Campanula cervicaria	0	7	4	0	3
Campanula glomerata subsp. *glomerata*	7	20	18	14	18
Campanula kladniana	0	4	0	0	3
Campanula patula subsp. *abietina*	24	26	4	13	19
Campanula patula subsp. *patula*	34	39	62	48	40
Campanula persicifolia	5	4	11	5	1
Campanula rotundifolia	5	3	4	3	1
Campanula serrata	4	5	4	6	8
Cardaminopsis halleri subsp. *halleri*	4	0	4	0	1

(continued)

Table 3 (continued)

Species name (alphabetic list)	*PA*	*LP*	*VC*	*T*	*SP*
Carduus nutans subsp. *nutans*	1	1	0	4	0
Carex caryophyllea	5	3	0	5	7
Carex distans	1	3	0	1	6
Carex flava	3	4	2	1	1
Carex hirta	4	3	0	0	1
Carex montana	1	5	7	4	7
Carex ovalis	16	13	9	11	10
Carex pallescens	9	8	13	16	10
Carex tomentosa	0	3	2	1	7
Carex vulpina	0	4	2	0	3
Carlina acanthifolia subsp. *acanthifolia*	0	3	4	3	0
Carlina acaulis subsp. *acaulis*	11	33	22	23	21
Carlina vulgaris subsp. *vulgaris*	1	8	7	3	17
Carum carvi	24	33	11	30	31
Centaurea apiculata subsp. *spinulosa*	0	0	4	3	0
Centaurea biebersteinii subsp. *biebersteinii*	*5*	*1*	*9*	*3*	*3*
Centaurea indurata	5	3	7	0	1
Centaurea jacea	3	7	13	14	11
Centaurea nigrescens	1	3	2	9	7
Centaurea pannonica	3	0	7	0	0
Centaurea phrygia subsp. *phrygia*	17	36	38	38	40
Centaurea scabiosa	1	0	4	5	0
Centaurea stenolepis	0	3	4	0	3
Centaurium erythraea subsp. *erythraea*	8	13	7	9	15
Cerastium fontanum subsp. *vulgare*	51	22	60	40	40
Chamaespartium sagittale	9	29	7	10	19
Cichorium intybus	8	12	9	8	11
Cirsium arvense	1	3	0	0	4
Cirsium canum	1	3	0	4	3
Cirsium erisithales	5	1	4	1	0
Cirsium vulgare	0	5	0	1	1
Clinopodium vulgare	0	3	0	6	3
Colchicum autumnale	9	11	16	14	25
Coronilla varia	3	8	11	6	4
Crepis biennis	3	9	13	6	22
Crepis conyzifolia	0	5	0	1	0
Crocus vernus subsp. *vernus*	*4*	*5*	*2*	*3*	*1*
Cruciata glabra	16	14	18	15	19
Cruciata laevipes	0	8	0	3	0
Cuscuta europaea	7	13	0	5	3
Cynosurus cristatus	53	49	62	56	56
Dactylis glomerata	13	21	18	21	28

(continued)

Table 3 (continued)

Species name (alphabetic list)	*PA*	*LP*	*VC*	*T*	*SP*
Dactylorhiza maculata	7	4	0	1	6
Dactylorhiza majalis	0	5	0	1	0
Dactylorhiza sambucina subsp. *sambucina*	*1*	*1*	*2*	*1*	*6*
Danthonia alpina	3	16	0	4	7
Danthonia decumbens	14	13	13	15	24
Daucus carota subsp. *carota*	*3*	*11*	*4*	*8*	*10*
Deschampsia cespitosa	11	18	9	8	8
Deschampsia flexuosa	13	1	7	8	4
Dianthus armeria subsp. *armeria*	8	1	2	3	3
Dianthus barbatus subsp. *compactus*	4	11	0	6	4
Dianthus carthusianorum	28	22	38	31	31
Dianthus superbus subsp. *superbus*	3	0	4	3	0
Digitalis grandiflora	5	0	0	1	0
Dorycnium pentaphyllum subsp. *herbaceum*	1	4	4	8	7
Echium vulgare	7	7	16	5	14
Elymus repens	0	0	4	0	1
Epilobium montanum	0	1	0	0	4
Equisetum arvense	4	1	4	6	4
Equisetum palustre	1	3	0	3	7
Equisetum pratense	3	3	0	0	4
Equisetum sylvaticum	1	1	0	0	4
Erigeron acer	1	5	7	5	6
Erigeron annuus subsp. *annuus*	9	3	4	4	13
Eryngium campestre	3	11	9	4	4
Euphorbia amygdaloides	3	4	0	0	0
Euphorbia cyparissias	9	16	13	9	21
Euphrasia pectinata	0	7	0	0	6
Euphrasia rostkoviana	13	24	31	21	39
Euphrasia stricta	20	24	27	25	17
Fagus sylvatica	4	0	0	0	0
Ferulago sylvatica	0	8	7	0	4
Festuca pratensis	5	20	13	19	24
Festuca rubra subsp. *rubra*	100	100	100	100	100
Festuca rupicola subsp. *rupicola*	4	0	2	3	3
Festuca valesiaca	0	1	0	4	4
Filipendula ulmaria	0	11	0	3	6
Filipendula vulgaris	12	21	29	24	32
Fragaria vesca	8	8	9	14	10
Fragaria viridis	5	3	2	0	4
Galeopsis speciosa	0	5	0	0	0
Galium album subsp. *album*	1	13	0	3	3
Galium mollugo	4	0	4	8	8

(continued)

Table 3 (continued)

Species name (alphabetic list)	*PA*	*LP*	*VC*	*T*	*SP*
Galium schultesii	0	4	0	0	3
Galium uliginosum	4	14	0	4	8
Galium verum	29	39	42	45	36
Genista tinctoria subsp. *tinctoria*	16	21	27	25	19
Gentiana asclepiadea	3	12	2	6	6
Gentiana cruciata subsp. *cruciata*	0	3	4	0	0
Gentiana cruciata subsp. *phlogifolia*	1	12	0	4	3
Gentiana utriculosa	0	1	0	0	6
Gentianella austriaca	7	7	7	5	3
Gentianella lutescens	3	13	4	8	6
Geranium phaeum	5	4	0	1	0
Geranium sanguineum	0	5	0	0	6
Gladiolus imbricatus	3	13	11	4	13
Glechoma hederacea	4	3	0	0	3
Gymnadenia conopsea	21	14	13	13	24
Gymnadenia odoratissima	1	3	0	0	4
Helianthemum nummularium subsp. *nummularium*	9	17	22	6	6
Helianthemum nummularium subsp. *obscurum*	7	4	13	9	6
Helleborus purpurascens	0	1	2	4	0
Heracleum sphondylium subsp. *spondylium*	1	11	4	14	7
Hieracium aurantiacum	9	16	2	10	17
Hieracium caespitosum	1	4	7	3	1
Hieracium cymosum subsp. *cymosum*	4	1	0	1	1
Hieracium pavichii	1	7	0	1	1
Hieracium pilosella	33	22	36	33	22
Hieracium umbellatum	4	4	4	3	3
Hieracium x floribundum	7	7	18	6	3
Holcus lanatus	17	25	31	31	42
Homogyne alpina	4	0	0	0	0
Hypericum hirsutum	4	5	0	1	0
Hypericum maculatum	20	9	20	19	31
Hypericum montanum	3	13	2	3	0
Hypericum perforatum	21	22	18	25	24
Hypericum tetrapterum	1	11	4	5	0
Hypochoeris maculata	12	28	33	19	14
Hypochoeris radicata	25	17	38	21	19
Hypochoeris uniflora	4	0	0	0	0
Inula britannica	0	4	0	0	3
Inula hirta	0	1	0	0	7
Iris sibirica	0	3	0	0	4
Juncus conglomeratus	0	4	0	4	7
Juncus effusus	4	0	2	5	8

(continued)

Table 3 (continued)

Species name (alphabetic list)	*PA*	*LP*	*VC*	*T*	*SP*
Juniperus communis subsp. *communis*	1	4	2	0	4
Knautia arvensis	13	32	33	29	38
Koeleria macrantha	3	5	0	3	1
Laserpitium latifolium	3	3	18	0	7
Lathyrus latifolius	0	0	2	5	0
Lathyrus pallescens	1	4	0	0	0
Lathyrus pratensis	3	3	7	9	8
Lembotropis nigricans	7	1	0	1	1
Leontodon autumnalis subsp. *autumnalis*	17	33	42	48	26
Leontodon crispus subsp. *crispus*	1	8	0	1	3
Leontodon hispidus subsp. *danubialis*	9	20	4	8	8
Leontodon hispidus subsp. *hispidus*	7	16	24	25	40
Leucanthemum vulgare	57	51	76	74	81
Leucanthemum waldsteinii	0	3	4	1	1
Linaria vulgaris	0	9	2	0	4
Linum austriacum subsp. *austriacum*	1	11	0	1	6
Linum catharticum	16	13	31	31	28
Listera ovata	4	4	0	3	1
Lolium perenne	9	25	0	4	8
Lotus corniculatus	41	64	71	63	72
Luzula campestris	37	28	16	23	29
Luzula luzuloides subsp. *cuprina*	4	9	2	4	3
Luzula luzuloides subsp. *luzuloides*	9	11	13	15	6
Luzula multiflora	1	3	2	3	4
Lychnis coronaria	4	8	0	1	0
Lychnis flos-cuculi	4	13	2	9	13
Lychnis viscaria	9	3	4	6	7
Lysimachia nummularia	0	3	2	1	6
Lysimachia vulgaris	1	8	7	9	10
Lythrum salicaria	4	8	0	1	1
Medicago lupulina	3	18	2	3	22
Medicago minima	1	5	0	4	7
Medicago sativa subsp. *falcata*	5	7	11	8	6
Melilotus officinalis	0	0	0	0	4
Moenchia mantica subsp. *mantica*	5	0	4	5	0
Molinia caerulea subsp. *caerulea*	0	3	4	0	8
Muscari comosum	1	9	0	1	7
Myosotis scorpioides	1	3	2	3	10
Myosotis stricta	0	3	0	0	4
Myosotis sylvatica	11	7	4	5	3
Nardus stricta	26	21	38	25	13
Nepeta nuda subsp. *nuda*	0	3	4	3	0

(continued)

Table 3 (continued)

Species name (alphabetic list)	*PA*	*LP*	*VC*	*T*	*SP*
Omalotheca sylvatica	18	8	18	10	8
Ononis arvensis	5	8	9	10	13
Ononis spinosa x arvensis	0	5	0	1	1
Orchis coriophora subsp. *coriophora*	8	14	7	4	3
Orchis morio subsp. *morio*	1	7	0	3	17
Orchis ustulata	5	7	2	0	6
Origanum vulgare	0	1	7	4	3
Ornithogalum pyramidale	0	1	0	4	0
Parnassia palustris	1	7	0	9	4
Pedicularis comosa subsp. *comosa*	1	3	4	0	1
Peucedanum cervaria	1	12	0	0	4
Peucedanum oreoselinum	14	14	22	10	21
Peucedanum rochelianum	0	0	0	0	6
Phleum alpinum subsp. *alpinum*	8	0	0	1	1
Phleum montanum	0	0	4	0	0
Phleum phleoides	4	7	0	0	0
Phleum pratense	1	9	2	10	17
Phragmites australis	1	4	0	1	4
Phyteuma spicatum	1	3	4	3	0
Picris hieracioides	1	5	0	1	0
Pimpinella major	5	9	4	5	3
Pimpinella saxifraga	16	21	36	29	33
Plantago altissima	5	9	0	0	1
Plantago lanceolata	47	53	53	64	57
Plantago major	0	13	2	4	10
Plantago media	29	29	47	40	40
Poa alpina	4	0	0	0	0
Poa annua	1	7	0	3	1
Poa compressa	5	7	0	4	0
Poa pratensis	11	14	7	11	21
Poa trivialis	5	1	0	4	0
Polygala amara	3	5	2	1	1
Polygala comosa	4	3	18	8	10
Polygala major	5	13	0	6	4
Polygala vulgaris	29	37	51	44	42
Polygonatum verticillatum	0	1	7	3	0
Polygonum viviparum	0	4	0	1	3
Potentilla argentea	9	8	13	1	10
Potentilla aurea subsp. *aurea*	9	1	0	0	0
Potentilla aurea subsp. *chrysocraspeda*	3	0	4	4	1
Potentilla chrysantha	3	13	2	3	3
Potentilla erecta	34	28	53	40	47

(continued)

Table 3 (continued)

Species name (alphabetic list)	*PA*	*LP*	*VC*	*T*	*SP*
Potentilla recta	0	3	0	6	3
Potentilla thuringiaca	0	3	2	4	1
Primula elatior	1	8	7	3	14
Primula veris subsp. *veris*	4	7	7	9	13
Primula veris subsp. *columnae*	3	11	0	0	0
Prunella grandiflora	5	13	7	6	13
Prunella laciniata	13	17	9	9	11
Prunella vulgaris	54	42	71	55	57
Pteridium aquilinum	8	11	7	3	6
Quercus robur	4	7	0	4	1
Ranunculus acris	13	18	9	30	31
Ranunculus auricomus	0	1	4	1	1
Ranunculus montanus	8	9	2	5	1
Ranunculus polyanthemos	38	22	42	34	21
Ranunculus repens	1	0	2	3	10
Rhinanthus angustifolius subsp. *angustifolius*	21	26	11	25	15
Rhinanthus minor	21	16	36	25	26
Rhinanthus rumelicus	11	21	11	13	31
Rhodiola rosea	1	8	0	1	1
Rorippa pyrenaica	13	1	11	4	1
Rosa gallica	1	12	0	1	8
Rubus caesius	4	13	0	1	1
Rumex acetosa subsp. *acetosa*	36	29	40	46	42
Rumex acetosella subsp. *acetosella*	18	14	20	18	19
Rumex acetosella subsp. *acetosella* var. *tenuifolia*	5	0	0	1	0
Rumex alpinus	7	0	2	0	0
Rumex crispus	3	0	2	4	7
Salix rosmarinifolia	1	5	0	0	1
Salvia pratensis	3	11	11	3	4
Salvia verticillata	5	3	4	5	3
Sanguisorba minor subsp. *minor*	3	1	9	4	8
Scabiosa columbaria subsp. *columbaria*	1	8	0	8	3
Scabiosa lucida subsp. *barbata*	1	4	0	0	0
Scabiosa ochroleuca	11	17	13	15	18
Scleranthus annuus subsp. *annuus*	4	1	0	4	4
Scorzonera purpurea subsp. *purpurea*	4	3	0	3	0
Scorzonera purpurea subsp. *rosea*	3	4	0	1	1
Senecio jacobaea	7	1	7	11	1
Senecio sylvaticus	3	4	0	0	0
Serratula tinctoria	1	13	0	3	13
Serratula tinctoria var. *lancifolia*	0	0	0	0	4
Seseli annuum subsp. *annuum*	1	0	9	3	1

(continued)

Table 3 (continued)

Species name (alphabetic list)	*PA*	*LP*	*VC*	*T*	*SP*
Silene nutans subsp. *nutans*	3	4	4	3	3
Silene vulgaris	0	0	4	3	0
Sisyrinchium montanum	0	0	0	0	4
Solidago virgaurea	0	0	4	3	0
Stachys germanica	4	9	0	4	1
Stachys officinalis	17	25	38	30	39
Stachys recta	5	14	2	3	4
Stellaria graminea	49	41	42	56	53
Succisa pratensis	4	7	7	6	19
Taraxacum officinale	14	28	18	15	32
Teucrium chamaedrys	4	11	4	6	14
Thalictrum aquilegifolium	0	0	7	1	0
Thalictrum lucidum	0	7	0	1	4
Thalictrum minus	0	0	7	3	1
Thalictrum simplex subsp. *simplex*	1	0	4	1	0
Thesium linophyllon	1	3	2	1	4
Thymus comosus	1	9	0	5	6
Thymus glabrescens	9	1	18	6	4
Thymus pannonicus	8	4	2	8	3
Thymus pulegioides	29	38	44	34	51
Thymus x porcii	4	13	4	4	6
Tragopogon dubius	0	4	0	3	1
Tragopogon pratensis subsp. *orientalis*	1	8	11	4	11
Tragopogon pratensis subsp. *pratensis*	4	11	9	13	24
Traunsteinera globosa	5	8	0	8	1
Trifolium alpestre	12	20	27	14	32
Trifolium arvense	7	17	2	5	6
Trifolium aureum	4	11	18	5	7
Trifolium campestre	26	16	18	18	17
Trifolium dubium	8	0	4	8	8
Trifolium hybridum	3	3	0	3	7
Trifolium medium	12	21	13	5	15
Trifolium montanum	30	36	33	41	57
Trifolium ochroleucon	5	16	24	5	10
Trifolium pannonicum	12	26	11	15	19
Trifolium pratense	61	50	76	59	54
Trifolium repens subsp. *repens*	58	46	49	60	51
Trifolium rubens	4	4	0	1	0
Trisetum flavescens	0	11	0	1	8
Trollius europaeus subsp. *europaeus*	7	7	18	3	15
Vaccinium myrtillus	5	1	2	0	1
Vaccinium vitis-idaea	4	4	0	0	0

(continued)

Table 3 (continued)

Species name (alphabetic list)	*PA*	*LP*	*VC*	*T*	*SP*
Valeriana officinalis subsp. *officinalis*	1	4	7	4	1
Valerianella locusta	1	5	0	0	0
Veratrum album	7	5	4	6	8
Verbascum nigrum	3	0	0	4	0
Veronica austriaca subsp. *austriaca*	7	9	0	1	1
Veronica chamaedrys subsp. *chamaedrys*	21	7	27	23	18
Veronica officinalis	20	9	20	20	6
Veronica serpyllifolia	7	7	4	9	7
Veronica spicata subsp. *spicata*	3	3	2	0	4
Veronica verna	1	7	0	4	0
Vicia cracca	4	12	7	13	8
Vicia sepium	4	3	2	3	0
Vicia tetrasperma	4	3	2	3	4
Vicia villosa	1	5	0	4	0
Viola arvensis	1	1	4	1	3
Viola canina subsp. *canina*	17	11	42	16	15
Viola declinata	13	11	7	9	7
Viola reichenbachiana	3	7	0	6	6
Viola suavis	0	5	2	1	3
Viola tricolor subsp*s*	16	8	18	13	21

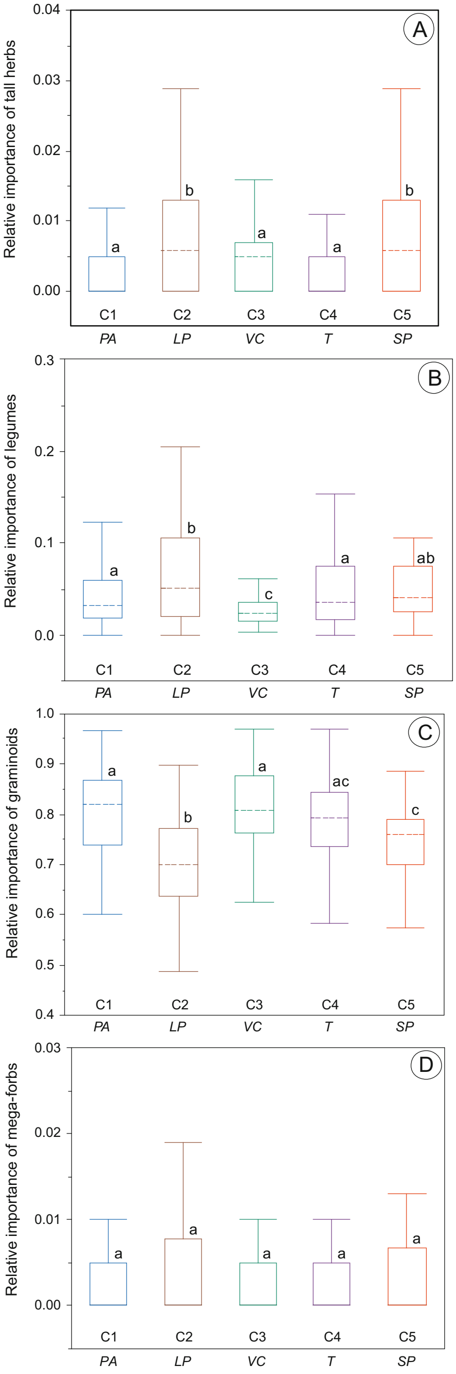
Cluster C1 (*PA*)—F-A *potentillosum aureae* (holotype: relevé 9, Table 8 in Csűrös and Resmeriţă 1960)
Differential species: *Potentilla aurea*, *Phleum alpinum*

This group includes montane pastures developed on moderately acidic soils with relatively high nitrogen content. Usually, these grasslands extend from 800 up to 1900 m. Because they are grazed intensively, some nitrophilous species may become frequent (e.g., *Rumex alpinus*) to the point of being considered differential with respect to the other facies. The montane and acidophilous character of this facies is indicated floristically by the preferential presence of some typical species for *Poion alpinae* grasslands, like *Phleum alpinum* and *Poa alpina*, and for *Potentillo-Nardion* pastures, such as *Potentilla aurea* and *Hypochoeris uniflora*.

Cluster C2 (*LP*)—F-A *loliosum perennis* (holotype: relevé 15, Table 15 in Drăgulescu 1984)
Differential species: *Lolium perenne, Danthonia alpina, Trifolium arvense*

This group contains fertilised meadows occurring in the colline belt on moderately acidic, N-rich soils. The high nitrification is confirmed by the preferential occurrence of some nitrophilous species like *Lolium perenne, Galeopsis speciosa* and *Cruciata laevipes*. The facies *loliosum perennis* is more thermophilous and

Fig. 5 Relative importance of four plant functional groups within each grassland community, by facies (A = tall herbs, B = legumes, C = graminoids, D = mega-forbs). Abbreviations are as in Table 1 and symbols as in Fig. 3



xerophilous, as indicated by the diagnostic species *Hypericum montanum, Peucedanum cervaria, Danthonia alpina, Trifolium arvense* and *Stachys recta*. Proximity to *Arrhenatherion* grasslands is suggested by the preferential occurrence of *Galium album*.

Cluster C3 (*VC*)—F-A *violosum caninae* (provisional holotype: relevé 16, Table 36 in Zanoschi 1971)
Differential species: *Viola canina, Laserpitium latifolium, Phleum montanum*

This group is composed of submontane pastures lying on sunny slopes and slightly acidic to neutral bedrocks. The good fidelity of *Phleum montanum* and *Seseli annuum* indicates slightly more xeric conditions, very likely due to shallow soils, and the proximity of grasslands in the class *Festuco-Brometea*. Apart from *Viola canina*, the other differential species have high requirements for soil base saturation. The preferential occurrence of the acidophilous species *Viola canina* is likely due to overgrazing but without excessive nitrification.

Cluster C4 (*T*)—F-A *typicum*
Differential species: *Ajuga genevensis*

Because this group of relevés lies in the middle of the first ordination axis and extends all along the second ordination axis (Fig. 4), it has neither distinct ecological features nor good differential species.

Cluster C5 (*SP*)—F-A *succisosum pratensis* (holotype: relevé 3, Table 15 in Peia 1978)
Differential species: *Succisa pratensis, Peucedanum rochelianum* (restricted to the southern Carpathian region), *Gentiana utriculosa, Orchis morio*

This facies represents colline meadows formed on gentle slopes or valley bottoms shaped by slow water run-off and deposition of fine, slightly acidic to neutral materials. The best ecological indicators of such site conditions (base-rich, moist soils) are *Peucedanum rochelianum* and *Gentiana utriculosa*. Along with *Succisa pratensis*, these species are typical for *Molinion* grasslands that probably occur nearby.

Discussion

The *Festuca rubra-Agrostis capillaris* (F-A) grasslands show low floristic variation in spite of their wide geographic distribution and range of environmental conditions. Such a situation is reflected in the predominance of generalist species in their floristic composition, which has also rendered the syntaxonomic assignment of these communities quite challenging at the alliance level.

The main ecological gradients underlying the floristic variation of F-A grasslands are edaphic (base and nitrogen availability) and, to a lesser extent, the thermal conditions and management type. Base saturation and nitrogen content are negatively related, probably because acidophilous grasslands have been used mostly as pastures or have been given more manure. Another confounding effect arises from the interaction between grassland management and local climate conditions. The thermal gradient is related somewhat to the intensity of grazing and the frequency of mowing. This is because grazing is the dominant use of grasslands at higher altitudes, whereas mowing is most common at lower elevations.

The five facies described are based on fuzzy clusters of relevés that show low floristic distinctiveness in terms of diagnostic species. None of them had a Phi coefficient larger than 0.30, which is considered a lower threshold for non-trivial effects of association (Osborn 2006). The strongest floristic and ecologic differentiation occurs between acidophilous grasslands (facies *potentillosum aureae* and *loliosum perennis*) and those formed on base-rich substrates (facies *violosum caninae* and *succisosum pratensis*). A much weaker differentiation is induced by elevation and the predominant land-use regime, i.e. colline-submontane meadows (facies *loliosum perennis* and *succisosum pratensis*) *versus* montane-subalpine pastures (facies *potentillosum aureae* and *violosum caninae*). With regard to these two categories, only two species (*Medicago lupulina* and *Trisetum flavescens*) show fidelity patterns that make them fairly good indicators of meadows as opposed to pastures. In addition, legumes and tall herbs, on the one hand, and graminoids, on the other hand, show contrasting guild proportionality between the two main grassland use modes. The relative cover of the graminoids seems to be enhanced by repeated grazing that stimulates the formation of a continuous, thick sod. Actually, graminoids have a competitive advantage by means of their high regeneration ability after browsing and low sensitivity to trampling (Wilmanns 1998). A similar pattern of increasing graminoid cover with grazing intensity was observed in subalpine meadows converted to pastures (Fischer and Wipf 2002). On the other hand, tall herbs and legumes appear to be more abundant in colline meadows, in which plants are usually clipped twice a year at several centimeters above ground level.

The montane variant described by Csűrös and Resmeriţă (1960) as *Festuco rubrae-Agrostidetum tenuis montanum* can be considered roughly as a synonym of the facies *potentillosum aureae*, which is definitely the most microthermal.

The facies *loliosum perennis* overlaps to a certain extent with the subass. *genistetosum sagitallis* Coldea 1991, given its acidophilous character and the presence of *Chamaespartium saggitale* among diagnostic species.

The grasslands corresponding to the provisional facies *violosum caninae* appear floristically like grazing-disturbed counterparts of those included by Coldea (2012) in the subass. *caricetosum montanae* (Raclaru et Barbu 1959) Chifu et al. 2006. In fact, three important differential species of the latter (*Anthylis vulneraria, Hypochoeris maculata* and *Laserpitium latifolium*), along with a series of character species of *Nardetalia* (*Viola canina, Nardus stricta, Polygala vulgaris, Potentilla erecta* and *Hieracium pilosella*), reach their maximum frequency just in the third cluster of relevés (C3), which is assigned provisionally to the facies *violosum caninae*. The co-occurrence of *Viola canina* and of species demanding high soil base saturation suggests an on-going depletion of cations due to high amount of biomass loss (through grazing) and lack of fertilisation.

The grasslands of the facies *succisetosum pratensis* are by far the most hygrophilous and potentially the most productive, given the underlying soils with their optimal water and base supplies. This facies has obvious floristic affinities with communities of the *Molinion caeruleae* alliance.

Despite the almost equal number of relevés employed in classification, the lower syntaxa proposed herein differ floristically from those retained by Coldea (2012). There are at least four reasons for this discrepancy. First, our data-set does not include a series of relevés from the eastern and southern extra-Carpathian zone that accounted largely for the distinction of the subassociations *caricetosum montanae* and *trifolietosum patens* (Coldea 2012). Second, we did not consider relevés in which "third-party" species were more abundant than both *Agrostis tenuis* and *Festuca rubra*, as the structure of such communities is—in our opinion—closer to other plant associations or assignable to unstable seral stages. Third, our input data also contained relevés from grasslands with floristic compositions that had been altered slightly by overgrazing. Fourth, the numerical classification used herein gave equal weight to all component species. On the contrary, in the classical classification of Coldea (2012), higher importance was given to character species from relevés that were probably selected carefully in order to exclude floristically degraded grasslands. Our approach was more objective and allowed the use of numerical analyses to draw inferences that can be generalised. On the other hand, the data contained more noise due to inconsistencies in the occurrence patterns of grazing-tolerant and ruderal species. Coldea's (2012) approach led to a more subjective (personal experience-based) selection and assignment of relevés to different syntaxa, and the resulting classification was sharper in terms of frequency patterns of the differential species. The different levels of classification, i.e. subassociation and facies, were determined partly by such differences in data structure. A good example is the contrasting occurrence patterns of *Nardus stricta* in the various syntaxa resulting from the two classifications. Whereas *N. stricta* occurs almost exclusively in the subass. *nardetosum* of Coldea (2012), it is more or less evenly distributed among the facies distinguished herein. Therefore, our results do not support the distinction of the subass. *nardetosum* Oroian 1998, as long as the abundance of *N. stricta* does not exceed that of any of the two presumed dominant species (*F. rubra* and *A. capillaris*). The empirical classification by Coldea (2012) may be more useful as a typologic reference for conservation and restoration purposes. In turn, our clustering output is probably more suitable for the practice of grassland management and provides a good basis for unravelling successional pathways under different environmental conditions and grassland use modes.

A regressive, dynamic tendency toward *Nardus stricta*-dominated communities has been observed largely in F-A grasslands affected by overgrazing (Puşcaru-Soroceanu 1963; Coldea et al. 2008). According to species frequency data, the least prone to such floristic degradation are the meadows assigned to the facies *succisosum pratensis* and *loliosum perennis*. Long-term overgrazing and lack of fertilisation usually result in regressive successions to *Gentianello lutescentis-Nardetum* Coldea et al. 2008 in the colline and submontane belts, or to *Violo declinatae-Nardetum* Simon 1966 in the montane and subalpine belts (Coldea et al. 2008). Similar shifts to *Nardus*-dominated communities have been observed in many other grassland types throughout central Europe (Ellenberg 1996).

It must be recalled that we excluded 65 relevés from the final classification as being marginal or outlying communities with respect to cluster medoids. However, these floristically "atypical" grasslands cannot be overlooked, as they are an expression of the floristic continuum of species composition (Mucina 1997). Although these 'odd' grasslands cannot be classified uniquely at the moment, at least some of the outliers might be assigned further to other syntaxa, e.g. *trifolietosum patens*, or to new ones. The marginal relevés are of interest for reconstructing coenoclines along ecological gradients and for inferring possible successional pathways.

Future research must consider the use of even larger data-sets in order to catch the entire floristic variation of F-A grasslands in the southeastern Carpathian region. In particular, more relevés from the eastern and southern extra-Carpathian zone are needed in order to assess numerically whether the grasslands assigned to the subass. *caricetosum montanae* and the facies *violosum caninae* do segregate into different clusters.

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The *Caricetum distichae* Association in Italy

Franco Pedrotti

Abstract *Carex disticha* Hudson (Fam. *Cyperaceae*) is a Eurasian species that is very rare in Italy. It is present at only a few sites in the Alps and at only two sites in the central Apennines, in the areas of Pian Grande (Umbria) and the Quarto di Santa Chiara (Abruzzo), both in the montane belt. This species forms the *Caricetum distichae* Noviński 1927 (syn. *Caricetum intermediae* Steffen 1931) association, all. *Magnocaricion*, ord. *Magnocaricetalia*, cl. *Phragmiti-Magnocariceta*, which occurs throughout Europe but is very rare in Italy.

Carex disticha Hudson (Family Cyperaceae) is a Eurasian species occurring in Italy at seven sites in the region Trentino-Alto Adige (Wallnöfer 1991; Venanzoni 1993; Wilhalm et al. 2006; Prosser 2004–2010); at one site in Umbria (Pedrotti 1977; Cortini Pedrotti and Pedrotti 1977; Pignatti 1982; Pedrotti et al. 2004); at one site in Abruzzo (Conti et al. 1991); and at one site in Lazio (Anzalone et al. 2010). All of these were also reported by Conti et al. (2005). Thus there are nine sites in all, all in the montane belt, except for the Lazio location, which is in the foothill belt. *Carex disticha* Hudson is a very rare species and is on the red list of plants of Italy, for both the national and regional level (Conti et al. 1992, 1997). The goal of this note is to examine the phytosociology of *Carex disticha* in Italy.

The Phytosociology of *Carex disticha*

Carex disticha is a species of the alliance *Magnocaricion elatae* W. Kock 1926 (the *Caricenion gracilis* Neuhäusl 1959; Oberdorfer et al. 1967 suballiance), in the order *Magnocaricetalia elatae* Pignatti (1953) 1954 and the class *Phragmiti-Magnocaricetea* Klika in Klika et Novák 1941. It forms the *Caricetum distichae* Noviński 1927 (syn. *Caricetum intermediae* Steffen 1931) association, which, though already known from a site in the Italian Alps (Trentino), is reported here

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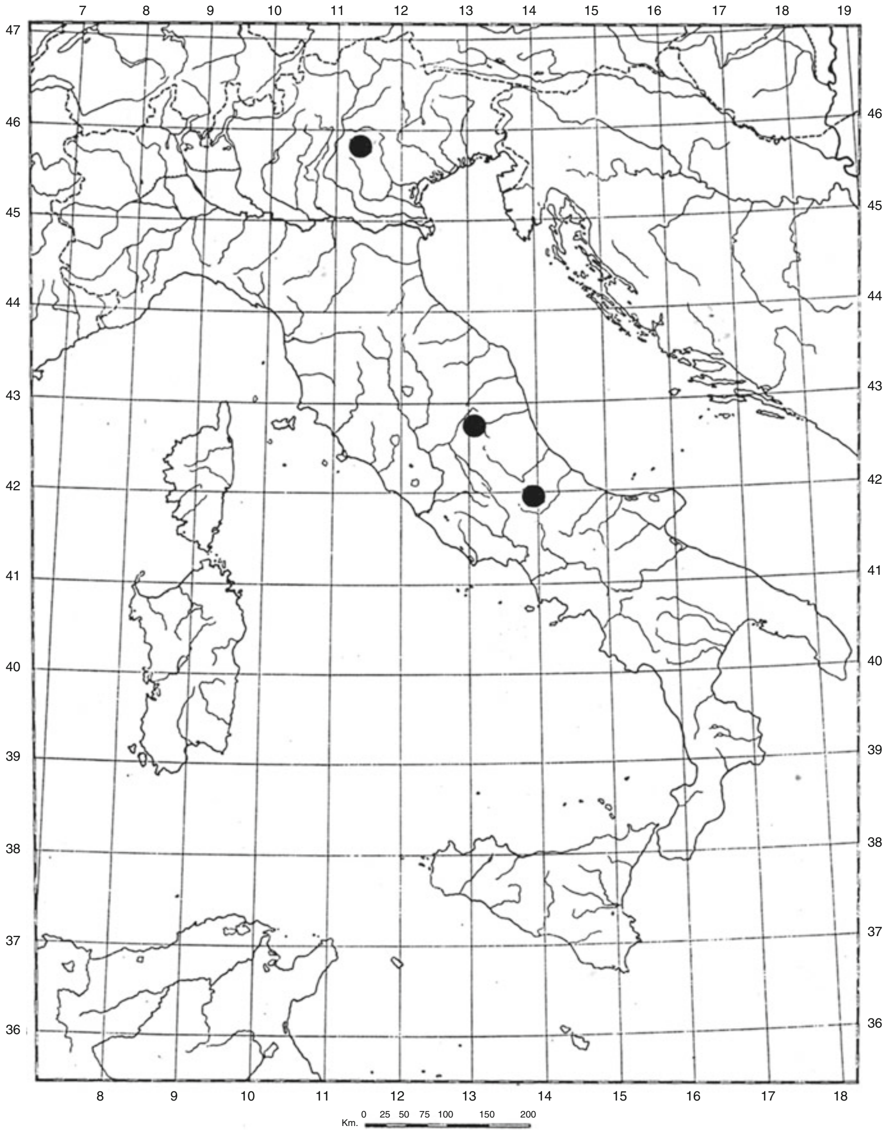

Fig. 1 Distribution of *Caricetum distichae* in Italy

for the first time for the central Apennines (see Fig. 1). It is not known whether this species also forms stands at sites of Alto Adige and Lazio.

Table 1 shows four relevés of this association, made on the Pian Grande of Umbria and the Quarto di Santa Chiara in Abruzzo. As can be seen, this association is almost monospecific, dominated by *Carex disticha*, joined by a few *Carex gracilis* tufts and a few other species. Each relevé has between seven and nine

Table 1 *Caricetum distichae*

Relevé number	1	2	3	4
Altitude (m.a.s.l.)	1268	1268	1250	1250
Aspect	–	–	–	–
Slope (°)	–	–	–	–
Cover (%)	100	100	100	100
Relevé area (m^2)	10	10	10	8
Carex disticha	4.5	5.5	4.4	5.5
Character. species of all. (*Magnocaricion elatae*), suball. (*Caricenion gracilis*), order. (*Magnocaricetalia*) and cl. (*Phragmiti-Magnocaricetea*)				
Galium constrictum	+	+	1.1	1.1
Carex gracilis	+	+	+	+.2
Heleocharis palustris	+	.	.	.
Companions				
Veronica scutellata	+	+	+	.
Ranunculus repens	.	+	+	+
Ranunculus flammula	1.1	+	.	.
Agrostis alba	.	+	+	.
Equisetum palustre	+	.	.	.
Leontodon autumnalis	,	+	.	.
Myosotis scorpioides	.	.	+	.
Polygonum amphibium var. *terrestre*	.	.	.	1.1
Mentha arvensis	.	.	.	+
Bryophytes				
Drepanocladus aduncus	1.2	1.2	.	1.2
Number of species per relevé	8	9	8	7

species. The relevés were very similar in both locations, with very few species differences.

On the Pian Grande, the *Caricetum distichae* develops in a few dolines and very small depressions of a few square meters, which are present in the meadowlands belonging to the *Polygono-Nardetum* association (Pedrotti 1982).

The soils of the Pian Grande are highly hydromorphic, submerged in water for about 7 months a year, and occur on clayey sediments with variable carbonate content. These soils are referred to in German as *Anmoor* soils (Histic Humaquepts), with an O horizon sometimes acidic, sometimes neutral, which merges, at 20–25 cm, to a strongly mottled Bg (gley) horizon with high base saturation (Cortini Pedrotti et al. 1973). In the summer, the water table is 60–70 cm deep, but the long roots of *Carex gracilis* and of *Carex disticha* reach it easily.

At Quarto di Santa Chiara, the association may occupy individual depressions (without other "magnocariceta") or it may form a band around depressions that have *Caricetum gracilis* in their center. On the basis of our observations, one may say that *Caricetum gracilis* occupies sites that are more flooded than those of *Caricetum distichae*.

In the Alps, *Carex disticha* is present in the glacio-karstic basin of Folgaria in Trentino (Pedrotti and Venanzoni 1987), where it was possible to conduct just one relevé, reported by Venanzoni (1993), which because of its species composition corresponds to that of Table 1; the same can be said for the *Caricetum distichae* in former Czechoslovakia (Balátová-Tuláčková 1976, 1978).

Often the *Carex disticha* plants are sterile, without flowers or with small spikelets with aborted flowers. This was observed both at Pian Grande and in Quarto di Santa Chiara, and also is the case for the spikelets of *Carex gracilis*. In part, this may be attributed to late-spring freezes that damage the spikelets during their formation, when the plant is beginning its development after the winter.

Conclusion

The two environments of the central Apennines in which *Caricetum distichae* is present, Pian Grande and Quarto di Santa Chiara, are very similar. Both are large basins with structural and karstic origins, with a partially impermeable bottom, a fact that enables the establishment of the associations of *Magnocaricion*. Both of these locations host two very rare species, *Carex disticha*—as already noted—and *Carex buxbaumii*, reported for Pian Grande by Pedrotti (1971) and for the Quarto di Santa Chiara by Conti et al. (1991). *Carex buxbaumii* is common at Pian Grande and forms its own association, *Ranunculo-Caricetum buxbaumii*, a new association of the *Magnocaricion* alliance, *Caricenion gracilis* suballiance, described by Pedrotti (in press). At Quarto di Santa Chiara only one site has been found to date, with these association.

The occurrence of "magnocariceta" at the two locations is as shown below; those marked by an * were already reported by Pirone (1987).

	Pian Grande	Santa Chiara
Caricetum vesicariae	+	+*
Caricetum gracilis	+	+*
Caricetum otrubae	+	+*
Caricetum distichae	+	+
Ranunculo-Caricetum buxbaumii	+	+
Caricetum paniculatae	.	+*

The presence of *Caricetum paniculatae* at Quarto di Santa Chiara is related to some springs found on the bottom of the plain, which are lacking at Pian Grande. The presence of *Ranunculo-Caricetum buxbaumii* at Pian Grande is explained by the vast area of clayey lacustrine deposits, as seen also in the vegetation map at scale 1:5000 (Cortini Pedrotti et al. 1973). However, within this area, *Caricetum* *distichae* is very rare and limited to three or four small areas, each of which covers only a few square meters.

The "magnocariceta" contribute to give a particular character to the plant landscape of the basins of the central Apennines, inasmuch as they are prevalently associations of Middle Europe, including the Padania plain. In the central Apennines some associations, such as *Caricetum distichae*, reach their southernmost limit, while *Rannunculo-Caricetum buxbaumii* is exclusive to the central Apennines, where it is known to grow at only two locations.

Locations of the relevés:

Number 1 and Number 2—Pian Grande di Castelluccio di Norcia (Umbria), June 28, 2012.

Number 3 and Number 4—Quarto di Santa Chiara (Abruzzo), July 12, 2013.

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The Vegetation of the Pie' Vettore Debris (Sibillini Mountains, Central Italy)

Kevin Cianfaglione and Franco Pedrotti

Abstract This work describes the vegetation that colonizes the rubble deposits of glacial origin on the southeast slopes of Monte Vettore (Sibillini Mountains, central Apennines), at altitudes between 1000 and 1800 m. Today these deposits are colonized by some pioneer herbaceous species (*Rumex scutatus*, *Epilobium dodonaei*, *Scrophularia canina*) and shrubby species (*Amelanchier ovalis*, *Lonicera caprifolium*, *Prunus spinosa*, *Cytisophyllum sessilifolium*, *Rosa canina*, *Clematis vitalba*, *Viburnum lantana*, *Juniperus communis* and *J. deltoides* = *J. oxycedrus* and others). The latter form the *Junipero oxycedri-Amelanchieretum ovalis* Pedrotti 1994 association, *Cytision sessilifolii* alliance*, Prunetalia spinosae* order and *Rhamno-Prunetea* class*,* already noted for other locations in the Sibillini Mountains. Where the soil is more developed, a shrubland dominated by *Prunus spinosa*, *Ligustrum vulgare*, *Cytisophyllum sessilifolium* and other species has grown up, attributed to the new association *Cytisophyllo sessilifolii-Prunetum spinosae* ass. nova hoc loco, *Cytision sessilifolii* alliance. This association occurs in many other locations of the montane belt of the Marche Region (central Apennines).

Introduction

This note describes the vegetation growing on the calcareous detritus left from Pie' Vettore in the Sibillini Mountain group in central Italy and also reports its dynamic tendencies. This shrubby vegetation may, in part, be considered primary, similar to that observed in other locations with detritus deposits in the Alps, and with which it shares some botanical and ecological characteristics.

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Description of the Study Area

The study area is in the Pie' Vettore locality on the southeastern slopes of Monte Vettore, part of the Sibillini Mountains, at 1000–1800 m above sea level, above the village of Pretare (Arquata del Tronto). The name Pie' Vettore means at the foot of Monte Vettore (2456 m). At this location, a great landslide of calcareous rocks (limestone of the lower and middle Liassic, i.e. early Jurassic) formed a complex of detritus deposits composed by compact limestone clasts of different sizes: large boulders of several meters in diameter together with finer elements of the dimensions of silt (Bisci and Dramis 1991). In some sections, the deposits have been moved onto small terraces and in part removed for a quarry for calcareous construction materials, especially sand and limestone. Nearby is a lime furnace called "Calcara" that has been abandoned for some time.

The body of the landslide has three gross forms, convex, flat or concave. The first form is made by the coarser deposits (Fig. 1), while the flat and concave areas correspond often to areas where debris was partly worked or removed.

The grassland vegetation is composed mainly of *Sesleria nitida*, *Brachypodium rupestre*, *Bromus erectus*, *Cerastium tomentosum*, *Teucrium chamaedrys* and other species of the *Crepido lacerae-Phleion ambigui* alliance of Biondi and Blasi (1982); the shrubby species are mainly: *Amelanchier ovalis* (Fig. 2), *Lonicera caprifolium*, *Prunus spinosa*, *Cytisophyllum sessilifolius*, *Rosa canina*, *Clematis vitalba*, *Viburnum lantana*, *Juniperus communis*, and *J. deltoides* (= *J. oxycedrus*) (*Cytision sessilifolii* alliance of Biondi et al. 1988). The detritus of the landslide is colonized by pioneer species like *Rumex scutatus*, *Epilobium dodonaei*, and *Scrophularia canina*. At the moment it is not possible to identify the pioneer association growing on the detritus at Pie' Vettore because only a few species are present, only sparsely, and the overall situation of the vegetation is too fragmentary.

Fig. 1 The association *Junipero oxycedri-Amelanchieretum ovalis* grows on limestone debris, with a strip of *Cytisophyllo sessilifolii-Prunetum spinosae* in a small valley within the debris; the xeric grasslands belong to the alliance *Crepido lacerae-Phleion ambigui*

Fig. 2 Landslide debris from Pie' Vettore (Sibillini Mountains), with *Amelanchier ovalis* on a large boulder; in the background: the "Calcara" and the Monte Vettore (2456 m) profile

The Vegetation of the Debris

Today three associations grow on the detritus, a shrubwood formed prevalently by *Amelanchier ovalis* (*Junipero oxycedri-Amelanchieretum ovalis* Pedrotti 1994); a shrubwood formed prevalently by *Prunus spinosa* (*Cytisophyllo sessilifolii-Prunetum spinosae* ass. nova hoc loco); in addition, there is a shrubwood of *Corylus avellana*, similar to the *Symphyto-Coryletum avellanae* Catorci and Orsomando.

Junipero oxycedri-Amelanchieretum ovalis *(Table 1)*

This shrubwood belongs to the *Junipero oxycedri-Amelanchieretum ovalis* association, which is part of the *Cytision sessilifolii* alliance, *Prunetalia spinosae* order and *Rhamno-Prunetea* class. On the basis of the relevés made (Table 1), the species composition is similar to that of other locations in the Sibillini Mountains and from the mountains of the Abruzzo region (Pedrotti 1994; Basnou and Pedrotti 2001; Catorci and Orsomando 2001; Rosi 2005; Pedrotti 2010), where *Junipero oxycedri-Amelanchieretum ovalis* normally grows on sites with detritus or with rocky outcroppings and sometimes in rocky pastures (*Crepido lacerae-Phleion ambigui*) that have been abandoned and are undergoing secondary succession, at 900–1000 m (upper limit of the hilly belt). At higher altitudes (1100–1800 m), i.e. the montane belt, this vegetation is replaced by the *Rhamno alpinae-Amelanchieretum ovalis* Pedrotti 1994, of the *Berberidion* alliance. At Pie' Vettore, the *Junipero oxycedri-Amelanchieretum ovalis* is developed as primary succession, though partly disturbed, and the first stage is formed by pioneer vegetation (*Rumex scutatus*, etc.); it tends to develop on convex landforms on substrates formed of coarser accumulations. Initial aspects of the association are also developed among the large boulders of the landslide; in this case the vegetation also reveals species typical of rock walls, such as *Asplenium trichomanes*, *A. ruta-muraria*, *Sedum dasyphyllum* and others.

In the surveys, the relevés included only species of the herbaceous stratum inside the shrubby vegetation and not those outside, because these were excluded due to

Table 1 *Junipero oxycedri-Amelanchieretum ovalis*

Relevé number	1	2	3	4	5	6	7	8	9	10	11	
Altitude (m.a.s.l.)	950	980	1000	1000	1050	1050	1000	1050	1100	1000	950	
Aspect	S	S	S	–	–	–	–	S-W	S-E	S-W	E	
Slope (°)	5	70	40	–	–	–	–	10	20	15	15	
Cover (%)	90	70	100	90	90	90	90	80	90	80	80	
Relevé area (m^2)	10	60	40	100	20	50	15	90	30	20	10	
Amelanchier ovalis	3.3	2.2	5.5	4.4	4.4	4.4	5.5	4.4	3.3	3.3	3.3	12
Juniperus deltoides (=*J. oxycedrus*)	+	1.1	+	+	.	+	.	.	.	.	.	6
Character. sp. of all. (*Cytision sessilifolii*)												
Cytisophyllum sessilifolium	.	+	1.1	1.1	.	+	.	+	3.3	+	.	7
Coronilla emerus	.	+	.	+	.	+	.	.	.	.	.	3
Character. sp. of ord. (*Prunetalia spinosae*) and cl. (*Rhamno-Prunetea*)												
Euonymus europaeus	.	.	1.1	+	+	+	1.1	+	.	.	.	7
Prunus spinosa	.	.	1.1	+	.	.	2.2	1.1	.	.	1.1	5
Cornus sanguinea	.	.	+	.	+	+	.	.	.	.	.	4
Clematis vitalba	.	.	+	.	.	+	.	+	.	+	.	3
Rhamnus alpina	.	+	.	.	.	.	.	+	.	.	.	3
Corylus avellana	.	.	.	+	.	1.1	.	.	+	.	.	3
Prunus mahaleb	.	1.1	.	.	.	.	.	.	.	.	.	1
Crataegus laevigata	.	.	.	+	.	.	.	.	.	.	.	1
Ligustrum vulgare	.	.	.	+	.	.	.	.	.	.	.	1
Companions												
Teucrium chamaedrys	+.2	+	+	+	.	+	+	.	+	1.1	+	10
Sanguisorba minor	+.2	.	+	+	+	+	.	1.1	.	1.1	+	9
Fraxinus ornus	.	+	+	+	+	+	.	+	.	+	+	9
Cerastium tomentosusm	.	+	1.2	.	+	.	1-1	+.2	.	+	+	8
Bunium bulbocastanum	.	.	1.1	1.1	1.1	+	+	+	.	+	.	8

Helianthemum nummularium	.	.	.	+.2	+	.	1.2	+.2	1.1	1.2	1.1	8
Brachypodium januense	+	.	.	+	1.2	.	2.2	2.3	+.2	1.2	.	8
Sesleria nitida	+	.	2.2	2.2	1.1	1.1	,	2.2	,	+	,	7
Viburnum lantana	.	.	+	1.1	1.1	+	.	+	+	.	.	7
Taraxacum officinale	+	.	+	+	+	+	+	+	.	.	.	7
Turritis glabra	+	+	.	.	.	+	.	+	.	+	+	6
Globularia cordifolia	1.1	.	,	+	.	.	.	.	1.1	1.1	.	4
Sedum album	+.2	+	.	.	.	.	+	.	.	.	+	4
Hypericum perforatum	.	+	+	+	.	.	+	.	.	.	.	4
Rubus fruticosus	.	.	.	+	.	+	.	+	.	+	.	4
Galium verum	.	.	.	.	+	.	+	.	+	+	.	4
Cyclamen hederifolium	.	.	.	+	.	+	.	+	+	.	.	4
Juniperus communis	+	.	.	.	.	+	.	.	.	+	.	3
Geranium pusillum	.	.	+	.	.	.	1.1	.	.	.	.	2
Galium mollugo	.	.	+	.	.	.	+	.	.	.	.	2
Geranium purpureum	.	.	.	+	.	.	.	.	.	.	+	2
Accidental species	2	4	–	3	–	1	2	1	1	3	2	
Number of sp. per relevé	14	16	18	26	13	20	16	19	11	19	12	

Accidental species—Rel. 1: *Geranium robertianum*, *Polygala major*; rel. 2: *Quercus pubescens*, *Quercus ilex*, *Mycelis muralis*, *Polygala major*; rel. 3: none; rel. 4: *Acer obtusatum*, *Acer pseudoplatanus*, *Pteridium aquilinum*; rel. 5: none; rel. 6: *Viola alba* ssp. *denhardtii*; rel. 7: *Geranium robertianum*, *Pteridium aquilinum*; rel. 8: *Acer campestre*; rel. 9: *Viola alba* ssp. *denhardtii*; rel. 10: *Ostrya carpinifolia*, *Sorbus aria*, *Sorbus aucuparia*; rel. 11: *Ostrya carpinifolia*, *Quercus cerris*

Relevé locations—Rel. 1–8: Pie Vettore; rel. 9: Bivio per Montegallo; rel. 10 and 11: Foce di Montemonaco (Sibillini Mountains)

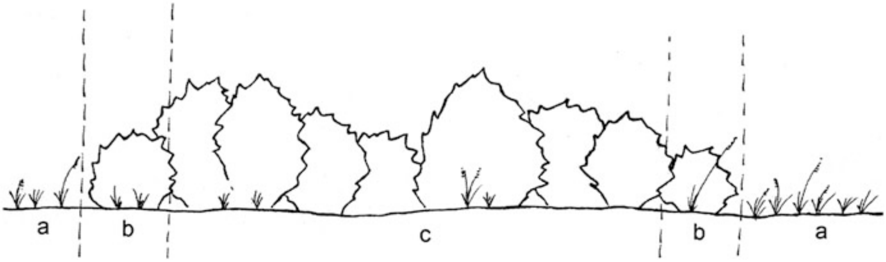

Fig. 3 Profile through a shrubland of Pie' Vettore (Sibillini Mountains): a = xeric grassland (*Crepido lacerae-Phleion ambigui*); b = ecotone; c = shrubland (*Junipero-Amelanchieretum* or *Cytisophyllo sessilifolii-Prunetum spinosae*). The relevés were made in the shrubland. Some species from the surrounding xeric grassland also grow in the shrubland

the ecotonal conditions (Fig. 3). This also applies to the other shrubby associations reported here.

Cytisophyllo sessilifolii-Prunetum spinosae *ass. nova hoc loco (Table 2)*

This *Prunus spinosa* shrubwood belongs to a new association, the *Cytisophyllo sessilifolii-Prunetum spinosae* ass. nova hoc loco (survey type no. 2, Table 2), which grows where the detritus has been partly worked or removed. This association belongs to the *Cytision sessilifolii* alliance, described by Biondi et al. (1988) for Central Italy. The *Cytisophyllo sessilifolii-Prunetum spinosae* includes a stratum of shrubby species, among them *Prunus spinosa*, *Rosa canina*, *Clematis vitalba*, *Lonicera caprifolium*, *Euonymus europaeus* and sometimes *Ligustrum vulgare*. The behaviour of *Cytisophyllum sessilifolius* varies considerably; it can attain notable degrees of cover, but not always, and sometimes it is absent. This association grows at slightly higher altitudes than does the *Cytiso sessilifolii-Spartietum juncei*, where it is cooler and *Spartium junceum* is rare or absent. At Pie' Vettore the substrate where *Cytisophyllo sessilifolii-Prunetum spinosae* grows has a concave or flat form, and thus the general site conditions are more favourable (because of the pedological characteristics) than are those of the *Junipero oxycedri-Amelanchieretum ovalis*.

This new association has been noted in various locations in the Umbria-Marche Appenines (see Table 2), in the Sibillini Mountain chain as well as in Colfiorito, Montelago, Copogna and other locations, always between the upper limit of the hilly belt and the montane belt. This association normally constitutes the mantle of the *Scutellario columnae-Ostryetum carpinifoliae*; in some cases it accompanies the *Carici sylvaticae-Quercetum cerris* (for example, in Popola di Colfiorito and around Montelago) or the *Lathyro veneti-Fagetum* (for example, in some parts of Pie' Vettore).

Table 2 *Cytisophyllo sessilifolii-Prunetum spinosae*

Relevé number	1	2*	3	4	5	6	7	8	9	10	11	
Altitude (m.a.s.l.)	1000	950	1010	900	950	920	850	780	800	900	880	
Aspect	–	S-E	–	E	E	W	W	W	S-W	N	N	
Slope (°)	–	5	–	10	15	20	20	40	30	5	20	
Cover (%)	90	100	100	90	100	100	100	100	100	100	100	
Relevé area (m^2)	10	20	20	20	100	100	50	100	60	120	100	
Prunus spinosa	1.2	1.1	2.2	2.2	4.5	4.4	5.5	4.5	3.4	4.4	5.5	11
Cytisophyllum sessilifolii	+	2.2	2.2	2.3	2.3	2.2	+.2	.	2.3	.	1.1	8
Character. sp. of ord. (*Prunetalia spinosae*) and cl. (*Rhamno-Prunetea*)												
Rosa canina	2.2	+	+	+	+	1.1	+	+	.	+	+	10
Clematis vitalba	+	+	+	1.1	.	.	1.1	.	1.1	1.1	1.1	9
Rubus fruticosus	+	+	.	+	+	1.1	+	+	.	1.1	+	9
Lonicera caprifolium	+	1.1	+	+	+	+	.	.	.	.	+	7
Euonymus europaeus	.	.	+	2.2	.	+	.	.	+	1.1	1.1	6
Crataegus monogyna	+	.	+	.	.	+	.	+	.	+	+	5
Crataegus laevigata	.	+	.	.	+	+	+	.	.	+	+	5
Viburnum lantana	1.1	1.1	+	1.1	.	.	.	.	.	.	.	4
Ligustrum vulgare	3.3	1.1	.	.	.	.	.	.	.	.	+	3
Cornus sanguinea	.	.	+	.	.	+	.	.	.	.	+	3
Lonicera etrusca	.	.	.	.	.	+	.	+	.	.	+	3
Prunus mahaleb	.	.	.	.	+	+	+	.	.	.	.	3
Pyrus pyraster	.	.	+	.	.	+	.	.	.	.	.	2
Cornus mas	.	.	.		.	+	.	.	.	.	+	2
Juniperus deltoides	.	.	1.1	.	.	.	.	.	+	.	.	2
Rhamnus cathartica	.	.	.	.	.	+	.	.	.	.	.	1
Ribes mutiflorum	.	.	.	.	.	.	.	.	.	2.2	.	1
Prunus cerasifera	.	.	.	.	.	.	.	.	.	.	+	1

(continued)

Table 2 (continued)

Relevé number	1	2*	3	4	5	6	7	8	9	10	11	
Altitude (m.a.s.l.)	1000	950	1010	900	950	920	850	780	800	900	880	
Aspect	–	S-E	–	E	E	W	W	W	S-W	N	N	
Slope (°)	–	5	–	10	15	20	20	40	30	5	20	
Cover (%)	90	100	100	90	100	100	100	100	100	100	100	
Relevé area (m^2)	10	20	20	20	100	100	50	100	60	120	100	
Companions												
Gallium mollugo	1.1	+	.	+	1.1	.	+	.	+	1.1	1.1	8
Brachypodium januense	.	+	+	+	1.1	1.1	+	.	1.1	+	1.1	7
Cruciata glabra	.	.	.	.	+	+	+	.	+	+	+	5
Silene italica	+	1.1	.	.	+	.	.	+	.	.	.	4
Corylus avellana	.	2.2	+	.	+	+	.	.	.	1.1	.	4
Fraxinus ornus	.	+	+	+	.	.	.	+	.	.	+	4
Prunus avium	.	.	+	.	+	.	.	.	+	.	+	4
Teucrium chamaedrys	.	+	.	.	+.2	1.2	.	.	.	.	+.2	4
Quercus cerris	.	.	.	.	+	.	.	+	.	+	+	4
Lathyrus sylvestris	.	.	.	.	+	+	.	+	.	+	.	4
Malus sylvestris	.	.	+	+	.	+	.	+	.	.	.	4
Viola alba denhardtii	.	.	.	.	.	1.2	.	.	+	2.3	+.2	4
Geranium purpureum	+	+	.	+	.	.	+	.	.	.	.	4
Sanguisorba minor	+	.	+	+	.	.	+	.	.	.	.	4
Turritis glabra	.	1.1	.	.	+	.	+	+	.	.	.	4
Acer obtusatum	.	+	+	.	.	+	.	.	.	.	.	3
Hypericum perforatum	.	+	+	+	.	.	.	.	.	.	.	3
Helleborus bocconei	.	.	.	.	+	.	.	+	.	.	+	3
Acer campestre	.	.	.	.	.	+	.	.	+		+	3
Geranium robertianum	.	.	.	.	.	+	.	.	+	+	.	3
Urtica dioica	.	.	.	.	.	+	+	.	.	+	.	3
Inula conyza	.	.	.	.	.	+	.	+	.	.	+	3

(continued)

Table 2 (continued)

Relevé number	1	2*	3	4	5	6	7	8	9	10	11	
Altitude (m.a.s.l.)	1000	950	1010	900	950	920	850	780	800	900	880	
Aspect	–	S-E	–	E	E	W	W	W	S-W	N	N	
Slope (°)	–	5	–	10	15	20	20	40	30	5	20	
Cover (%)	90	100	100	90	100	100	100	100	100	100	100	
Relevé area (m^2)	10	20	20	20	100	100	50	100	60	120	100	
Ostrya carpinifolia	.	+	+	.	.	.	.	.	+	.	.	3
Pteridium aquilinum	.	+	.	1.1	.	.	.	.	.	.	.	2
Tamus communis	.	+	.	.	.	.	.	+	.	.	.	2
Malus domestica	.	.	.	.	+	.	.	.	.	.	+	2
Sorbus domestica	.	.	.	.	+	.	.	.	.	.	+	2
Aristolochia rotunda	.	.	.	.	.	+	.	+	.	.	.	2
Daphne laureola	.	.	.	.	.	.	.	+	.	1.1	.	2
Accidental species	.	1	1	1	.	2	.	3	1	1	2	
Number of sp. per relevé	13	23	21	17	20	29	14	19	14	19	29	

*Holotypus

Accidental species—Rel. 1: none; rel. 2: *Juniperus communis*; rel. 3: *Quercus pubescens*; rel. 4: *Galium verum*; rel. 5: none; rel. 6: *Mycelis muralis*, *Hypericum montanum*; rel. 7: none; rel. 8: *Lilium croceum*, *Arum italicum*, *Potentilla micrantha*; rel. 9: *Melittis melissophyllum*; rel. 10: *Brachypodium sylvaticum*; rel. 11: *Hedera helix*, *Acer pseudoplatanus*

Relevé locations—Rel. 1–3: Pie Vettore; rel. 4: Foce di Montemonaco; rel. 5: Nocria (Sibillini Mountains); rel. 6: Copogna, Serravalle del Chienti; rel. 7: Colfiorito; rel. 8: Popola; rel. 9 and 10: Montelago; rel. 11 Gelagna (Central Apennines near Camerino)

Shrubwood of Corylus avellana *(Table 3)*

Above 1000 m, *Corylus avellana* is sometimes present in a *Cytisophyllo sessilifolii-Prunetum spinosae*, and may become very frequent and dominant, and so there is a passage to another vegetation unit, that is to a shrubwood of *Corylus avellana*. Based on the relevé shown in Table 3, this shrubwood cannot be attributed for the moment to any certain association, even though it is similar to the *Symphyto-Coryletum avellanae* (Catorci and Orsomando 2001) for the zone of Nocera Umbra (Umbria-Marche Apennines). One relevé made not at Pie Vettore but at another site in the Sibillini Mountains, above Sarnano (1100 m), corresponds well to this association, because of the presence of *Symphytum bulbosum* and many

Table 3 Shrubwood of *Corylus avellana*

Relevé number	1	2	3	
Altitude (m.a.s.l.)	1050	1050	1100	
Aspect	N-E	N	S-E	
Slope (°)	5	15	25	
Cover (%)	100	100	90	
Number of relevés	2	3	4	
Relevé area (m^{2})	100	70	60	
Corylus avellana	5.5	5.5	4.4	3
Digitalis micrantha	+	+	1.1	3
Lonicera caprifolium	1.1	+	1.1	3
Fragaria vesca	1.1	1.1	+	3
Calamimintha nepeta	1.1	+	+	3
Listera ovata	+	1.1	+	3
Clematis vitalba	+	1.1	+	3
Juniperus communis	+	+	+	3
Acer obtusatum	+	+	+	3
Geranium robertianum	+	+	+	3
Urtica dioica	+	+	+	3
Turritis glabra	+	+	+	3
Neottia nidus-avis	+	+	+	3
Primula veris	+	+	+	3
Mycelis muralis	+	+	+	3
Melica uniflora	+	+	+	3
Chamaecytisus hirsutus	+	+	+	3
Teucrium chamaedrys	+	+	+	3
Cruciata glabra	+	.	+	2
Poa nemoralis	+	.	+	2
Viola alba denhardtii	+	.	+	2
Crataegus monogyna	+	.	+	2
Sanicula europaea	1.1	1.1	.	2
Cyclamen hederifolium	1.1	+	.	2
Euphorbia dulcis	1.1	+	.	2
Aremonia aremonioides	+	1.1	.	2
Viola riviniana	+	1.1	.	2
Dactylorrhiza maculata	+	+	.	2
Rubus caesius	+	+	.	2
Salix caprea	+	+	.	2
Cephalanthera longifolia	+	+	.	2
Veronica chamedryis	+	+	.	2
Viburnum lantana	+	+	.	2
Tamus communis	+	+	.	2
Crataegus laevigata	+	+	.	2
Prunus avium	+	+	.	2

(continued)

Table 3 (continued)

Relevé number	1	2	3	
Altitude (m.a.s.l.)	1050	1050	1100	
Aspect	N-E	N	S-E	
Slope (°)	5	15	25	
Cover (%)	100	100	90	
Number of relevés	2	3	4	
Relevé area (m^2)	100	70	60	
Cytisophyllum sessilifolium	+	+	.	2
Malus sylvestris	.	+	+	2
Rhamnus alpina	.	+	+	2
Hypericum montanum	.	+	+	2
Ostrya carpinifolia	.	+	+	2
Acer pseudoplatanus	.	+	+	2
Carex flacca	.	+	+	2
Rosa canina	.	+	+	2
Gallium mollugo	.	+	+	2
Quercus pubescens	.	+	+	2
Sorbus aria	.	+	+	2
Accidental species	12	13	4	
Number of species per relevé	49	56	36	

Accidental species—Rel. 1: *Primula acaulis*, *Euonymus europaeus*, *Cornus sanguinea*, *Prunus spinosa*, *Asperula taurina*, *Cephalanthera pallens*, *Thalictrum aquilegiifolium*, *Silene nutans*, *Acer campestre*, *Orchis purpurea*, *Rhamnus cathartica*, *Astragalus glycyphyllos*; rel. 2: *Brachypodium sylvaticum*, *Corallorhiza trifida*, *Euonymus latifolius*, *Lathyrus venetus*, *Solidago virgaurea*, *Polystichun aculeatum*, *Hepatica nobilis*, *Geranium purpureum*, *Campanula trachelium*, *Lilium croceum*, *Euphorbia amygdaloides*, *Festuca heterophylla*, *Epipactis latifolia*; rel. 3: *Quercus cerris*, *Juniperus deltoides*, *Inula conyza*, *Bunium bulbocastanum*
Relevé locations: 1–3 at Pie’ Vettore (Sibillini Mountains)

species of the *Fagetalia* order. On the other hand, in the other relevés of Table 3, many species are missing that appear in the relevés of Catorci and Orsomando (2001), such as *Poa nemoralis*. It’s possible to hypotize that similar plant communities follow each other altitudinally, one in the montane *Fagus* (beech) belt and another in the hilly belt of *Ostrya* (hop hornbeam), but this hypothesis needs further confirmation. At Pie’ Vettore, the *Corylus avellana* shrubwood is followed by the *Melico uniflorae-Populetum tremulae*, which sometimes forms thickets or pre-forest and preludes the formation of beech forest (Pedrotti 1995).

Concluding Considerations

The vegetation studied seems to be very similar to that in Marocche di Dro (debris from the Dro) in the Valle del Sarca, Trentino (northern Italy), which is formed on impressive detritus deposits from landslides; a similar plant phenomenon is observed, albeit with other associations (Pedrotti and Minghetti 1994; Pedrotti et al. 1996). The detritus is colonized by the pioneer association *Stipetum calamagrostis*, which is followed by *Cotino-Amelanchieretum ovalis* scrub, in the *Berberidion* alliance, which is a geographic vicariant of the *Junipero oxycedri-Amelanchieretum, Cytision sessilifolii* alliance, of the central Apennines. The potential vegetation of the detritus of the Marocche di Dro corresponds to the *Fraxino orni-Ostryetum carpinifoliae* on the Pie' Vettore landslide, to the *Scutellario columnae-Ostryetum carpinifoliae* up to about 1000 m, and to the *Lathyro veneti-Fagetum* above that altitude. In any case, classification of the vegetation, its ecological significance, and the dynamic tendencies of the vegetation are analogous in the two locations, even if the associations are different.

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Microtopography-Induced Differentiation of Moss Synusiae in Wet Grasslands Covering a Karst Plain in Central Italy (Pian Grande, Central Apennines)

Michele Aleffi, Franco Pedrotti, and Dan Gafta

Abstract This study examines the relationships between the occurrence of epigeic moss assemblages in different grasslands and the microhabitats (pits, dolines, brooks and mounds) occurring in a karst, almost flat basin. The bryophytes tend to form specific synusiae in grassland communities that cover particular microhabitats differentiated on the basis of microtopography. Except for pits and mounds, all other microhabitats are clearly distinguishable in terms of bryophyte composition. The most discriminant species between the moss synusiae of dolines, brooks and pits are *Drepanocladus aduncus*, *Fontinalis antipyretica* and *Polytrichum commune*, respectively. The mounds have no differential species and are poorly distinguished from pits based only on the low cover of *Polytrichum commune*. A combined soil acidity-moisture gradient determined by both land microtopography and surface water runoff is responsible for the good compositional distinctiveness of dolines and brooks from pits and mounds. A relatively broad section of this gradient is occupied by the niche of *Calliergonella cuspidata*, which could be the indicator of a different synusia occurring in microhabitats with ecological conditions intermediate between dolines and brooks. A weaker gradient of soil organic matter content accounts for the distinction of pits from dolines and brooks in the species multidimensional space. Overall, there is a good agreement between the structure of epigeic bryophyte assemblages and the corresponding type of vascular plant communities developed in the same karst habitat, which supports the hypothesis of their dependence and the methodological approach of integrated relevés in phytocoenosis sampling.

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Introduction

Bryophyte assemblages differ in their degree of dependence on the surrounding communities of vascular plants, according to the type of substrate. For instance, epilithic bryophytes have been acknowledged to form distinct, independent communities. On the contrary, epigeic bryophytes intermix frequently with vascular plants, and their assemblages are generally considered as dependent structural parts (e.g. synusiae) of a concrete vegetation unit (phytocoenosis). The differentiation of synusiae is based on at least four important features (Barkman 1973): specific microhabitat, characteristic species composition, spatial extent limited to one stratum, and a similar way of exploiting the environment by all component species.

Irrespective of their substrate or degree of dependence, bryophyte assemblages have been subjected to syntaxonomical classification that parallels the phytosociological nomenclature (Dierssen 2001; Marstaller 2006). However, Hübschmann (1986) notes that the syntaxa used to denominate synusiae, for example *Moos-Unionen* (moss unions) or *Moos-Vereine* (moss alliances), do not correspond conceptually to plant associations *sensu* Braun-Blanquet (1964). Although less encountered in the recent literature, the synusial approach to cryptogamic vegetation analysis is far from being obsolete. Fine-scale analysis of bryophyte, lichen and fungus synusiae within vascular plant communities has proven to be useful for inferring patterns in community organisation and species interactions, revealing good ecological indicators, providing science-based conservation measures, and so on (Vellak and Paal 1999; Ódor and Standovár 2002; Lindlar and Frahm 2002; Dierssen and Dierssen 2005; Bao et al. 2009).

The goal of this work is to examine the moss synusiae (*sensu* Barkman 1973) occurring on the soil of a karst plain covered by hygrophilous and meso-hygrophilous grasslands strictly conditioned by the micromorphology and the water content in the substrate. In particular, we sought to answer the following questions: Is there any floristic differentiation of the moss synusiae induced by different karst microhabitats? Which are the most discriminant species between habitats distinguished according to microtopographic features? Which are the main ecological gradients accounting for the floristic differentiation of moss synusiae between different karst landforms?

Study Area

The Pian Grande of Castelluccio of Norcia is a vast basin of karst and structural origin at an altitude of 1270 m in the Sibillini Mountains (central Apennines). It is about 6.5 km long and 3 km wide, and has an overall surface area of about 1300 km^2 (Pedrotti 1982). The highest point of the plain is at 1278 m, and the lowest is at 1268 m, but the wide central part lies between 1270 and 1268 m.

This almost flat area is grooved by a natural ditch that collects surface water and channels it toward a sinkhole. Here and there one finds shallow dolines (50–80 cm) with flat bottoms that are partly impermeable. The soils of Pian Grande are highly hydromorphic, submerged under water for about 7 months a year, and developed on clayey sediments with a variable content of carbonates. These soils are generally rich in *Anmoor*-type humus and feature an A horizon sometimes acidic, sometimes neutral, which merges, at a depth of 20–25 cm, into a strongly mottled Bg (gley) horizon that is highly base-saturated (Cortini Pedrotti et al. 1973).

The flat bottom of Pian Grande is occupied by grassland vegetation that can be grouped into the following alliances: (a) *Caricion gracilis*, which occurs in the impermeable zone of lacustrine clays on the bottom of the dolines, with the associations: *Caricetum gracilis, Caricetum vesicariae* and *Caricetum otrubae* (plus the following associations found later, thus not in Tables 2 and 6: *Caricetum distichae* and *Ranunculo-Caricetum buxbaumii*; cf. Pedrotti 2015); (b) *Nardo-Agrostion*, which develops on the lacustrine clays but outside the dolines, with *Polygono-Nardetum* and *Filipendulo-Nardetum*; and (c) *Cynosurion*, on well-drained soils with the *Cynosuro-Trifolietum repentis* association. For the species composition of these associations, see the tables published in Cortini Pedrotti et al. (1973).

The distribution of the plant associations is strictly linked to the microtopography, as can be seen in Fig. 1. In the flat zone with impermeable bottom, the *Polygono-Nardetum* association is present and is divided into two subassociations, *polygonetosum* and *polytrichetosum.* The two subassociations, in turn, occupy different conditions, the first on sod that is a few centimetres higher than the soil, and the second in microdepressions of the soil (Fig. 2). *Caricetum vesicariae* and a *Caricetum gracilis* variant with *Veronica scutellata* occur on the bottom of the dolines (Fig. 3), and at the external border of the doline they develop in contact with a *Polygono-Nardetum.* On the banks of the natural ditch there is always *Caricetum gracilis*, but with the variant with *Cardamine amara* (Fig. 1).

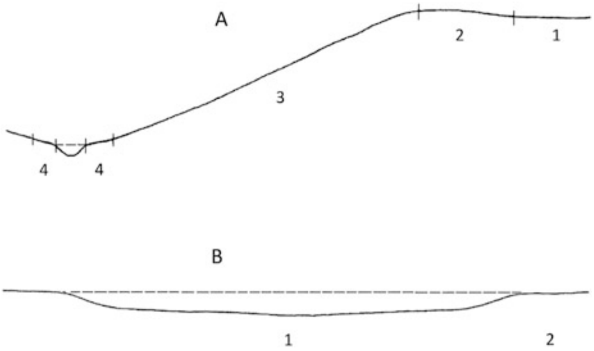


Fig. 1 (**a**) Profile and distribution of the vegetation of Pian Grande: 1—flat bottom with impermeable bottom due to the presence of lacustrine clays, vegetation of *Polygono-Nardetum*; 2—flat bottom subject to drainage with vegetation of *Filipendulo-Nardetum*; 3—slopes subject to drainage of a natural vallecula that cuts through Pian Grande, with vegetation similar to *Filipendulo-Nardetum*; 4—banks of the stream that runs through the bottom of the vallecula, vegetation of *Caricetum gracilis* variant with *Cardamine amara*. (**b**) Profile of a doline and of the flat bottom: 1—doline with *Caricetum vesicariae* and *Caricetum gracilis* variant with *Veronica scutellata*; 2—flat bottom with *Polygono-Nardetum*

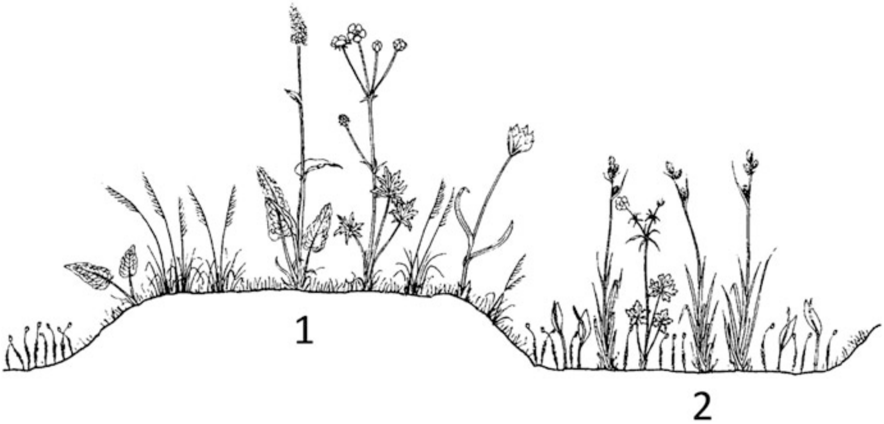


Fig. 2 Profile of *Polygono-Nardetum* (detail); 1—small sods (10–15 cm higher than the bottom) with *Polygono-Nardetum polygonetosum* and its moss synusia of *Aulacomnium palustre*. *Nardus stricta, Polygonum bistorta, Ranunculus acer, Tulipa australis* and *Aulacomnium palustre* can be recognized, represented with brief sections; 2—depressions with *Polygono-Nardetum polytrichetosum* and the moss synusia with *Polytrichum commune, Carex buxbaumii*, *Ranunculus pedrottii*, *Ophioglossum vulgare* and *Polytrichum commune* can be recognized

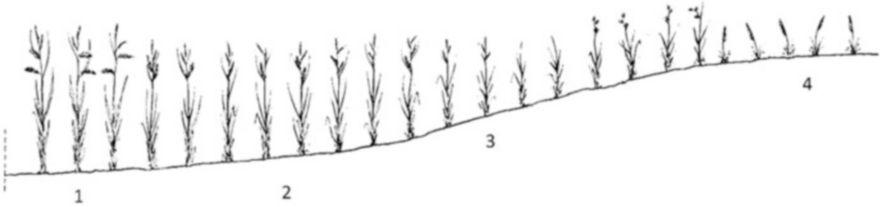


Fig. 3 Profile of a doline; 1—*Caricetum vesicariae*; 2—*Caricetum gracilis* variant with *Veronica scutellata*; 3—ecotone between *Caricetum gracilis* and *Polygono-Nardetum polygonetosum*; 4—*Polygono-Nardetum polygonetosum*

Bryophytes appear sporadically and with very low degree of cover in some plant associations found in Pian Grande, such as *Caricetum vesicariae, Caricetum otrubae,* and *Filipendulo-Nardetum*. Therefore, these were not considered in the present study.

Materials and Methods

Floristic Data Collection

A study of the vegetation of Pian Grande was conducted during June–July 1969 and identified the plant associations mentioned above (Cortini Pedrotti et al. 1973).

During the field work, the bryophytes present were also noted, and all were reported in phytosociological tables.

For the present study on bryophyte synusiae in the grassland associations, the bryophytes of Table 2 (associations of the *Caricion gracilis* alliance) and Table 6 (associations of the *Nardo-Agrostion* alliance) in Cortini Pedrotti et al. (1973) were considered. The relevés were conducted on areas of variable size and form, according to the extension and configuration of the habitats on the terrain. The species cover was estimated visually using Braun-Blanquet's abundance-dominance scale. The moss samples were identified and deposited by C. Cortini Pedrotti in the Bryological Herbarium of the University of Camerino (CAME) (Cortini Pedrotti 2001, 2006).

Data Preparation and Numerical Analyses

Species scores on the Braun-Blanquet scale were converted to percentages by using the mid-values of the cover classes. Species ecological indicator values for soil reaction and moisture in Düll (1992) were used to calculate the species cover-weighted mean at the synusial level for each of the two soil variables.

The compositional distinction between habitats was assessed by a one-way analysis of similarity (ANOSIM, Clarke 1993) based on the Sørensen index. Only (binary) species presence-absence values were employed to calculate within-group and between-group similarities. The closer the R coefficient was to 1, the more floristically dissimilar was the corresponding habitat pair. The one-tailed significance of overall and pair-wise floristic dissimilarity was estimated through 9999 permutations. To prevent the increase in type I error when running these statistical tests repeatedly, sequential Bonferroni corrections of p-values were done manually.

To assess which *taxa* are primarily responsible for differences in moss composition and dominance between habitats, we used the Similarity Percentage method (Clarke 1993) by performing one overall multi-group calculation based on a quantitative measure of floristic dissimilarity, namely the Bray-Curtis dissimilarity index.

The significance of differences in total moss cover between all habitat pairs was assessed through a non-parametric analysis (the Steel-Dwass test) that automatically adjusts the p-values for multiple comparisons.

The main ecological gradients driving the variation in species composition and abundance were inferred through indirect ordination of moss synusiae. For this purpose, we employed a principal coordinates analysis (PCoA) applied on the Bray-Curtis matrix of floristic dissimilarities. These were raised to the power 4 (transformation exponent) before the eigenvalue analysis, in order to increase the variance explained by the first axis and to decrease the "horseshoe" effect (Podani and Miklos 2002).

The monotonic relationship between ecological variables was explored with the aid of Spearman's non-parametric coefficient (rho) and its associated transgression probability. The moss coenocline (synusial cline) along the first PCoA axis was modelled by fitted Gaussian curves of species relative cover. The algorithm was based on weighted averaging according to Braak and van Dam (1989).

All numerical analyses were performed in PAST 2.17c (Hammer et al. 2001), except for the Steel-Dwass test, which was run in JMP 10.0 (SAS Institute 2012).

Results and Discussion

Habitat-Based Distinction of Moss Synusiae

The bryophyte species form evident synusiae in some herbaceous, marshy or hygrophilous communities that cover particular habitats differentiated on the basis of microtopography (Table 1).

The synusia featuring *Drepanocladus aduncus* (Table 1, relevés 1–26) develops on dolines covered by *Caricetum gracilis* var. with *Veronica scutellata*. The dominant species forms mostly monospecific carpets, more or less dense, with prostate or sub-erect stems.

The synusia with *Fontinalis antipyretica* (Table 1, relevés 27–30) occurs along the natural ditch with slightly flowing water. The phanerogam vegetation is formed by *Caricetum gracilis* var. with *Cardamine amara*. At Pian Grande, *F. antipyretica* grows entirely underwater in thick monospecific tufts, irregularly ramified, that adhere to the rocky substrate of the watercourse.

The synusia of *Polytrichum commune* (Table 1, relevés 11–19) occurs in the micro-depressions of the soil where the phanerogam vegetation is represented by *Polygono-Nardetum polytrichetosum*. The species grows in loose tufts of medium size and has always been reported in association with *Aulacomnium palustre*. This synusia probably corresponds to the one called "*Polytrichum commune* Union" by Hübschmann (1986) and is part of the *Mnio-Climacion* von Krusenstjerna 1945 alliance.

The *Aulacomnium palustre* synusia (Table 1, relevés 20–33), which occurs on sod, is less evident because of the low degree of moss cover; it can be differenced only slightly from the previous synusia only on the basis of species dominance relationships. The phanerogam vegetation is represented by *Polygono-Nardetum polygonetosum*. *Aulacomnium palustre* grows on these small hummocks as more or less dense clumps or tufts with *Polytrichum commune* or *Dicranum bonjeanii*.

Finally, a possible *Calliergonella cuspidata* synusia is not clearly distinguishable, for the moment, because it is not ecologically bound to a particular habitat on Pian Grande. In fact, this species appears both on the dolines and in the ditch (Table 1). However, a homonymous synusia called "*Calliergonetum cuspidati*" or "*Calliergonella cuspidata* Union" (Hübschmann 1986) has been described elsewhere and attributed to the *Mnio-Climacion* von Krusenstjerna 1945 alliance.

Table 1 Species composition of the bryophyte synusiae developed in four different microtopographic habitats distinguished on the karstic tableland (Pian Grande)

Relevé no.	1	2	3	4	5	6	7	8	9	10	11	12	13
Altitude (m a.s.l.)	1268	1272	1272	1268	1268	1270	1272	1273	1270	1271	1271	1268	1269
Vegetation cover (%)	100	100	100	100	100	100	100	100	100	100	100	100	100
Bryophytes cover (%)	1	1	1	5	5	25	25	25	25	25	25	50	50
Relevé area (m^2)	60	50	20	100	100	30	50	40	20	20	8	50	10
Habitat type	d	d	d	d	d	d	d	d	d	d	d	d	d
Vascular plant association	CGv	CGv	CGv	CGv	CGv	CGv	CGv	CGv	CGv	CGv	CGv	CGv	CGv
Drepanocladus aduncus	+.2	+.2	+.2	1.2	1.2	2.1	2.3	2.3	2.3	2.3	2.3	3.4	3.4
Acrocladium cuspidatum	.	.	.	.	.	.	.	.	.	.	.	.	.
Fontinalis antipyretica	.	.	.	.	.	.	.	.	.	.	.	.	.
Polytrichum commune	.	.	.	.	.	.	.	.	.	.	.	.	.
Aulacomnium palustre	.	.	.	.	.	.	.	.	.	.	.	.	.
Dicranum bonjeanii	.	.	.	.	.	.	.	.	.	.	.	.	.
Campylium polygamum	.	.	.	.	.	.	.	.	.	.	+	.	.

Relevé no.	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Altitude (m a.s.l.)	1273	1270	1270	1268	1269	1271	1269	1268	1270	1271	1271	1271	1271	1259
Vegetation cover (%)	100	100	100	100	100	100	100	100	100	100	100	100	100	100
Bryophytes cover (%)	50	50	75	75	75	50	50	25	5	5	25	50	50	50
Relevé area (m^2)	10	50	4	10	20	50	10	60	50	50	50	8	8	30
Habitat type	d	d	d	d	d	d	d	d	d	d	d	d	d	b
Vascular plant association	CGv	CGv	CGv	CGv	CGv	CGv	CGv	CGv	CGv	CGv	CGv	CGv	CGv	CGc
Drepanocladus aduncus	3.4	3.4	4.4	4.4	4.4	3.4	3.4	2.3	1.2	1.2	1.2	1.2	1.2	.
Acrocladium cuspidatum	.	.	.	.	+.2	+.2	.	.	.	1.2	1.3	2.3	2.3	2.3
Fontinalis antipyretica	.	.	.	.	.	.	.	.	.	.	.	.	.	1.2
Polytrichum commune	.	.	.	.	.	.	+.2	+.2	+.2	+.2	.	.	.	.
Aulacomnium palustre	.	.	.	.	.	.	+	+.2	+.2	.	.	.	.	.
Dicranum bonjeanii	.	.	.	.	.	.	.	.	.	+.2	.	.	.	.
Campylium polygamum	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Table 1 (continued)

Relevé no.	1A	2A	3A	4A	5A	6A	7A	8A	9A
Altitude (m a.s.l.)	1272	1273	1272	1273	1273	1272	1273	1272	1273
Vegetation cover (%)	100	100	100	100	100	100	100	100	100
Bryophytes cover (%)	25	25	25	50	50	100	75	75	75
Relevé area (m^2)	100	20	50	20	20	20	50	20	60
Habitat type	p	p	p	p	p	p	p	p	p
Vascular plant association	Npt	Npt	Npt	Npt	Npt	Npt	Npt	Npt	Npt
Drepanocladus aduncus	.	.	.	.	.	.	.	.	.
Acrocladium cuspidatum	.	.	.	.	.	.	.	.	.
Fontinalis antipyretica	.	.	.	.	.	.	.	.	.
Polytrichum commune	2.3	2.3	2.3	2.3	2.3	2.3	3.4	3.5	3.3
Aulacomnium palustre	+.2	+.2	+.2	1.2	1.2	3.4	1.2	1.2	1.2
Dicranum bonjeanii	.	.	.	.	.	.	.	.	+.2
Campylium polygamum	.	.	.	.	.	.	.	.	.

Relevé no.	10A	11A	12A	13A	14A	15A	16A	17A	18A	19A	20A	21A	22A	23A
Altitude (m a.s.l.)	1272	1271	1271	1272	1271	1272	1272	1271	1273	1271	1272	1270	1271	1270
Vegetation cover (%)	100	100	100	100	100	100	100	100	100	100	100	100	100	100
Bryophytes cover (%)	5	5	5	5	5	5	5	5	1	1	1	1	1	1
Relevé area (m^2)	100	50	50	100	100	100	50	100	50	40	100	50	50	50
Habitat type	m	m	m	m	m	m	m	m	m	m	m	m	m	m
Vascular plant association	Npg	Npg	Npg	Npg	Npg	Npg	Npg	Npg	Npg	Npg	Npg	Npg	Npg	Npg
Drepanocladus aduncus	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Acrocladium cuspidatum	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Fontinalis antipyretica	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Polytrichum commune	+.2	+.2	+	+	.	.	.	.	+.2	+	+	.	.	.
Aulacomnium palustre	1.2	1.2	1.2	1.2	1.2	1.2	1.2	1.2	+.2	+.2	+.2	+.2	+.2	+.2
Dicranum bonjeanii	.	.	.	+.2	+.2	+.2	+.2	.	.	.	.	.	.	.
Campylium polygamum	.	.	.	.	.	.	.	.	.	.	.	.	.	.

The relevés were drawn from the tables 2 (relevés 1-27) and 6 (relevés 1A-23A) in Cortini Pedrotti et al. (1973)

Abbreviations: b = brook, d = doline, p = pit, m = mound, CGv = *Caricetum gracilis* var. with *Veronica scutellata*, CGc = *Caricetum gracilis* var. with *Cardamine amara*

Npt = *Polygono-Nardetum polytrichetosum*, Npg = *Polygono-Nardetum polygonetosum*

Floristic and Ecological Differentiation of Moss Synusiae

The pits (Schlenken) and mounds (Bulten) are not significantly different in terms of bryophyte composition (Table 2). Conversely, all other habitats are clearly distinguishable as revealed by the high R-values and low p-values (Table 2).

The species that discriminate best among the moss synusiae are *Drepanocladus aduncus* for doline habitats, *Fontinalis antipyretica* for streams, and *Polytrichum commune* for pit habitats (Table 3). The hummock habitat has no differential species and is poorly distinguished from the pit habitat based only on the low cover of *Polytrichum commune*, that is, through higher species equitability (Table 3). Actually, the mound habitat has less favourable ecological conditions for the growth of mosses, as seen in the fact that their total cover is significantly lower on mounds than in all other habitats (Fig. 4).

Along the first PCoA axis (Fig. 5), dolines and brooks are well separated from pits and mounds, lying at opposite ends of the axis. This separation is determined by a combined soil acidity-moisture gradient that is determined by both microtopography and surface water runoff. The dolines and brooks are deeper, more basic and are permanently wet due to flowing water, whereas the smaller pits (and especially mounds) are more acidic and become drier in summer, due to lack of water input other than precipitation. This inference is supported by the strong, significant negative relationships between the scores of the first ordination axis and the weighted means of indicator values for soil reaction and moisture at synusia level (Spearman's coefficients equal to −0.815 and −0.805 respectively, both with $p < 0.0001$). A similar response of bryophytes to soil base richness and maximum water level was observed in *Sphagnum*-dominated mires (Hájková and Hájek 2004).

The second PCoA axis is positively correlated with total moss cover (Spearman's coefficient: +0.663, $p < 0.0001$), which is probably a consequence of higher accumulation rates of partly decomposed organic matter on concave landforms. Even the latter are partly separated along the second ordination axis, i.e. pits (to the upper end) *versus* dolines and brooks (Fig. 5). This distinction is very likely due to the surface water flowing through sinkholes and ditches that leaches away a part of the underlying litter and humus. Therefore, the second ordination axis may represent a positive gradient of organic matter content or thickness of the (near-surface) *Anmoor* layer.

Table 2 Output of the ANOSIM showing the pairwise R statistics (upper right semi-matrix) and the associated, adjusted probabilities (lower left semi-matrix)

Habitat	Brook	Doline bottom	Pit	Mound
Brook		0.982	1.000	1.000
Doline bottom	0.0002		0.876	0.917
Pit	0.0012	0.0001		0.042
Mound	0.0005	0.0001	0.2041	

The overall test is also significant ($R = 0.792$, $p = 0.0001$)

Table 3 Relative and cumulative contributions of species to the observed difference between the four microtopographic habitats based on taxon-specific dissimilarities

Moss species	Average dissimilarity	Relative contribution (%)	Cumulative contribution (%)	Mean relative cover (%)			
				Brook	Doline bottom	Pit	Mound
Drepanocladus aduncus	40.59	41.72	41.72	0	**20.80**	0	0
Polytrichum commune	26.25	26.98	68.70	0	0.08	**22.50**	0.25
Aulacomnium palustre	11.68	12.01	80.71	0	0.06	6.00	1.93
Fontinalis antipyretica	10.82	11.12	91.83	**17.60**	0	0	0
Calliergonella cuspidata	7.23	7.44	99.27	3.75	1.42	0	0
Dicranum bonjeanii	0.65	0.67	99.94	0	0.02	0.06	0.14
Campylium polygamum	0.06	0.06	100.00	0	0.02	0	0

The bold values correspond to the highest within-habitat mean cover values of the best discriminant species

Fig. 4 Distribution of the sum of moss species relative cover in the four habitat types. Different letters indicate significant differences in location (**p < 0.001; *p = 0.01–0.001)

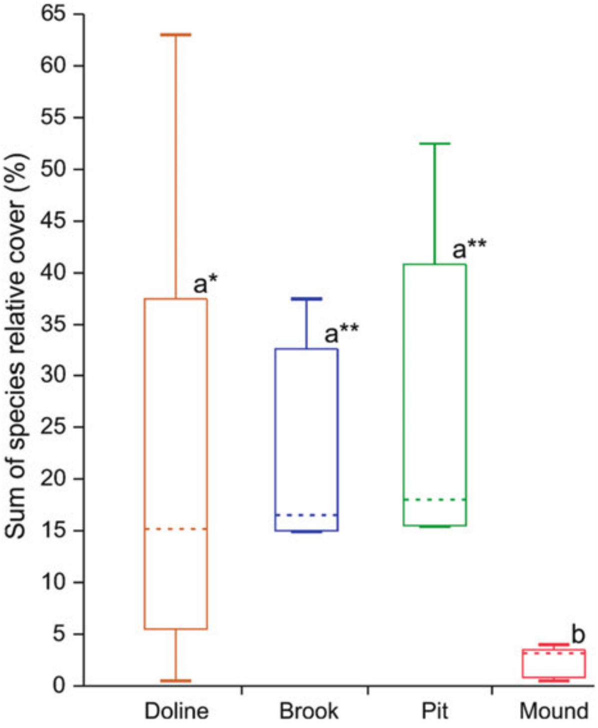
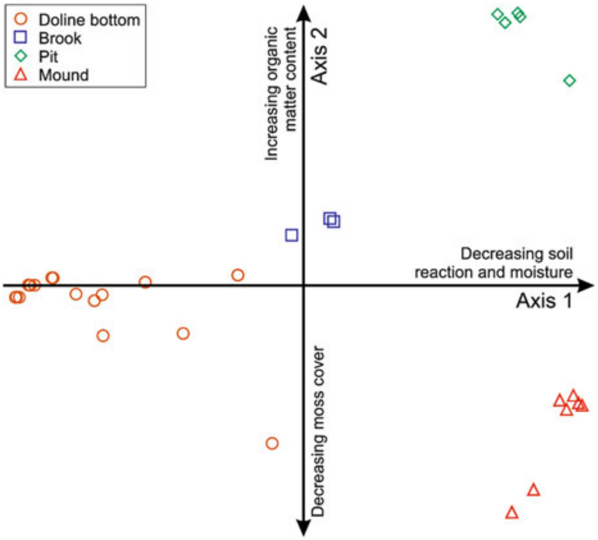


Fig. 5 Ordination of the moss synusiae sampled in different microtopographic habitats. The first two PCoA axes account for 36.4 % and 14.8 % respectively of the total variation in species composition and relative cover



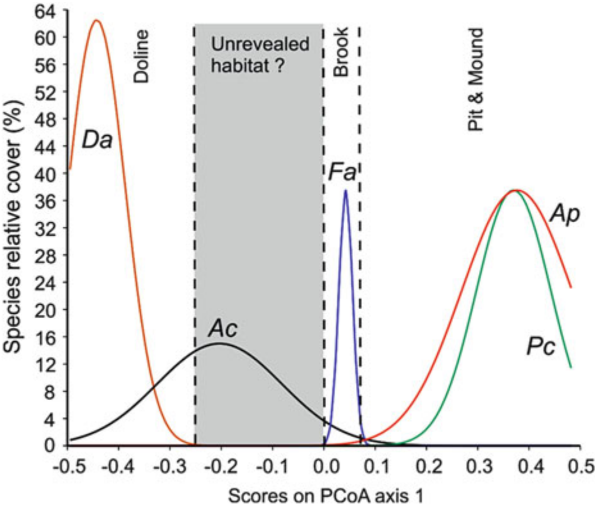


Fig. 6 Moss coenocline (synusial cline) based on the response curves of species relative cover along the PCoA axis 1 (the two least abundant species are not shown). The *dashed lines* indicate approximately the limits between synusiae. *Da - Drepanocladus aduncus*, *Ac - Calliergonella cuspidata*, *Fa - Fontinalis antipyretica*, *Pc - Polytrichum commune*, *Ap - Aulacomnium palustre*

Fontinalis antipyretica has the narrowest niche breadth and lies in the middle of the soil reaction-moisture gradient (Fig. 6). A relatively broad section of this gradient is occupied by the niche of *Calliergonella cuspidata*, which can become the dominant or the only moss species. Such synusiae could be indicators of a different, unrevealed habitat with ecological conditions intermediate between typical dolines and streams. The habitat that could theoretically host a *Calliergonella cuspidata* synusia is indicated as a gray area in Fig. 6; in Table 1, the relevés 23–27 could belong to a synusia dominated by *Calliergonella cuspidata*. In central Italy *Calliergonella cuspidata* is a species reported in moist environments with peat, as found in another karst plain of the central Apennines, the Piano di Montelago (Pedrotti et al. 2004; Aleffi et al. 2008). At this location the moss synusia is also composed of some turficolous species such as *Palustriella falcata* and *Warnstorfia exannulata*. The limited differentiation of this synusia at Pian Grande is probably due to the absence of peat.

Finally, the synusiae of pits and mounds are practically indistinguishable along the combined soil reaction-moisture gradient (Fig. 6). This pattern is consistent with the output of the analysis of similarities performed on presence-absence data only (Table 2). However, the two synusiae are well separated along the second ordination axis, due to obvious differences in the cover of *Polytrichum commune*. This species has found more favourable conditions in pits, which are very likely to be richer in organic matter (*Anmoor*) than are the mounds. An analogous but opposite dependence of bryophytes on nanotopography was observed in *Hylocomium splendens*, which appeared more abundant on small hummocks than in concavities in the understorey of a boreal spruce forest (Vellak et al. 2003).

Overall, there is a good agreement between the structure of epigeic bryophyte assemblages and the corresponding type of vascular plant communities developed in the same karst habitat. This supports our approach, according to which the moss assemblages inventoried are synusiae of the wet grasslands and not independent communities. However, such dependence does not imply a constant occurrence of moss synusiae in these grasslands, as bryophytes may be completely absent even from favourable habitats such as dolines. Moreover, divergent ecological responses between ground bryophytes and herbaceous plants have often been reported in various vegetation types, such as grasslands (Herben 1987), mires (Hájková and Hájek 2004) and forest understoreys (Vellak et al. 2003).

Conclusions

The microtopography of the karst plain induces differentiation in upper-soil moisture, acidity and humus accumulation, which is followed closely by a conspicuous species turnover or, at least, a change in species dominance among the moss synusiae. Their distribution suggests a high degree of specialisation to karst habitats from concave landforms. The moss synusiae in karst-plain grasslands are generally species-poor, and their cover seems to be controlled by variation in both soil moisture and thickness of the upper organic layer. *Polytrichum commune* is a key differential species for the distinction of both moss synusiae and subassociations of *Polygono-Nardetum* grasslands that occur in pits and on mounds.

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At What Scales and in What Vegetation Types Should We Sample Non-vascular Plants?

Gillian L. Rapson

Dedicated to Kazue Fujiwara, a modern representative of that increasingly diminutive taxon, the scholar and gentlewoman.

Abstract Scientists usually avoid sampling non-vascular plants (particularly bryophytes and lichens) for a variety of reasons. However, non-vascular plants often respond differently to the environment than do vascular plants for a range of vegetation types. There is increasing evidence that including them in a sampling programme conveys additional information about the study sites. Such sampling can be important at all scales and in any vegetation type, depending on the subtlety of information sought. Situations which appear likely to benefit from sampling of non-vascular plants are those involving some or all of the following: (1) high-stress environments, (2) relatively long environmental gradients, (3) suspected occurrence of subtle niche-based differences, and (4) need for sensitivity to environmental changes at micro-spatial or temporal scales. Knowledge and use of non-vascular plants in vegetation science will become increasingly important as anthropogenic impacts such as climate change intensify.

Introduction

Plants are surveyed at different descriptive and spatial scales depending on the purpose of the research. For example, the growth- or life-form scale is appropriate when considering biomes, and the scale of vegetation types when surveying continental-level variation, the macro-environment or geological differences. More taxonomic resolution is needed when looking at finer-scale effects, such as variation due to the local terrestrial environment. However, most such sampling

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includes only vascular (or higher) plants at the species' level, because these are relatively easy to identify (technically, to determine). They can usually be identified by eye simply from visible morphological features, and often just from vegetative material. By contrast, identification of non-vascular (lower) plants often requires input from experts or professionals who specialise in just some of the plant groups involved. Consequently these groups are often omitted by non-specialists.

Difficulties in Sampling Non-vascular Plants

The non-vascular plant groups of most significance are the lichens and bryophytes, macro-algae not being found in most terrestrial systems, while unicellular or microscopic algae are routinely excluded by all. None of the above groups are easy to identify, even when adequate keys are available, and many, if not most, require microscopes as minimal identification tools (Fig. 1). Lichens are really communities of two or more species, a mycobiont and a photobiont sharing a common thallus, but they are named as units according to the binomial nomenclatural system (see Knight 2014, for an example). Many lichens require chemical tests to clarify the alga and fungus involved (Knight 2014). Bryophytes, subdivided into mosses, liverworts and hornworts (Fig. 1), may require dissection of gametophytes or sporophytes, and detailed study of anatomical structure (e.g., Beever et al. 1992; Malcolm and Malcolm 2006; Knight 2014). Such work is often time-limited; e.g. the study of oil bodies in leafy and thalloid liverworts has to be completed while material is very fresh (Rodney Lewington, pers. comm.). Non-vascular plants can also be too small to be included feasibly in most terrestrial sampling systems. For example, epiphyllous bryophytes, many of which are members of the liverwort family Lejeuneaceae (Zartman 2003), are often host-specific and much less than 1 cm tall. These are routinely omitted, even in studies of bryophytes, being the domain of a specialist group of bryologists.

In addition to the taxonomic and size-related problems above, there is also the issue of the relative diversity of non-vascular plants, which can greatly increase the workload. Diversity is high at national scale. For example, New Zealand has 1163 bryophytes and probably 2000 or more lichens, against a vascular flora of 2360 native vascular plants, and 2500 naturalised exotic vascular plants (Fife et al. 2010; Knight 2014; see http://www.nzpcn.org.nz). Similarly, the bryophytes of Estonia number 550 and lichens 800, while there are around 1400 vascular plants (http://www.estonianwildlifetours.com/about-estonia). Grau et al. (2007) recorded 480 mosses and 368 liverworts for their Nepalese altitudinal gradient, and found very similar maximum numbers (about 230) for mosses and higher plants in the optimal altitudinal range, though numbers of ferns (not considered here) and liverworts were 85 % and 75 % of those respectively. Even at the scale of individual sites, the diversity of non-vascular plants can be enormous. Cornelissen and Gradstein (1990)

Fig. 1 Non-vascular plants of New Zealand: (**a**) Moss *Cyathophorum bulbosum* with capsules and calyptra, inverted; Det: Patrick Brownsey; (**b**) Lichen *Parmotrema perlatum* in a matrix of *Xanthoria parietina*, with, above, fruticose *Ramalina* sp. (*left*) and foliose *Flavoparmelia* sp. (*left* and *right*), all epiphytic on a street tree, *Betula pendula*; Dets: Allison Knight; (**c**) The world's tallest moss, *Dawsonia superba*, to 50 cm tall; (**d**) Hornwort *Anthoceros* sp., with horn-like sporophyte

recorded 52 mosses, 82 liverworts (30 % Lejeuneaceae), and 36 macrolichens on 16 trees in tropical lowland rainforest of Guyana. Steel et al. (2004) found an average of 10.2 bryophytes in 10 × 10 cm quadrats across a range of vegetation types in New Zealand. Species lists for non-vascular plants ranged from 7 to 29 for 10 m^2 in a range of forest types in the Canadian Rocky Mountains (Lee and La Roi 1979), and 0 to 64 for 4 m^2 for alvar grassland on Öland, Sweden (Löbel et al. 2006). And the work in obtaining such complete lists cannot be underestimated, so that bryologists are notoriously slow-moving. For example, bryologists once got engrossed in a roadside ditch on Great Barrier Island, New Zealand, for half an hour, ignoring Warren's Waterfall Track through kauri (*Agathis australis*) forest. Another group took 3 happy hours to walk halfway round a 10-minute-track in coastal hardwood forest at Ratapihipihi Reserve, New Plymouth, New Zealand, despite the inducement of coffee and cake ahead. Hutsemekers et al. (2008) reported that surveying even one Belgian slag heap (averaging about 0.1 ha) for non-vascular plants took a whole day for a team of 2-4 bryologists. Even more detailed work is horrendously more time-consuming. Steel et al. (2004) found a maximum of 18.3 species of bryophytes per 10 × 10 cm quadrat in a wet southern beech forest and commented that it took up to 3 days to sort a single quadrat by species for biomassing. And none of these include lab time actually identifying and cataloguing the finds. Further, surveys for non-vascular plants are very sensitive to sampling intensity and method (McCune and Lesica 1992), so obtaining reliable information is very problematic.

Thus it is very time-consuming for ordinary terrestrial plant ecologists to develop the skills to identify (or even to adequately sample and collect) specimens of non-vascular plants, in addition to doing their standard sampling of vascular plants. Consequently, the decision is often made not to sample them. But this decision is difficult to justify. Here I examine the available evidence on the relative relationships of non-vascular and vascular plants, and the contribution non-vascular plants make to structuring communities, and then evaluate the need to sample them.

Are Vascular Plants Surrogates for Non-vascular Plants?

If vascular plants are good, or even reasonable, surrogates (term of Pharo et al. 2000) for non-vascular plants, then there might be a strong case for sampling just the former. But there are reasons for thinking surrogacy could be at least partially ineffective.

Bryophyte-environment relations
Intuitively, bryophytes should respond differently to environmental parameters than do vascular species, due to their crucial morphological differences, such as absence of vasculature, roots and water-retaining cuticles, and due to their being evergreen and dispersing by spores. While there are few head-to-head comparisons of the respective ecologies of vascular and non-vascular plants, many researchers have reported close environmental relations for bryophytes. For example, Werth et al. (2005) related macrolichen diversity to a range of human impacts and climatic factors. Bradfield and Scagel (1984), Bruun et al. (2006) and Grau et al. (2007) recorded bryophytic species' patterns with altitude (see Table 1). Bradfield and Scagel (1984) also noted relations with moisture regimes, as did Lee and La Roi (1979) and Kantvilas and Minchin (1989). Sun et al. (2013) noted bryophyte distributions in Gongga Mountain, China, related to depth of litter, air temperature and precipitation. Bryophyte diversity in spring water is related to conductivity (Spitale et al. 2009; Sekulová et al. 2012) or to pH (Zamfir et al. 1999). Löbel et al. (2006) noted different habitat requirements in relation to soil and microtopographical characters. However, these relationships are not often linear. For example, Pharo et al. (1999) noted that correlations varied depending on the forest type, with patterns being strongest in wet sclerophyll forests.

While examination of the literature suggests these responses can differ from those of vascular plants, such evidence is inferential at best. Identification of such patterns requires appropriate databases, where both vascular and non-vascular species have been sampled, fully or representatively, in the same habitats. Unfortunately such databases are uncommon, and in need of development.

Table 1 Relationships between vascular and non-vascular plants and type of vegetation sampled. An asterisk (*) in the first column denotes a direct test of the effect of including bryophytes in a sample scheme. Symbols +, ± or − in brackets in the last column summarise the extent of the contribution of bryophytes as positive, mixed or negative respectively

Vegetation type, study location and source reference	Sampling method and analytical approach	Plant taxa sampled	Comparison of contribution of the different taxa
Forest			
**Abies grandis* forest layers, Swan Valley, Montana (McCune and Antos 1981).	42 stands of 375 m^2, each containing 100 plots of 300 cm^2 for bryoids. Bray-Curtis dissimilarities compared using various correlations; agglomerative cluster dendrograms.	Bryophytes and non-crustose lichens; vascular plants.	Weak (<0.3) though significant correlations (+). Little overlap of dendrograms. (−)
Subalpine spruce-fir forest strata, British Columbia, Canada (Bradfield and Scagel 1984).	110 plots of 400 m^2. Pearson's correlations between PCAs of each stratum.	122 bryophytes; 15-177 vascular plants per stratum.	First axes of PCAs weakly correlated (+). Environmental relations similar for both taxa (+).
Pinus sylvestris forest understorey, eastern Pyrenees Range, Spain (Pausas 1994).	57 plots of 314 m^2. GLM on species richness.	13 epigeic mosses; 53 vascular plants.	Environmental models fit woody and herbaceous vascular plants and mosses differently. (−)
*Dry eastern forest, near Newcastle, New South Wales, Australia (Pharo et al. 1999, 2000).	35 plots of 20 × 50 m for vascular species, with 5 small quadrats each of 20 × 20 cm for non-vascular species. Correlations of similarity matrices and minimum reserve set analysis.	78 bryophytes; 69 lichens; 472-477 vascular plants.	Bryophytes correlated with richness of overstorey and of ferns. (+) Spp. turnover through space similar for bryophytes and vascular spp. (+) A random subset of 20 sites can capture 90 % of vascular plants, 65 % of moss and 87 % of lichens. (±)
*Mountain forests > 60 years old, Bavarian Alps, Germany (Ewald 2009).	93 plots of 144 m^2. Linear regression of bryophytes against residuals of vascular relationship.	103 bryophytes; 316 vascular spp.	The two groups differed in their relationships to Ellenberg values. (−) Combining both groups increased fit only slightly. (−)

(continued)

Table 1 (continued)

Vegetation type, study location and source reference	Sampling method and analytical approach	Plant taxa sampled	Comparison of contribution of the different taxa
Altitudinal gradient			
Montane forests to alpine heath-tundra stands, Jasper National Park, Canadian Rockies (Lee and La Roi 1979).	30 stands of 500 m^2 plots, each containing 50 0.2 m^2 bryophyte plots on either rock or detritus. Beta diversity correlations.	7-29 bryophytes and 5-34 vascular plants per stand.	Bryophyte and vascular floras similar for non-xerophytic communities along moisture gradients. (+) Floras dissimilar for altitude. (−)
Lowland to cloud forest, to subalpine scrub, to open mossfields, Nepal (Grau et al. 2007).	Vascular spp. excluding ferns. Correlations of species richness.	480 mosses; 368 liverworts; vascular plants.	Vascular spp. peak at 1500–2500 m in altitude, ferns at 1900 m, mosses at 2500 m and liverworts at 2800 m. (−) Vascular spp. have a wider altitudinal range. (−) High correlation between moss and liverwort richness. (−)
Latitudinal gradient			
Spruce forest of north-eastern American seabord (Nekola and White 1999).	60 plots of 300 × 300 m. Distance decay rates of pairwise comparisons of compositional similarity. PCA axis eigenvalues.	118 or 79 bryophytes and 252 or 195 vascular spp. in white or black spruce forest.	Vascular plants have 1.5-1.9 times higher rates of distance decay than bryophytes (±), though wind-dispersers are similar.
Natural grasslands of *Chionochloa* and *Festuca*, southern New Zealand (Wilson and Meurk 2011).	226 sites with plots of 1000 m^2. Abundance by 100 height frequency samples per plot. Relations with variables by regression and Mantel tests.	262 vascular, bryophytic and lichen species.	Spp. abundance more informative for non-vascular spp. than presence, opposite to vascular spp. (−) Abundance of non-vascular spp. more related to latitude than vascular spp. (−), and less related to environment (−).
Grassland			
*Grassland communities, Czechoslovakia (Herben 1987)	Subsets of relevés comparing vascular plants with randomly selected communities of vascular and non-vascular plants, but with the same total biodiversity. PCA axis eigenvalues.	17-49 bryophytes and lichens; 88-179 vascular plants.	Replacing vascular plants with bryophytes increases a community's variance. (−)

Calcareous wooded meadow, regularly mown, Laelatu, Estonia (Ingerpuu et al. 1998).	2 fertilised and 2 control plots of 10 m × 30 m, containing 31 × 1 m bryophyte plots and 20 plots of 20 × 7.5 cm for vascular plants.	21 bryophytes; 94 vascular spp.	Both taxa have similar relations to their species' pool. (+) Fertilisation decreases vascular diversity, and increases bryophytic diversity. (−)
Dry grassland, Öland, Sweden (Löbel et al. 2006).	452 plots of 2 × 2 m. GLM with environmental conditions. GLM on richness and biomass. Ordination with splines.	153 bryophytes and 84 non-epilithic crustose lichens; 300 vascular spp.	Larger patches enhanced non-vascular plant richness only. (−) Vascular plant richness is negatively related to non-vascular plant richness. (−)
Grazed grassland, Hirta, St Kilda, Scotland (Virtanen and Crawley 2010).	90 plots of 20 × 20 cm.	Bryophytes; vascular spp.	Bryophyte spp. richness peaks at high elevations; vascular spp. richness declines with altitude. (−)
Species-rich grasslands of *Festuco-Brometea*, Transylannia (Turtureanu et al. 2014).	20 plots at 100 m^2, with 40 nested sub-plots at 6 scales. GLM on richness, with model selection of predictors of species richness using Akaike.	Mean of 83.3 ± 24.2 vascular species in the largest plots, 3.8 ± 2.2 bryophytes and 1.2 ± 2.3 lichens.	Both vascular species and bryophytes were partially modelled by heat load. (±) Both bryophytes and lichens were partially modelled by humus. (±)
Wetland			
Alpine springs, Italy (Spitale et al. 2009).	86 springs, whole area sampled. SEM of direct and indirect effects of environment on species richness.	167 bryophytes; 201 vascular spp.	Similar responses of vascular spp. and bryophytes, (+) sometimes for different reasons. (−)
Subalpine springs, Switzerland, Bulgaria, Slovakia (Sekulová et al. 2012).	177 plots of 4 × 4 m. Correlations with environmental variables, PCoA.	53-101 bryophytes; 137-177 vascular spp.	Bryophytes form more similar assemblages across countries than do vascular spp. (−)
Alpine			
Dwarf shrubland to barren areas, Fennoscandia (Bruun et al. 2006).	874 quadrats of 0.8 m × 0.8 m. GLM with altitude and local topography.	39 bryophytes; 54 macrolichens; 113 trees, dwarf-shrubs, forbs and graminoids.	Vascular spp. richness peaked at 300 m altitude, lichens at 400 m, while mosses and liverworts increased with altitude. (−)

Gradient Tests

Several authors have measured both vascular and non-vascular species along gradients and evaluated the similarity of their responses (Table 1). If vascular plants are adequate surrogates, then they should follow the same trends as non-vascular plants. This was reported by Bradfield and Scagel (1984) using correlations between various strata in spruce-fir forest, and by Pharo et al. (1999) who found positive correlations between the species richness of bryophytes and vascular taxa in dryland forest, and similar turnover for all understorey taxa.

Other authors have recorded opposing patterns for vascular and non-vascular plants (Table 1). Löbel et al. (2006) found a negative relation between richness of vascular spp. and bryophtyes or lichens in a dry Swedish grassland. Bruun et al. (2006) looked at alpine areas in Fennoscandia and found different peaks in species richness along an altitudinal gradient for lichens and vascular species, particularly graminoids, and forbs, while moss or hepatic richness increased with altitude. Similar results were found for Pyranean *Pinus sylvestris* forest (Pausas 1994), Nepalese vegetation (Grau et al. 2007), and subalpine springs in central Europe (Sekulová et al. 2012). Studies of latitudinal gradients have revealed differing patterns for rates of distance decay for vascular and non-vascular spp. (Nekola and White 1999; Wilson and Meurk 2011).

Variable results, in terms of similarity in responses of vascular and non-vascular species, were found by Lee and La Roi (1979) for altitudinal gradients in Rocky Mountain alpine vegetation, while moisture gradients elicited similar responses. Ingerpuu et al. (1998) recorded similar relations to species' pools, but differences in response to fertilisation (Table 1). Virtanen and Crawley (2010) examined trends in sheep-grazed grassland in Scotland, showing that the two groups have the same richness relations (negative) to grazing pressure but different responses to altitudinal gradients (bryophytes being positive). In terms of biomass effects, both groups showed greater richness at medium biomass, but the linear trend was positive for bryophytes and negative for vascular plants (Virtanen and Crawley 2010). Turtureanu et al. (2014) reported some overlap in variables modelling taxon ranges, but many differences. In a study of Italian springs, Spitale et al. (2009) found that both groups increased in richness with altitude, and size of each spring, and decreased with conductivity. However, the cause of the response to altitude was primarily lithology for bryophytes and reduced canopy cover for vascular species. So the same response was obtained for different reasons.

With both positive and negative responses to gradients between non-vascular and vascular plants, and with relations which may be different in different situations or for different reasons, it is clear that the case for surrogacy fails.

Direct Tests

The correlative approaches above give only inferential evidence. A direct approach would check whether the explanatory powers of vegetation analyses are improved by the inclusion of non-vascular plants in sampling, allowing, preferentially, for the effects of differences in species' numbers. McCune and Antos (1981), looking at a spruce forest in Montana, compared dendrograms of different taxa by inspection and found them dissimilar (Table 1). In 1987, Tomáš Herben provided the most scientific comparison of the relative contribution of non-vascular and vascular plants available, using grassland communities of Czechoslovakia. Herben (1987) compared communities in PCA space which were composed only of vascular plants, with randomised constructions containing the same total diversity but with subsets of vascular plants and bryophytes. Inclusion of bryophytes mostly increased the variance in the ordination, demonstrating the response of bryophytes to different environmental conditions, and thus the absence of surrogacy.

Subsequently, Pharo et al. (2000) used pattern analysis, confounded by several species being unique to single sites, to demonstrate that sites reserving 90 % of vascular species also reserved relatively high proportions of bryophytes and lichens (Table 1). Ewald (2009) compared the explanatory power of epigeic bryophytes with vascular understorey plants in the Bavarian Alps using Mantel tests on Ellenberg values. He found that the bryophytes responded differently in terms of environmental scores and were less responsive to scores than were vascular plants, contributing little to the explanatory power of the vascular data.

In a recent highly relevant study, Turtureanu et al. (2014) explored biodiversity patterns in species-rich grasslands in Transylvannia, using species-area relations, and included non-vascular plants as a comparison to the standard vascular species. They found low cryptogamic diversity, but in some plots, very high cover. Bryophytes were similarly affected by heat load as vascular plants, but lichens were not, while humus content affected both lichens and bryophytes, the latter in two different ways in relation to acrocarpy or pleurocarpy as life style. Vascular species and lichens responded to micro-relief, while bryophytes did not. They concluded, forcefully that "none of the groups could reasonably be used as a surrogate for the diversity of any of the others".

In conclusion, these direct tests unfortunately yield very mixed, and unencouraging, results on the issue of potential surrogacy.

Other Indications of Surrogacy

Steel et al. (2004) identified species from a range of un-pairable (i.e., not a direct test) bryophytic and vascular-plant sites from around New Zealand and found bryophytes to show less evenness, due to the smaller size of their photosynthetic units (generally leaves or leaflets); they noted, though, that their overall community organisation was similar. Some non-vascular plants have been examined for within-species' variation, such as commonly occurs with vascular species. For example, Cronberg et al. (1997) detected 79 genotypes amongst 298 shoots of *Hylocomium splendens* (implying potential for small-scale adaptation), but the populations were usually genetically similar, suggesting poor potential for surrogacy at the genetic level. Experimental manipulations of communities comprised of both groups can also demonstrate differences in their response. For example, by fertilising pots in a competition experiment for meadow communities, Ingerpuu et al. (2005) showed bryophytes were facilitated by the vascular plants.

Taxa other than "vascular spp." may have more potential as surrogates for bryophytes. Pharo et al. (1999) notes that species richness of ferns is highly correlated with bryophytes, and thus ferns are potential surrogates. Nekola and White (1999) note similarities between distance decay rates of bryophytes and wind-dispersed vascular plants, i.e., those with spores, plumes or microseeds, a view supported by the work of Wilson and Meurk (2011).

Are Non-vascular Plants Drivers or Passengers in Vegetation?
Drivers are species normally seen as interactive in their community, so they are important structurally, bioenergetically, abundance-wise, or in terms of facilitation or engineering roles (see Hodges and Rapson 2010, for an atypical engineer). Passengers are species whose populations are structured by the environment. Although not customarily applied to higher taxonomic groupings, the terminology can be insightful.

Bryophytes are most easily imagined to be drivers in vegetation in which they form a substantial portion of the "canopy", the heliophilic vegetation which is exposed to direct sunlight. Examples are the lichen-rich tundra of the Scandinavian arctic, or the bryophyte cushions of the exposed Andean scoria fields (Fig. 2), in which these early-successional pioneers form the only temperature-tolerable habitat where nitrogen-fixing shrubs can germinate.

However, there is evidence of bryophytes instead being facilitated by vascular species (Ingerpuu et al. 2005), building a case for bryophytes as passengers. This is especially the case for heliophobic taxa, such as the lower strata within forest communities, where surrogacy is especially weak (Table 1). For example, ferns and bryophytes are probably both passengers in forests (following Nekola and White 1999), positive relations there being determined primarily by moisture (following Lee and La Roi 1979). Consequently, epiphyllous and canopy bryophytes (*sensu* Cornelissen and Gradstein 1990) are obligate passengers. But other common passengers include bryophytes epiphytic on trunks and dead or fallen wood, especially large debris (Ódor and Standovár 2001; Mills and MacDonald 2005; Fig. 2). These passengers may in turn facilitate germination and establishment of vascular plants by providing seed-catching sites, becoming drivers.

In summary, when differences in the ecology of non-vascular and vascular plants have been sought, they have most commonly been found, though sometimes there are similarities, as well as a number of bipartisan results, and also apparently accidental similarities (e.g., Spitale et al. 2009), suggesting that one taxon is not a reliable surrogate for the other.

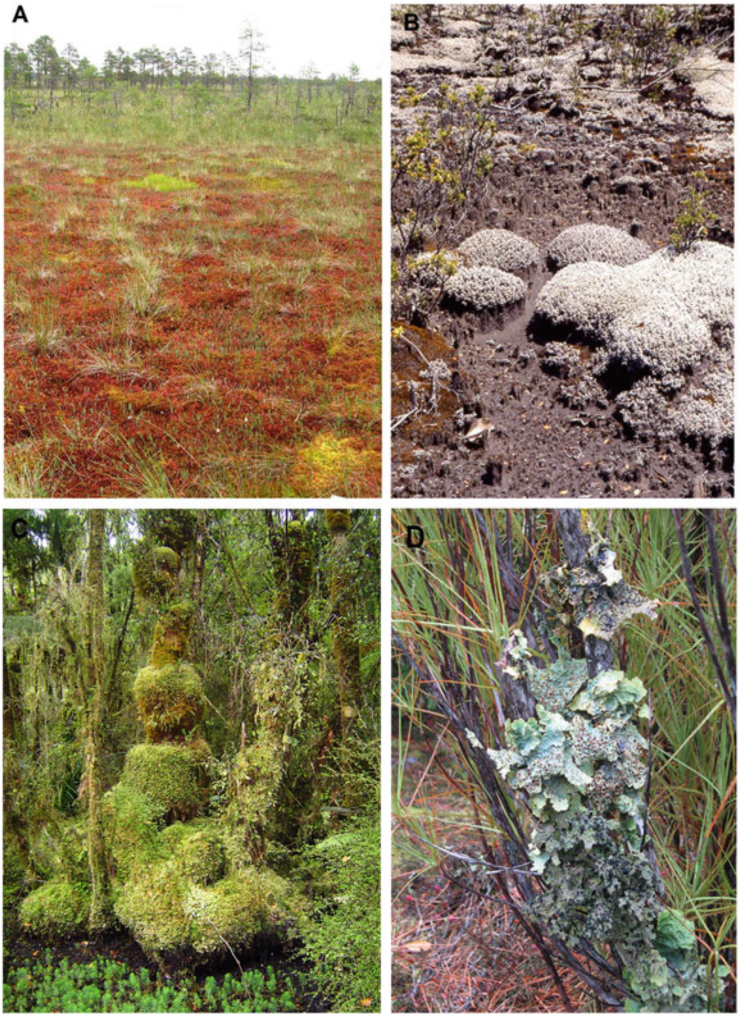

Fig. 2 Important roles and habitats for non-vascular plants: (**a**) *Sphagnum* spp. as ecosystem engineers of Fen-Bog Transitions (*sensu* Hodges and Rapson 2010) in Suursoo mire, Estonia; (**b**) *Racomitrium pruinosum* as facilitator of establishment of vascular plant seedlings on the scoria fields of Volcan Osorno, Parque Nacionale de Vicente Pérez Rosales, Chile; (**c**) Clumps of sponge-like bryophytes on *Leptospermum scoparium* trees at Sponge Swamp, West Coast, New Zealand; (**d**) Epiphytic lichens (*Stereocaulon* spp.) on grass tree of genus *Dracophyllum* above litter on sand dunes of Hellfire Pass, Stewart Island, New Zealand (Murphy et al. 2012)

When Should We Sample Non-vascular Plants?

In what vegetation types and at what scales should we sample non-vascular plants? The situation regarding scale of the study, or of the plot or of the environmental patterning is straight-forward: finer-scale studies can afford to include bryophytes, and may need to do so, since the effects being investigated are probably already subtle. For vegetation types, the answer from Table 1 is that there is direct evidence of bryophytes giving a different view of vegetation in at least some forests, and increasing evidence that the same might apply to grasslands. Indirect evidence, though equally mixed, suggests that responses of non-vascular plants can show extensive differences from those of vascular plants, making a case for sampling both taxa in all vegetation types! However, in many instances, such a goal is simply not practicable, due to the time and effort needed. The choice of sampling all plants or of limiting effort to vascular plants depends upon how much we want to know. Do we need to obtain as much information as possible from our environmental phytometers, or is a rough idea enough? Only the practitioner can decide how subtle the information content of their data has to be, but some guidelines are presented below for circumstances in which adding non-vascular plants to the sampling methodology may be particularly rewarding.

(1) **High-stress environments** may be the standard situation for incorporation of non-vascular plants, especially where many form the "canopy" and so are exposed to direct solar radiation, i.e., are heliophilic. Examples are high-altitude or high-latitude zones (e.g. Molau and Alatalo 1998), where non-vascular plants are seen as integral members of the community, or in very dry areas such as grasslands, deserts or dunes (Murphy et al. 2012), or dry forests which often have open canopies (Pharo et al. 1999, 2000). Here non-vascular plants are more likely to be drivers of vegetation dynamics, due to community-wide low values for biomass and productivity.

(2) **Long environmental gradients** are generally clearly depicted ecologically by vascular floras, and so sampling of non-vascular plants is probably unnecessary (e.g. Lee and La Roi 1979, for altitudinal gradients). However if these gradients extend into the heliophilic zone, as defined above, then non-vascular plants could usefully be included (e.g. Grau et al. 2007; Medina et al. 2013), perhaps recording them only when they form an extensive portion of the "canopy", thus allowing many under-canopy and epiphytic species to be omitted. The results of Wilson and Meurk (2011) make a case for only sampling bryophytes in such a situation, and not bothering with vascular species at all!

(3) Suspected existence of **subtle niche-based differentiation** might also represent a case for the inclusion of non-vascular plants, based on the logic that extra or "vacant" niche space should result in occupation by novel species and some of these could be non-vascular. There is considerable evidence of niche specialisation in non-vascular plants, many being epiphytes (Kantvilas and Minchin 1989; Grau et al. 2007; Medina et al. 2013), some even canopy specialists (Cornelissen and Gradstein 1990), and others inhabiting dead

wood, especially coarse woody debris (Ódor and Standovár 2001; Fig. 2). However, when the habitat of non-vascular plants is as un-subtle as woody debris, it is probably more economic and sensible to measure the debris rather than its occupants (which are probably highly diverse), and instead, to collect and fit niche-space descriptors of the debris etc. as covariates in any analysis of the vascular flora.

(4) When **sensitivity to environmental change**, either spatial or temporal, is desired, then monitoring changes in non-vascular taxa, especially bryophytes, might be the best choice. Bryophytes appear very responsive to environmental changes as their reserves are less, they are more opportunistic, and are regulated by their immediate microclimate (Herben 1987; Lee and La Roi 1979). Additionally, non-vascular species are often well-dispersed (Nekola and White 1999; Hutsemekers et al. 2008; Wilson and Meurk 2011; Sekulová et al. 2012; but see Löbel et al. 2006), accelerating their rate of response. This suggestion is against a background where considerable stability in bryophyte populations has been noted, even over 30 years of monitoring (Ingerpuu et al. 1998). Including non-vascular plants in subtle studies (e.g. Molau and Alatalo 1998) could become increasingly important as monitoring of effects of climate change accelerates, lichens at least, being well-known phytometers of environmental pollution (Hawksworth and Rose 1970). Habitat fragmentation, also an accelerating research field, is another situation in which non-vascular plants might usefully be included; Zartman (2003), studying epiphyllous Lejeuneaceae, noted a link between decline in epiphyll communities and loss of common, but not rare, non-vascular hosts induced by declining fragment size.

Conclusions

Non-vascular plants give extensive evidence of responding differently to environmental gradients or changes than do vascular plants, so logically they should give additional insight into a community's relations and dynamics. Their inclusion may substantially reduce what is currently seen as noise or variability between samples of vascular plants. Following Herben (1987), construction of databases is needed from studies which include full sampling and identification, at least to morphotypes, of both non-vascular and vascular plants. Such databases can be analysed by ordination or via Mantel tests to investigate whether the two groups differ in explanatory power, desirably correcting for differences in β diversity (*sensu* Herben 1987) and applying randomisation testing. However the technical problems of sampling non-vascular plants remain, and sampling will likely be restricted to crucial cases only. Vegetation scientists may need to consider increasing their budgetary requirements for sampling or using metagenomics (common in studies of other groups of small organisms) to better characterise vegetation communities in quest of more subtle understanding.

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Part IV
Conceptual Methodologies

Moving from Patterns to Processes: A Challenge for the Phytosociology of the Twenty-First Century?

Guillaume Decocq

Abstract Phytosociology and ecology are often viewed as two distinct scientific disciplines though both emerged from phytogeography in the second half of the nineteenth century. Here we propose an epistemological essay of the “science of plant communities” in which the reasons behind the divergence between phytosociology and ecology are analyzed. While ecology incorporated the progress made by life chemistry, making ecology more functional than descriptive, syntaxonomy and synsystematics rapidly made phytosociology an esoteric science and contributed to the conflicts among the different European schools. As animal ecology began to develop ecology became “the science of ecosystems”, a field of biology, phytosociology stayed closer to geography. However, with the emergence of the integrated synusial method, phytosociology began to re-connect with ecology, by taking into account functional considerations provided by general system theory, hierarchy theory and landscape ecology. We stress on three challenges that phytosociology should meet to find its niche in plant ecology: being more functional; incorporating recent advances in dispersal vs. niche assembly rules; and withdrawing old-fashioned, static concepts such as the climax. The future of phytosociology includes providing ecology with high-quality field data through its robust methodology, but perhaps with a more process-oriented sampling strategy. In this respect, the integrated synusial approach is inherently better suited to serve ecology by reflecting the complexity of plant communities in both space and time.

Phytosociology as a science deals with plant communities at various spatial and temporal scales. It is based on the postulate that, at a given place and time, vegetation reflects the combined influence of biotic and abiotic environmental factors. Hence, a plant community is considered as a discrete repetitive combination of plant species sharing the same ecological requirements, which occupies an ecologically homogeneous piece of land. Phytosociology became very popular in Europe and in other countries worldwide, such as Japan, but hardly permeated the Anglo-Saxon world, which turned to a closely related science, namely plant

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ecology. While the latter improved continuously its theoretical background, concepts, and tools to meet the emerging challenges of a globally changing world over the twentieth century, phytosociology remained a "conservative" science, devoted to the description and naming of plant communities worldwide, sometimes with never ending debates on syntaxonomy and synsystematics that rendered it esoteric to most scientists. Doing so, phytosociology diverged widely from ecology, so that the gap between the two sciences has never been so large as now. The time has come to bridge this gap: this is the challenge for the twenty-first century. This contribution first summarizes the (hi)story of phytosociology from its roots to the most recent developments, as a first attempt in an epistemology of the "science of plant communities". Next, the reasons behind the divergence between phytosociology and ecology are analyzed. In the last part of this essay, I will discuss some examples that, in my opinion, are among the most important challenges that the phytosociology of the twenty-first century should meet in order to bring it back together with ecology, to become a modern science and to find its niche.

A Brief Story of Phytosociology

Nineteenth Century: Before Phytosociology

Phytosociology is rooted in phytogeography, and as such is often considered as a field of geobotany. Following the great scientific expeditions of the eighteenth century, a wind of change affected botany during the nineteenth century, with the seminal work of Alexander von Humboldt, who may be considered as the founding father of the Plant Geography. In his famous book "*Essai sur la Géographie des plantes*" published in 1805, he was the first to deal with the sociology of plants, the importance of climate and geological history for plant distribution, and the various life forms (*Hauptformen*) patterning the various landscapes (Deléage 1991). Though the Danish botanist Schouw had already proposed, in 1822, to add the suffix -*etum* to the genus name of the dominant plant species that characterize plant communities, phytosociology really emerged at the end of the nineteenth century. Three precursors must be mentioned: the German Grisebach, who introduced the concepts of vegetation formation (*Vegetationsformation*) and plant forms (*Vegetationsformen*) in 1884 and related them to climate; the Dane Warming, who claimed in 1895 that plant communities should be studied at a finer spatial scale than previously done by phytogeographers and interpreted in the light of ecological and social factors; and the Frenchman Flahault, who assessed the relative importance of climatic, edaphic and biotic factors in determining plant communities (1907).

Early Twentieth Century: The Birth of a New Science

Phytosociology emerged simultaneously in several European countries, particularly Poland (the Central-Eastern European School of Paczoski, where the term "phytosociology" was born in 1896); France (the Zürich-Montpelier school of Braun-Blanquet); and Sweden (the Uppsala school of Du Rietz). It was first formalized as a science, though, only in 1922, with the "*Vocabulaire de Sociologie végétale*" (Braun-Blanquet and Pavillard 1922). Phytosociology rapidly became a reference method for the study of plant communities but hardly penetrated the Anglo-Saxon world. Its aim was defined as follows: describing and understanding vegetation, which is the spatial and temporal, qualitative and quantitative organisation of plants on Earth (Braun-Blanquet and Pavillard 1922). From a theoretical point of view, phytosociology postulates that any plant community can be considered as the juxtaposition of "individuals of association" (IA, i.e., the group of such associated species) that are separated by more or less fuzzy discontinuities, from which different "plant associations" may be basically defined. Hence, the concept of "plant association" is at the core of phytosociology and broke historically with the continuum paradigm, which prevailed in the Anglo-Saxon world. The continuum paradigm considers that plant species colonize a given place for individual reasons, which are independent of any social relationships between them, so that species composition varies continuously along environmental gradients and is partly random (Gleason 1926, 1939; Curtis 1959). In other words "*species populations are variously distributed, each according to its own physiology and genetic pattern, so that community types are not organized units of many species, but can be interpreted and defined in terms of population distributions along gradients and understood as part of the complex population pattern of climaxvegetations to which the method of gradient analysis is appropriate*" (Whittaker 1956).

From the very beginning, phytosociology proceeded in three consecutive steps. It starts with an analytical inventory of plant communities, i.e., a semi-quantitative record of the IA called a relevé, which is an exhaustive list of plant species that occur in a given sample area together with species-specific indices of cover-abundance (often using the Braun-Blanquet scale). The sampled area has to be homogeneous floristically, representative of the studied community, and at least equal to the "minimum area" as determined by a species-area curve. Secondly, relevés are sorted according to the species they share, using a variety of similarity metrics implemented by various classification and ordination algorithms (e.g., hierarchical classification, correspondence analysis, TWINSPAN) that have replaced the manual "tablework" after the emergence of micro-informatics. The emergent groups of relevés, called syntaxa, are then characterised by a set of environmental factors that explain the species composition, and subsequently named according to the International Code of Phytosociological Nomenclature (Weber et al. 2000). This second step is called syntaxonomy. Finally, synsystematics consists of classifying and ranking the syntaxa themselves in a hierarchical system, where the plant association is the basic unit.

The plant association is an abstraction, similar to the species in taxonomy. A number of plant communities that are sufficiently similar in terms of species composition are considered to belong to the same plant association, just as plant individuals sharing the same suite of traits belong to the same species (though the recent emergence of phylogeny has changed this definition substantially). The concrete object studied by phytosociology is the "individual[s] of association" (IA), just as the "plant individual" is the concrete object behind plant species. The IA is what the phytosociologist can observe in the field and what can be described in a phytosociological relevé.

The concept of plant association was refined through time, especially with the work of Tüxen. From a simple "original, repetitive combination of plant species", it turned to "an abstraction emerging from a set of individuals of association that share more or less the same floristic, statistic, ecological, dynamic, chorologic and historical characters" (Géhu and Rivas-Martínez 1981). In other words, from a purely floristic definition the concept of plant association came to incorporate progressively more ecological considerations. The related key concept of "characteristic species" which prevailed in Braun-Blanquet's approach progressively lost its importance.

In his epistemological analysis of phytosociology, de Foucault (1986) demonstrated that this science can be considered a "morphophysics". Firstly, phytosociology is a morphology, since it aims at describing forms (i.e., the IAs) that one encounters in nature; the resulting descriptions are then named (syntaxonomy) and classified (synsystematics); hence, phytocociology is a taxonomy of forms. But phytocociology is also a physics, since it aims at clarifying laws that govern the relationships between plant communities (i.e., the syntaxa) and environmental factors (e.g., climate, soil, relief, biota). In this way, phytosociology is an indirect, inductive way of studying the environment.

Mid Twentieth Century: Sorting New Ideas and Reaching Maturity

Historically, the most widespread method in phytosociology is called the "Braun-Blanquet method", after Josias Braun-Blanquet, who is considered the founder of the method of "Sigmatist phytosociology" after the name of his lab (Station Internationale de Géobotanique Méditerranéenne et Alpine or SIGMA) or also the "Zürich-Montpellier method" after the cities where Braun-Blanquet came from and worked.

During the twentieth century, other methods with new concepts emerged in the field of phytosociology, but few permeated the "official" paradigm. Among the most famous were the Swedish school of Uppsala, with the concept of "sociation" introduced by Du Rietz (1930, 1966), and the Estonian school with the theory of "unistratum associations" elaborated by Lippmaa (1933, 1939). Both were disputed strongly by the partisans of the sigmatist approach and faded from memory until their rehabilitation by the synusial method.

The concept of ecological groups was at the basis of phyto-ecological approaches, conceived by vegetation scientists who found that phytosociology was giving too much importance to plant species as compared with environmental factors. These phyto-ecological approaches do not consider the plant community as a unit but rather as the superposition of more or less inter-dependent groups of species sharing the same ecological requirements (Gounot 1969). These approaches were developed more particularly by Duvigneaud (1946) and by Ellenberg (1954).

Landscape phytosociology appeared in Du Rietz (1917) and Osvald (1923), who were the first to describe landscapes in terms of complexes of associations (*Assoziationskomplexe*, later re-qualified as *Gesellschaftskomplexe* by Braun-Blanquet in 1928). But the method was developed the most by Tüxen (1956, 1973) and by Schmithüsen (1968), who applied to landscapes the same inductive approach as used in phytosociology. So were born two sub-disciplines: the synphytosociology and geosynphytosociology which study "associations of associations". Synphytosociology focuses on *sigmeta*. The corresponding concrete object is the "individual of synassociation", defined as the spatial mosaics composed by all plant communities associated to a same *tesela*, i.e., a series of plant communities corresponding to a single potential natural vegetation or climax (Géhu and Rivas-Martínez 1981). In contrast, geosynphytosociology focuses on *geosigmeta*. The corresponding concrete object is the "individual of geosynassociation", defined as the spatial mosaics composed by all plant communities associated to the same *catena*, i.e., the plant communities hosted by a single geomorphic unit (Géhu and Rivas-Martínez 1981). Usually, a catena supports several teselas.

The success of phytosociology worldwide—with the notable exception of the Anglo-Saxon world—may be attributed to the rather robust method used to describe, characterize and classify plant communities, although the synsystem remains esoteric to the vast majority of vegetation scientists. However, while phytosociology proved to be efficient in temperate—where it was developed—and boreal biomes, it has hardly been applied to more complex ecosystems such as tropical forests (e.g., Granville 1993).

Late Twentieth Century: Towards a New Phytosociology?

A new method emerged at the end of the twentieth century, namely integrated synusial phytosociology (Gillet 1986; Gillet et al. 1991; Gillet and Gallandat 1996), which incorporates the recent theoretical advances in ecology, especially hierarchy theory (Allen and Starr 1982), general systems theory (von Bertalanffy 1968) and the theory of landscape ecology (Forman and Godron 1986). It was first applied successfully to complex forest plant communities of the Jura Mountains (Gillet 1986).

This new method aimed first at accounting for both the nested levels of complexity of plant communities (from synusiae to catenas, through phytocoenoses and teselas) and the temporal dimension of plant communities (Gillet et al. 1991). The major difference with sigmatist phytosociology relates to the conception of the IA: it is now defined at the synusial level (hence “synusial phytosociology”), instead of the phytocoenotic level. A synusia was defined as a single or spatially fragmented ensemble of plants that are sufficiently close to each other with respect of their physical environment, behaviour (including tolerance to disturbance and constraints, exploitation of resources) and temporality, to coexist locally at a given time (Gillet et al. 1991). A phytocoenosis is often composed of several synusiae and thus, a coeno-association (defined at the phytocoenotic level) may be characterized by its composition in terms of associations (defined at the synusial level); hence “integrated” phytosociology. For example, in forest ecosystems, according to the sigmatist approach, the IA encompasses all plants rooted in a given piece of floristically homogeneous land, thus including trees, shrubs, lianas, herbs and mosses (excluding those not on the ground); all corresponding species are thus recorded over the same sample area, eventually at different times of the year if the vegetation shows significantly differing phenophases. In contrast, according to the synusial approach, the same piece of land contains one or more tree synusiae, shrub synusiae, herb synusiae, bryophyte synusiae (including epiphyte synusiae, saxicolous synusiae, humicolous synusiae, dead-wood synusiae…), which are described separately. The sigmatist IA thus became an “individual of coeno-association”. Of course, for many vegetation types, such as grasslands or heathlands, the two approaches lead to very similar results as long as a phytocoenosis is composed of only one synusia; the difference appears mainly for plant communities that are structurally complex in space (multi-layered or in mosaics) or time (with contrasting phenophases or strategies), such as forests, pioneer communities or aquatic communities.

A great advantage of Integrated Synusial Phytosociology (ISP) is that it delivers results that allow the reconstruction of the temporal dimension of vegetation. Since vegetation is primarily characterized at an organisation level that is spatially and temporally relevant, a systemic approach can be implemented. The systemic approach was introduced in phytosociology by de Foucault (1984) and developed further by Decocq (2000). It involves relating the syntaxa to each other within a tesela, according to their dynamic relationships: syntaxa are represented by labels and relationships by symbolic arrows. Several phytosociological systems built for various regions (e.g., different temperate forests) can be compared subsequently in order to identify isomorphic systems and invariant relationships, paving the way for a true structuralism, making generalisations and predictions more possible. With these new methodological developments, phytosociology not only describes patterns in plant communities, but also infers processes behind these patterns, hence provides a functional approach to studying plant communities. In so doing, the ISP may contribute to bridging the growing gap between phytosociology and ecology.

Phytosociology *Versus* Ecology: Toward a Reconciliation?

It is usually ignored that ecology, like phytosociology, is rooted in phytogeography. For example, the importance of island size and distance from the continent for species richness on islands, which is at the basis of MacArthur and Wilson's theory of island biogeography (1967) was still pointed out by de Candolle more than a century earlier in the introduction of his "*Géographie botanique raisonnée*" (1855). Similarly, the basics of population ecology were already addressed by Darwin in his "Origin of species" (1859), through the roles of intra- and inter-specific competition in the dynamics and evolution of species populations and the "web of life" (later renamed food web). Darwin also introduced the concept of the ecological niche, as the "place" of a species in nature. The term "ecology" itself was introduced by Haeckel in 1866 to design "the science of relationships between organisms and their environment"; subsequently, during the last decades of the nineteenth century, it developed rapidly as a new sub-discipline of geobotany (mostly among plant ecologists) or physiology (mostly among animal ecologists). One of the most important seminal books in ecology is Warming's "*Plantesamfund: Grundträk af den ökologiske plantegeografi*" published in 1895, which was influential to both traditions, namely European phytosociology and American ecology.

The conceptual divergence between ecology and phytosociology probably originated in the mid-nineteenth century, when ecology incorporated the progress made by life chemistry leading to new concepts such as the biosphere (1875), biocoenosis (1877) and biogeochemical cycles, making ecology more functional than descriptive, closer to biology than to geography (Deléage 1991). The schism between phytosociology and ecology became more final, though, at the beginning of the twentieth century. While European phytosociologists were focusing on static vegetation units, young American ecologists stressed the dynamic nature of vegetation by studying succession in plant communities, as expressed in the seminal works of Cowles (1899, 1901) and Clements (1905, 1916), the latter introducing the "climax" concept. This led progressively to the continuum concept (Gleason 1917), which pervaded the American tradition. The fact that syntaxonomy and synsystematics rapidly made phytosociology an esoteric science and contributed to the conflicts among the different European schools probably finalized the rupture. In the wake of plant ecology, animal ecology began to develop, at the instigation of Elton (1927), and contributed to make ecology "the science of ecosystems" (Tansley 1935), ecosystems being functional units with energy fluxes (Lindeman 1942) and material cycles (Odum and Odum 1953). Ecology clearly became a field of biology, while phytosociology stayed closer to geography. Remarkably, in France, where phytosociology was born as a science, the word "ecology" appeared in the Larousse dictionary for the first time only very late, in 1956 (Droin 1991).

With the emergence of the integrated synusial method, phytosociology began to re-connect with ecology, since the revised concept of IA took into account functional considerations. Especially, it incorporated the concepts provided by general system theory (von Bertalanffy 1968), hierarchy theory (Allen and Starr 1982) and the emerging landscape ecology (Forman and Godron 1986). The IA is no longer considered a community formed by all species rooted in a given habitat but as an ensemble of plants sharing the same ecological strategy (to respond to environmental filters and exploit resources) and the same ecologically homogeneous space at the same time (Gillet et al. 1991). Hence, the synusial association takes into account assembly rules provided by plant ecologists. Roughly, the sigmatist IA becomes a "coeno-association individual", that is a complex of synusiae (hence of different IA) organized spatially, temporally and functionally within a biogeocoenosis, with emergent properties such as homeostasis and resilience. The coeno-association is thus a functional unit that is relevant for ecological studies of ecosystem functioning. At upper integration levels, the tesela (i.e., complexes of phytocoenoses coverging theoretically towards the same climax) and the catena (i.e., complexes of tesela assembled within the same geomorphological unit) are relavant units for the purposes of landscape and global ecology.

New Challenges for the Phytosociology of the Twenty-First Century

Ecology has made substantial progress during the twentieth century, and the way forward promises to be fertile (Sutherland et al. 2013). What about phytosociology? For the purpose of this short note, I choose three challenges that phytosociology should meet in order to find its place in plant ecology: being more functional; incorporating recent advances in dispersal vs. niche assembly rules; and withdrawing old-fashioned, static concepts such as the climax. I acknowledge that many more challenges should be mentioned, but perhaps these represent a good starting point and to pave the way for a modern science.

Let Plant Associations Be Functional!

Raunkiaer was the first, in 1905, to categorize plants in biological types according to the position of buds during winter (Raunkiaer 1934). This classification was used to characterize some vegetation types; for example, a forest is dominated by phanerophytes (woody plants having their buds on aerial stems), a heathland by chamaephytes (woody shrubs with buds just above ground), a grassland by hemicryptophytes (perennial herbs with buds at ground level), etc. Other trait-based classifications emerged later, such as the integrative CSR strategy scheme of Grime (1974) and the morphological types of Barkman (1988). These trait classifications have been used largely by phytosociologists to characterize plant associations, but mostly in a descriptive way.

In the 1990s there was a renewed, growing interest in species classification that was related directly to response or function, based on shared life-history traits (Lavorel and Garnier 2002; Lavorel et al. 1997; Stearns 1989; Violle et al. 2007; Weiher et al. 1999; Semenova and van der Maarel 2000). This is because functional attributes of diversity relate to life-history traits that are sorted specifically by the environment, and because of a growing awareness that functional diversity, rather than species numbers *per se*, strongly determines ecosystem processes such as resource dynamics and biomass production (Díaz and Cabido 2001). These approaches relate ecophysiological attributes of plants to community and ecosystem functioning implicitly, a crucial step in modelling vegetation under changing environmental conditions.

The most common way of linking species traits to environment has been to group species into plant functional types (PFTs) using clustering algorithms based on their shared traits and, subsequently, to relate these groups to environmental variables using ordination techniques (Díaz and Cabido 1997; Lavorel and Garnier 2002). PFTs are sets of plant species exhibiting similar responses to environmental conditions ("response traits") or having similar effects on ecosystem processes ("effect traits") (Díaz and Cabido 1997). As an alternative to PFTs, multivariate statistical methods can be used to treat several large data matrices simultaneously, such as the three-table method of "RLQ analysis" (Dolédec et al. 1996; Ribera et al. 2001), which can link species traits directly to environmental variables.

To describe plant associations, classical phytosociologists used L matrices (i.e., relevés x species) and, quite often, simultaneously, used R matrices (i.e., relevés x environmental variables) in canonical multivariate methods. Now that large trait data-bases are available (e.g., LEDA in Europe: Kleyer et al. 2008), it has become easier and easier to build large Q matrices (i.e., species x traits), paving the way for more functional studies through RLQ analyses. This offers a great opportunity to phytosociology for relating the huge number of patterns it has described over the decades to ecosystem processes. For example, the distribution area of most plant associations ranges from a region to a sub-continent, and for a similar set of environmental conditions, plant associations replace each other over large geographic areas. Though they differ by their species composition, these plant associations are predicted to share the same traits that are filtered by similar environment conditions. Surprisingly, this prediction has been poorly tested so far by phytosociologists. Yet this has the potential to reveal the influence of the biogeographic history of floras on current ecosystem functioning worldwide and to answer questions such as: Do European temperate forestsfunction like their Japanese or North American counterparts, despite their differences in plant species composition and lowerspecies richness? Are they less resilient due to lower functional redundancy? In the phytosociological synsystem, many classes are subdivided according to the place of plant associations along (composite) environmental gradients that are reflected by species composition. For example, in the *Agrostio stoloniferae—Arrhenatheretea elatioris* (Tüxen 1937 em. 1970) de Foucault 1984 class of grasslands, the *Agrostienea stoloniferae* (Oberdorfer & Müller ex Görs 1966) de Foucault 1984 subclass groups hygrophilous communities and the *Arrhenatherenea* *elatioris* (Braun-Blanquet 1947) de Foucault 1984 subclass groups meso-hydric communities. How these changes in species composition are reflected by trait composition deserves attention, as this may increase greatly our ability to predict vegetation response to environmental changes, such as eutrophication and climatic warming. This higher level of abstraction in comparison with species-based analyses is essential for comparing vegetation dynamics and ecosystem processes across different biogeographical regions (Díaz and Cabido 1997). Rendering plant associations more functional than they currently are is probably one of the greatest challenges for phytosociology.

Are Plant Communities Niche-Assembled or Dispersal-Assembled?

Phytosociology is clearly a deterministic science, assuming that species differ in their response to resources, are not competitively equal, and have spatial distributions controlled by ecological conditions. Hence, phytosociology is based implicitly on niche theory and related species-sorting models. The ecological niche is a key concept in ecology and has been influential since the very beginning. Among other definitions, the Hutchinsonian view is that of an *n*-dimensional hypervolume, where the dimensions are environmental conditions and the resources that define the requirements of a species to survive and reproduce. In the absence of interacting species, a given plant species can theoretically use the full range of environmental conditions and resources in which it can live, which is called its *fundamental* niche. Due to inter-specific competition, species are supposed to be constrained to occupy a niche that is narrower than their fundamental niche, which is called the *realized* niche.

Within the last two decades, however, this traditional view has been challenged by Hubbel's neutral theory (Hubbell 2001), and growing attention has been paid to dispersallimitation (Primack and Miao 1992; Freestone and Inouye 2006) and the regional species pool (Zobel 1997) as important factors explaining local species assemblages. Whether plant assemblages are driven by neutral (random) or niche (deterministic) factors is still debated, despite the growing evidence that both sets of factors may operate simultaneously (Cadotte 2007). The question to be answered is rather when and how far neutral, stochastic processes on the one hand and niche-structuring processes on the other hand act together to organize species assemblages. To date, this question has largely been ignored by phytosociologists, despite the potential of dispersal limitations and differences in regional species pools for explaining the variability of plant associations.

Plant associations are traditionally defined on the basis of repetitive species combinations; in other words, the association individuals should share the same suite of species. That being said, all phytosociologists know that this statement is rarely achieved in the real world: some expected species (the so-called "characteristic" species) are sometimes missing, while some unexpected species (the so-called "accidental" species) sometimes do occur.

Characteristic species may be absent simply because they do not belong to the regional species pool; this often happens at the distributional margins of an association and phytosociologists usually consider the community as a "geographic race" of the association. Otherwise, a species may be missing from an IA [group] either because the area over which the relevé was compiled was too small (i.e., below the so-called "minimal area", as defined by the asymptote of the species-area relationship) or because the community had not achieved maturity yet. In the latter case, this means that the species-time relationship did not reach its asymptote yet (Adler et al. 2005) and slow colonizers had not had time to become established yet, usually because of dispersallimitations. Hence some characteristic species are missing simply because they have not immigrated from a source population yet. A remarkable example is provided by studies comparing ancient and recent forests (e.g., Hermy et al. 1999): many true forest species characteristic of the *Anemono nemorosae-Caricetea sylvestris* synusial class of temperate European forests were actually missing from more recent forests not because the habitat is unsuitable for them but because they are slow dispersers and had not had enough time to colonize the habitat. Surprisingly, although species-area relationships have been used by phytosociologists since the very beginning, species-time relationships have largely been neglected so far. The result, though, is the same: some characteristic species may be absent from a local plant community while they are present in the regional species pool; hence the individual association is fragmentary and does not reflect the so-called "normal taxonomic ensemble" (Gillet et al. 1991).

Accidental species are often neglected by phytosociologists (who often do not even report them in phytosociological tables) because they are considered to be stochastic artefacts that simply should not be there. Of course, by acknowledging the existence of accidental species, phytosociologists tacitly recognize that not only determinism but also stochasticity is at play! If a species occurs in an IA, it is because it was able to disperse there, to recruit and to become established, at least transiently. In brief, it found a suitable niche. It should be noted, however, that, for a species, being accidental means occurring very infrequently compared to the other species, hence its occurrence is not statistically significant. In no way does this mean that the species is not ecologically significant! The rarity of a species in a set of relevés may have various origins. It happens when a species is rare in the regional species pool, because it is going extinct or has invaded the region only recently; also when a species is a relict from a former successional stage or when it anticipates a future stage. Some plant communities may receive immigrants from a neighbouring, distinct plant community: despite *a priori* unsuitable habitat conditions, they may become established anyway. In this respect, growing awareness about the crucial role of propagule pressure has come from invasionecology (e.g., Lockwood et al. 2005): a local plant community can maintain a species that would otherwise go extinct without immigration from elsewhere through a "mass effect", because local filters operate slowly relative to the speed at which species immigrate.

In the future, phytosociology should acknowledge that plant communities are not only niche-assembled but also dispersal-assembled. This does not mean that phytosociology must be less deterministic (dispersal is a deterministic process!), but that it should also incorporate stochasticity and recent advances in dispersal ecology and metacommunity dynamics.

It has indeed been shown repeatedly that local species assemblages can only be understood by being placed in their historical and spatial contexts (Ricklefs and Schluter 1993). This led to the metacommunity concept, defined as a set of local communities linked by dispersal of multiple potentially interacting species (Leibold et al. 2004). Metacommunity theory has added new insight into mechanisms behind diversity by considering regional processes that regulate the arrival of organisms into local communities (e.g., habitatconnectivity and regional heterogeneity), local processes that regulate the success of species following their arrival or the arrival of other species (e.g., niche differentiation, competition, predation), and their interactions in structuring local communities. The grain at which plant communities are assessed by metacommunity ecology is coarser than in phytosociology. Being closely related to landscape ecology, metacommunity ecology considers rough vegetation types (e.g., forest, heathland, dry grassland) but puts local communities into an ecosystem context, hence is more functional and process-based. On the contrary, phytosociology is more pattern-based but distinguishes different IAs within vegetation types, hence providing the basis for a finer analysis of fine-scale processes.

Should We Bury the Climax Concept?

The idea that one final stage of vegetation exists for any given geographic location dates back to the nineteenth century but was formalized through the climax concept of Clements (1936). It was then applied to phytosociology, since Tüxen (1956), through the concept of potential natural vegetation (PNV). This PNV is the mature plant community which would become established given a particular set of environmental factors, in the absence of any disturbance, hence excluding any human influence. In practice, the climax is inferred from the existing mature stages observed in the wild, hence using a space-for-time substitution procedure. However, the climax concept faces some methodological problems that have been reviewed recently by Chiarucci et al. (2010). The climax concept assumes that one “final stage” in vegetation succession is reached under stable environmental conditions, but ecosystems rarely experience stable environmental conditions, especially in the context of contemporaneous global changes. The idea itself that a climax can be characterized by reference to existing mature vegetation simply ignores vegetation dynamics. Being static, the climax concept overlooks biological uncertainties and natural temporal variability completely.

Succession has been reviewed critically in the light of the roles of determinism, stochasticity and chaos (Decocq 2006). It has been suggested, for example, that there may be two or more climaxes for a single set of ecological conditions, resulting in two or more alternative states for the same community (Sutherland 1990). But probably the most important drawback of the climax concept involves our view of human impact. The climax refers to vegetation free from any significant outside influence—but is this realistic in a biosphere where *Homo sapiens* is definitely not an external disturbance but a keystone species within the system and has disrupted ecological recovery and stability mechanisms for a long time and over vast spatial scales. As claimed by O'Neill (2001), "*Homo sapiens* is moving ecological systems outside the envelope of conditions that have existed over evolutionary history. This is *terra incognita*, and the assumption that ecological systems will respond stably is unjustified". In a biosphere patterned by *Homo sapiens* it is illusive that any plant community may be freed from human influence. Among other factors, the extinction of large mammals, biological invasions (including plants, pests, etc.), changes in soil properties or fire regimes, and management have been shown to alter successions dramatically. So, what kind of climax could a plant community left alone reach when it is embedded in a human-managed landscape? In their 2010 paper, Chiarucci et al. pleaded for a change of paradigm (i.e., an *a priori* intellectual framework to look at nature), to move from a static and unrealistic concept of potential natural vegetation to a dynamic and more useful concept of vegetation. As a starting point they proposed to model individual species distributions and investigate potential associations that might emerge when environmental conditions change. I would add here that *Homo sapiens* should be included in the definition of potential vegetation, which cannot be longer "natural" since even when an area is abandoned to "natural" succession, it is largely influenced by human activities at broader spatial and temporal scales. The Earth has a tremendous capacity for self-healing and recovering after various disturbances, as illustrated remarkably by Weisman's *The World Without Us* (2007). But even if humans suddenly disappear tomorrow, some artefacts are probably indelible and, thus, ecosystems on Earth will definitely bear the human imprint. It is obvious, for example, that due to the human-induced extinction of big herbivores, the savanna-like Medieval landscape of temperate Europe will never recover even if *Homo sapiens* disappears; instead, a closed-canopy forest is more likely to develop.

There are so many uncertainties in predicting successional pathways and "final" states of succession that, in order to be operational, a climax concept must refer to a vague vegetation type, defined on the basis of the species that are more likely to dominate, such as a common beech forest. So the question is: do we still need the concept? (And the answer is: probably no!)

Conclusion: The Future of Phytosociology in a Globally Changing World

Ecology is a dynamic science, which regularly revisits old questions that are still seen as essential to answer and raises new questions about global environmental changes, complex ecosystem interactions and evolutionary ecology (Sutherland et al. 2013). Adapt or die: is it the challenge for phytosociology at the beginning of the twenty-first century? Phytosociology has accumulated an amazing number of vegetation records worldwide and provides us with a robust description of many plant communities (Dengler et al. 2011). Phytosociological data have long been used and are still used as a basis for sound ecological analyses, currently published in top-ranked journals (e.g., Lenoir et al. 2008; Bertrand et al. 2011). There is even a growing interest in unearthing old relevés, resurveying vegetation and assessing the impacts of global changes (Chytrý et al. 2014). The long-lasting debate about whether communities are discrete or continuous entities is now over, with the vast majority of scientists acknowledging that it is a matter of scale. But still, some vegetation scientists record vegetation at random, ignoring heterogeneity, although the purpose of their study would require floristically homogeneous communities. To move forward in the twenty-first century, phytosociology must no longer lock itself into dogma: it has to go beyond the syntaxonomy and synsystematics that make it esoteric to most plant ecologists. Although syntaxonomy can be useful for nature conservation and biogeography, for example to map vegetation, it is not essential to plant ecology, the main goal of which is to assess the processes behind the patterns. Above I suggested three needs for a renewed phytosociology: being more functional, paying more attention to dispersal and metacommunity dynamics, and dropping old-fashioned, misleading concepts such as the climax. The future of phytosociology includes providing ecology with high-quality field data through its robust methodology, but perhaps with a more process-oriented sampling strategy. In this respect, the integrated synusial approach is inherently better suited to serve ecology by reflecting the complexity of plant communities in both space and time, and by taking into account the ecological strategy of species. It also has the potential to cast light on the processes underlying metacommunity dynamics, since plant communities are described at a finer scale than is done by landscape ecology. This puts local species assemblages into the context not only of regional species pools but also habitat species pools. In conclusion, phytosociology is an empirical science that may help ecology greatly in testing some of its theories and models that otherwise might remain as esoteric as syntaxonomy may be perceived. Phytosociology can no longer afford to be a static science in a globally changing world.

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A Multi-scale Analysis of Plant Diversity Along Soil Nutrient Gradients

Brooke E. Wheeler and Robert K. Peet

Abstract Although edaphic variation is common in natural systems, and has often been described as a major driver of plant species diversity, the effect of this edaphic variation on plant diversity has not been described in a comprehensive, synthetic fashion. Understanding this variation is essential, however, as soil nutrients are important drivers of plant community structure. This study takes advantage of multi-scale vegetation sampling along with plot-level soil data from the Carolina Vegetation Survey to examine the relationships between soil nutrients and diversity in forests and woodlands at multiple spatial scales and across floristic regions. We find that there is greater variation in soil characteristics that predict diversity between regions than across scales within regions. In Atlantic Coastal Plain longleaf-pine communities, nitrogen, sulfur, iron, soil pH, organic matter, and silt are important predictors of diversity. In the Fall-line Sandhill longleaf-pine communities of the Carolinas, manganese, nitrogen, soil pH, and silt are the measured variables that predict diversity best. In longleaf-pine communities of Florida, soil pH, iron, nitrogen, and silt are consistently the strongest indicators across all scales from 0.01 to 1000 m^2. In southern Appalachian Mountain forest communities, soil pH, manganese, and calcium are the best diversity indicators. By tailoring models to individual regions, soil characteristics can predict between 39 and 54 % of the variance in diversity at the 0.1 ha scale.

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Introduction

Multiple factors affect plant species diversity, including climatic factors, species pool, dispersal abilities of species, disturbance, and environmental favorability, which includes nutrient availability. Describing diversity is complicated, however, by the fact that patterns of diversity have also been shown to vary with scale of observation (Gaston 2000; Peet et al. 2014). Giladi et al. (2011) emphasize the importance of studying the multiple drivers of diversity across scales of observation in order to determine influences on plant diversity accurately. Soil attributes are critical in driving plant community diversity, but variation in soil attributes is poorly represented in most regional data (Waring and Running 1998; Box and Fujiwara 2011). In particular, soil nutrients and texture vary between regions because of differences in geological history and context, but diversity may also track fine-scaled variation in soil attributes. If the significant correlates of diversity vary with scale, this could shed light on which mechanisms are influencing species coexistence. However, if correlates vary less with scale and more with region, this highlights the dominance of broader-scale factors, such as soil, climate and regional geology, over local coexistence mechanisms.

Path models and structural equation models provide a basis for determining the complex relationship of diversity with soil resources and its variation with scale. We use these approaches to examine the relationship between soil characteristics and species diversity across multiple scales in forests of two floristic regions: the longleaf-pine woodlands of the southeastern United States coastal plain and the forests of the southern Appalachian Mountains.

Small changes in soil moisture and soil texture translate into distinct compositional differences in longleaf-pine communities. In fact, a combination of soil moisture and percent silt has been used as the primary basis for classification of longleaf-pine communities (Peet 2006; Peet et al. 2014). Soil texture has consequences for water relations and nutrient storage that affect the availability of moisture and nutrients to plants. Based on prior research (e.g., Peet 2006), we expected soil texture to be a key factor driving variation in diversity across spatial scales from 0.01 to 1000 m^2 within the coastal plain. In contrast, previous work in southern Blue Ridge Mountains forests has demonstrated a close relationship between soil pH and species diversity (Peet et al. 2003, 2014). This is consistent with the correlation between diversity and pH seen in other temperate forest communities (e.g., Schuster and Diekmann 2005). Because these distinct regions differ in expected importance of soil characteristics, they provide a case study for examination of consistency of patterns across scales in a wide range of community types.

Examination of the herbaceous richness of forests and woodlands in eastern North American indicates the changing importance of edaphic variables, both across scale of observation and across regions (Peet et al. 2014). This study takes advantage of multi-scale vegetation sampling (Peet et al. 1998, 2012) along with plot-level soil data to examine the relationships between soil nutrients and diversity

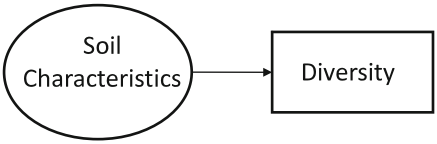

Fig. 1 Initial conceptual model showing the influence of soil characteristics on diversity

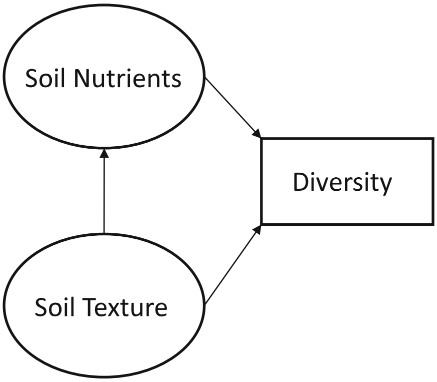

Fig. 2 Refined conceptual model illustrating the direct and indirect influence of soil texture on diversity

of vascular plants at different scales. Path analysis is used to determine the relative strength of soil variables in predicting plant species richness and to determine the loadings of soil variables onto latent variables in order to build structural equation models of soil nutrients and diversity. We hypothesize that texture is the driving influence on diversity in longleaf-pine communities, while soil pH and manganese are the essential variables in the southern Appalachian Mountains. We expect soil minerals to influence diversity collectively in the mountains (Fig. 1) but that there will be distinct soil mineral and soil texture influences in longleaf-pine communities (Fig. 2).

Methods

Data were assembled from the Carolina Vegetation Survey database (CVS; Peet et al. 2012) for forests of the southern Appalachian Mountain region (578 plots) and longleaf-pine woodlands of the Southeastern Coastal Plain (642 plots). The longleaf-pine data were subdivided into three geographic regions: one representing the Atlantic Coastal Plain ($n = 343$), the second the Fall-line Sandhill region of North and South Carolina ($n = 94$), and the third Florida ($n = 203$). These plots are 1000 m^2 and were surveyed using the CVS methodology (Peet et al. 1998, 2012). Plant species richness was measured in 0.01, 0.1, 1, 10, and 100 m^2 subplots within the 1000 m^2 plot, with two nests in each of four 100 m^2 intensive modules within the 1000 m^2. Richness values were averaged across the four intensive modules for each subplot size.

Soil samples were taken from the A horizon in at least one intensive module. Because soil samples were generally taken from each intensive module, they were typically located inside each 100 m^2 subplot, and in all cases there was a sample within the 1000 m^2 plot. All soil samples were analyzed by Brookside Laboratories, New Oxford, Ohio, using Mehlich-3 extraction (Mehlich 1984) for nutrient analyses. Soil analyses included texture (percent clay, silt, and sand), cation exchange capacity (CEC), pH, organic matter (Org), and availability of nitrogen (N), phosphorous (P), sulfur (S), manganese (Mn), calcium (Ca), and iron (Fe). Soil nutrient measurements were log-transformed to normalize the distributions in order to facilitate the comparison of covariances to diversity through structural equation modeling.

Conceptual models were initially specified for structural equation modeling (see above, Figs. 1 and 2), based on theory, previous work, and knowledge of the systems (e.g., Peet et al. 2003, 2014; Peet 2006). An iterative process was used to refine the models: (1) checking the specification of a model, (2) using the estimates based on the model fit to the covariance data and model fit indices to evaluate the model, and (3) making adjustments to the model if necessary. A model with suitable fit can then be interpreted. In this analysis, we used path models (only including measured variables) to eliminate unnecessary measured variables before running the structural equation models that include conceptual variables (e.g., soil nutrients). For a more thorough description of structural equation modeling, see Bollen (1989), or Grace (2006). For each dataset, correlations and covariances were calculated for plant species richness at each scale and for all soil variables. The strongest 5–6 soil variables (correlations $r > 0.24$) were selected to model diversity at four scales: 1, 10, 100, and 1000 m^2. Finer scales were excluded because they were further from the soil sample; also, because of weaker correlations, the models either fit poorly or did not converge. All path models were run initially with the strongest correlates for a given scale and region (Table 1). Correlates with strong co-linearity with other predictors were removed. Initial models were refined based on the significance of paths (i.e., insignificant paths were removed from the models until the best model fit was achieved). Confirmatory factor analyses were run on all models to determine the appropriateness of predictors loading onto latent variables (e.g., conceptual variables, such as soil nutrients and soil texture). The confirmatory factor analyses were used to test structural equation models (Bollen 1989) of soil and diversity. All analyses were conducted using the MPlus6.1 statistical package (Muthén and Muthén 1998–2010) with maximum likelihood estimation.

Table 1 Strongest correlates of diversity at different scales in Atlantic Coastal Plan (ACP), Sandhills, and Florida (FL) longleaf-pine communities, and southern Appalachian Mountain forest (Mountain) communities. The strongest correlate is listed on the left, and they decrease from left to right

ACP longleaf	0.01 m^2	N	Sand	Silt	S	Fe	Org
	0.1 m^2	N	Sand	Silt	S	Fe	Org
	1 m^2	N	Fe	S	Sand	Silt	Org
	10 m^2	Fe	S	N	Sand/Org	Silt	Clay
	100 m^2	Fe	S	N	Org	Sand	Silt/pH
	1000 m^2	Fe	S	N	Org	pH	Clay
Sandhills longleaf	0.01 m^2	N	Sand/pH	Silt	Org		
	0.1 m^2	N	pH	Sand	Silt/Mn	Ca/Org	Clay
	1 m^2	pH	N	Mn	Ca	Sand	Silt
	10 m^2	pH	N/Mn	Ca	Sand	Silt	Org
	100 m^2	Mn	pH	N	Ca	Silt/Sand	Org
	1000 m^2	Mn	Silt/Sand/pH	N/Ca	Org		
FL longleaf	0.01 m^2	N	Silt/Org	Fe	Sand		
	0.1 m^2	Silt	N	Sand	Org	Fe	P
	1 m^2	Silt	Sand/Fe/pH	N			
	10 m^2	pH	Fe	Mn	Silt	Sand	
	100 m^2	pH	Mn	Fe	Silt		
	1000 m^2	Fe	pH	Mn	Silt	Sand	
Mountain	0.01 m^2	Ca	pH	CEC	Mn		
	0.1 m^2	pH	Ca	Mn	CEC		
	1 m^2	pH	Mn	Ca	Fe	CEC	
	10 m^2	pH, Mn	Ca	Fe	S		
	100 m^2	pH	Mn	Ca	Fe	S	
	1000 m^2	pH	Mn	Ca	Fe	S	

Results

Longleaf Pine Communities

In all three longleaf-pine regions, the correlates of diversity had some turnover between scales (Table 1 summarizes the strongest correlates at each scale). Silt was a strong correlate across almost every scale in all three regions. Iron, nitrogen, and sulfur had the strongest relationship with diversity across all scales of observation in longleaf pine of the Atlantic Coastal Plain, followed by soil organic matter, silt, and sand (Table 2). In the Sandhills, longleaf diversity correlated most strongly with manganese, pH, and nitrogen, but silt, sand, and calcium were also highly correlated with diversity (Table 3). In Florida longleaf stands, soil pH, iron, manganese, and silt were the strongest correlates of diversity (Table 4).

Table 2 Correlations between soil nutrients and plant species richness at six scales in Atlantic Coastal Plain (NC, SC, GA) longleaf-pine communities

	$0.01\ m^2$	$0.1\ m^2$	$1\ m^2$	$10\ m^2$	$100\ m^2$	$1000\ m^2$	logCEC	logPH	logOrg	logN	logS	logP	logCa	logFe	logMn	Silt	Clay	Sand
$0.01\ m^2$	1.00																	
$0.1\ m^2$	0.94	1.00																
$1\ m^2$	0.87	0.95	1.00															
$10\ m^2$	0.77	0.86	0.96	1.00														
$100\ m^2$	0.66	0.77	0.89	0.97	1.00													
$1000\ m^2$	0.60	0.70	0.83	0.92	0.97	1.00												
logCEC	0.06	0.06	0.05	0.03	0.04	0.03	1.00											
logPH	0.01	0.07	0.20	**0.30**	**0.33**	**0.37**	−0.15	1.00										
logOrg	**0.28**	**0.29**	**0.37**	**0.40**	**0.40**	**0.41**	0.12	0.18	1.00									
logN	**0.49**	**0.51**	**0.51**	**0.49**	**0.47**	**0.45**	0.39	−0.20	0.53	1.00								
logS	**0.39**	**0.42**	**0.48**	**0.52**	**0.53**	**0.51**	0.23	0.14	0.58	0.45	1.00							
logP	0.00	0.04	0.10	0.16	0.18	0.19	0.21	0.24	0.39	0.31	0.47	1.00						
logCa	0.04	0.08	0.16	0.21	0.24	**0.26**	0.76	0.48	0.17	0.16	0.25	0.33	1.00					
logFe	**0.36**	**0.40**	**0.50**	**0.58**	**0.61**	**0.64**	−0.01	0.27	0.58	0.46	0.64	0.42	0.16	1.00				
logMn	−0.15	−0.10	0.03	0.13	0.16	0.19	0.05	0.70	0.08	−0.11	−0.03	0.34	0.48	0.11	1.00			
Silt	**0.46**	**0.48**	**0.43**	**0.36**	**0.33**	**0.28**	0.17	−0.27	−0.04	0.53	0.25	−0.05	−0.04	0.18	−0.27	1.00		
Clay	0.23	0.24	**0.27**	**0.31**	**0.31**	**0.35**	0.01	0.19	0.27	0.26	0.32	−0.03	0.06	0.33	0.06	0.20	1.00	
Sand	**−0.48**	**−0.50**	**−0.46**	**−0.40**	**−0.36**	**−0.33**	−0.16	0.23	−0.01	−0.54	−0.29	0.06	0.02	−0.23	0.25	−0.99	−0.36	1.00

Correlations greater than 0.25 are in bold (see columns 1–7). Organic matter, nitrogen, sulfur, iron, silt, and sand are strong correlates across all scales

Table 3 Correlations between soil nutrients and plant species richness at six scales in North Carolina Sandhills longleaf-pine communities

	0.01 m^2	0.1 m^2	1 m^2	10 m^2	100 m^2	1000 m^2	logCEC	logPH	logOrg	logN	logS	logP	logCa	logFe	logMn	Silt	Clay	Sand
0.01 m^2	1.00																	
0.1 m^2	0.86	1.00																
1 m^2	0.74	0.93	1.00															
10 m^2	0.64	0.85	0.95	1.00														
100 m^2	0.60	0.79	0.90	0.97	1.00													
1000 m^2	0.52	0.72	0.81	0.88	0.95	1.00												
logCEC	0.00	0.02	0.08	0.06	0.09	0.18	1.00											
logPH	**0.36**	**0.53**	**0.61**	**0.61**	**0.55**	**0.44**	−0.20	1.00										
logOrg	**0.32**	**0.32**	**0.36**	**0.30**	**0.32**	**0.35**	0.57	0.09	1.00									
logN	**0.45**	**0.58**	**0.60**	**0.55**	**0.50**	**0.42**	0.14	0.42	0.51	1.00								
logS	0.20	0.22	0.23	0.19	0.19	0.19	−0.14	0.19	0.48	0.47	1.00							
logP	−0.02	−0.06	−0.02	0.00	0.03	0.11	0.23	0.07	0.43	−0.23	0.11	1.00						
logCa	0.21	**0.32**	**0.42**	**0.41**	**0.41**	**0.42**	0.78	0.41	0.56	0.30	−0.07	0.33	1.00					
logFe	−0.22	**−0.25**	**−0.28**	**−0.28**	−0.24	−0.19	0.17	−0.22	0.05	−0.02	0.14	−0.11	−0.03	1.00				
logMn	0.23	**0.35**	**0.48**	**0.55**	**0.57**	**0.54**	0.14	0.62	0.29	0.30	0.10	0.37	0.54	−0.18	1.00			
Silt	**0.35**	**0.35**	**0.38**	**0.34**	**0.39**	**0.44**	0.50	0.10	0.65	0.40	0.23	0.03	0.43	0.05	0.11	1.00		
Clay	0.22	**0.31**	**0.32**	**0.26**	**0.25**	**0.25**	0.11	0.19	0.45	0.59	0.51	−0.11	0.10	−0.15	−0.04	0.45	1.00	
Sand	**−0.36**	**−0.37**	**−0.39**	**−0.35**	**−0.39**	**−0.44**	−0.47	−0.12	−0.67	−0.46	−0.28	−0.01	−0.41	−0.03	−0.09	−0.99	−0.56	1.00

Correlations of 0.25 and above are in bold (see columns 1–7). Soil pH, organic matter, nitrogen, and silt are strong correlates across all scales

Table 4 Correlations between soil nutrients and plant species richness at six scales in Florida longleaf-pine communities

	0.01 m^2	0.1 m^2	1 m^2	10 m^2	100 m^2	1000 m^2	logCEC	logPH	logOrg	logN	logS	logP	logCa	logFe	logMn	Silt	Clay	Sand
0.01 m^2	1.00																	
0.1 m^2	0.88	1.00																
1 m^2	0.73	0.91	1.00															
10 m^2	0.54	0.75	0.93	1.00														
100 m^2	0.39	0.62	0.83	0.95	1.00													
1000 m^2	0.33	0.55	0.74	0.86	0.94	1.00												
logCEC	−0.06	−0.05	−0.03	−0.09	−0.12	−0.12	1.00											
logPH	−0.01	0.16	**0.33**	**0.45**	**0.50**	**0.45**	−0.19	1.00										
logOrg	**0.31**	**0.32**	0.24	0.10	0.04	0.10	0.56	−0.31	1.00									
logN	**0.33**	**0.36**	**0.28**	0.14	0.08	0.13	0.52	−0.26	0.98	1.00								
logS	0.13	0.09	0.11	0.11	0.12	0.13	0.39	−0.13	0.42	0.44	1.00							
logP	−0.22	**−0.25**	−0.15	−0.07	−0.02	0.00	0.35	0.14	0.14	0.16	0.59	1.00						
logCa	−0.11	−0.03	0.08	0.10	0.09	0.08	0.88	0.26	0.37	0.36	0.33	0.46	1.00					
logFe	**0.28**	**0.31**	**0.33**	**0.38**	**0.41**	**0.46**	−0.31	0.22	0.02	0.05	0.15	−0.01	−0.21	1.00				
logMn	−0.24	−0.05	0.17	**0.35**	**0.47**	**0.44**	−0.09	0.66	−0.24	−0.21	0.01	0.17	0.23	0.13	1.00			
Silt	**0.31**	**0.37**	**0.37**	**0.32**	**0.28**	**0.30**	−0.12	0.07	0.30	0.34	0.09	−0.25	−0.10	0.33	−0.02	1.00		
Clay	0.06	0.16	0.14	0.09	0.08	0.09	0.14	0.03	0.18	0.20	0.05	−0.09	0.11	0.19	0.02	0.26	1.00	
Sand	**−0.25**	**−0.35**	**−0.33**	**−0.27**	−0.24	**−0.26**	0.01	−0.06	−0.32	−0.35	−0.09	0.22	0.01	−0.33	0.01	−0.84	−0.74	1.00

Correlations of 0.25 and above are in bold (see columns 1–7). Iron and silt are strong correlates across all scales. Soil pH is a strong correlate at the larger scales

Table 5 Model fit values for path models and structural equation models of plant diversity and soil attributes

Location	Scale	CFI	SRMR	RMSEA	90 % CI	χ^2	df	P	AIC
ACP longleaf	1 m^2	0.60	0.09	0.26	0.22–0.30	123.16	5	0.00	1004.84
	10 m^2	1.00	0.00	0.00	0.0–0.0	230.954	4	0.00	2381.84
	100 m^2	1.00	0.00	0.00	0.0–0.0	240.706	4	0.00	2714.44
	1000 m^2	1.00	0.00	0.00	0.0–0.0	265.78	5	0.00	1452.47
	SEM	0.74	0.12	0.25	0.23–0.27	1079.23	21	0.00	346.55
Sandhills longleaf	1 m^2	1.00	0.00	0.00	0.0–0.0	75.636	4	0.00	500.79
	10 m^2	1.00	0.00	0.00	0.0–0.0	72.734	4	0.00	607.95
	100 m^2	1.00	0.00	0.00	0.0–0.0	68.285	4	0.00	731.18
	1000 m^2	1.00	0.00	0.00	0.0–0.0	57.518	4	0.00	414.56
	SEM	0.87	0.11	0.19	0.11–0.27	138.51	10	0.00	101.08
FL longleaf	1 m^2	0.00	0.00	0.00	0.0–0.0	80.461	4	0.00	1195.02
	10 m^2	1.00	0.00	0.00	0.0–0.0	83.75	4	0.00	1404.92
	100 m^2	1.00	0.00	0.00	0.0–0.0	107.453	4	0.00	1609.93
	1000 m^2	1.00	0.00	0.00	0.0–0.0	106.528	4	0.00	848.40
	SEM	0.82	0.11	0.17	0.13–0.21	259.49	14	0.00	368.75
Mountain	1 m^2	1.00	0.00	0.00	0.0–0.0	193.38	4	0.00	2299.71
	10 m^2	1.00	0.00	0.00	0.0–0.0	229.064	5	0.00	649.65
	100 m^2	1.00	0.00	0.00	0.0–0.0	314.19	5	0.00	3734.31
	1000 m^2	1.00	0.00	0.00	0.0–0.0	289.88	4	0.00	1446.17
	SEM	0.94	0.04	0.16	0.13–0.19	1153.43	15	0.00	1818.53

Models are organized by region and scale: Atlantic Coastal Plain (ACP) longleaf-pine woodlands, Sandhills longleaf pine, Florida longleaf pine, and southern Appalachian mountain forests (Mountain). The comparative fit index (CFI), standardized root mean square residuals (SRMR), and the root mean square error of approximation (RMSEA), 90 % confidence interval for the RMSEA (90 % CI), chi-squared value, degrees of freedom (df), p value (p), and Akaike information criterion (AIC) are presented. The path models for each region had excellent fit based on CFI, SRMR, and RMSEA, with the exception of the 1 m^2 scale Atlantic Coastal Plain model, which had a marginal fit. SEM models in each region had marginally acceptable fit values

Path models predicting diversity using the strongest soil indicators for the 10, 100, and 1000 m^2 scales (Table 1) had excellent model fit based on standardized root mean square residuals (SRMR), the comparative fit index (CFI), and the Root Mean Square Error of Approximation (RMSEA) (Table 5). The chi-squared values ($p = 0.000$) suggest a poor model fit to the covariance data, but this fit value is influenced heavily by the relatively large sample size. The one exception to the excellent path-model fit values was the 1 m^2 path model for Atlantic Coastal Plain longleaf pine, which had a poor to marginal fit (see Table 5). Although the model fit is not ideal, the 1 m^2 Atlantic Coastal Plain longleaf-pine path model has patterns similar to those of models at coarser scales, with nitrogen, sulfur, and iron as strong indicators of diversity.

The path models indicated that nitrogen, sulfur, iron, and pH are the best indicators of diversity at all scales in Atlantic Coastal Plain longleaf-pine communities, while sand is important at the 1 m^2 scale and organic matter at the 1000 m^2 scale (Fig. 3). In the Sandhill longleaf-pine path models, manganese and silt were strong predictors of diversity across all scales, and pH and nitrogen became more

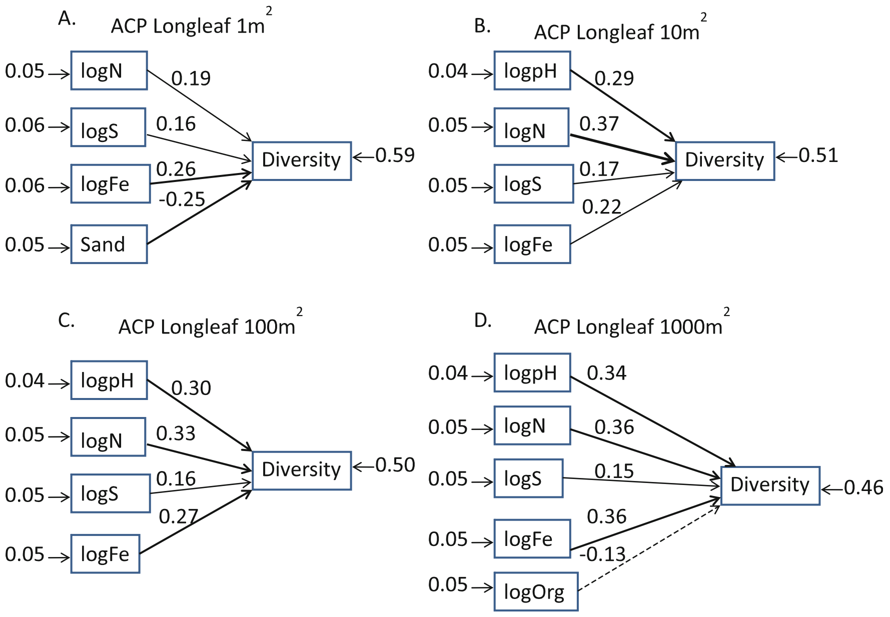

Fig. 3 Path models of Atlantic Coastal Plain longleaf-pinediversity and soil nutrients at the 1, 10, 100, and 1000 m^2 scales. The paths show standardized model estimates. The direction of the *arrow* represents the direction of the regression, with x, or observed variables, pointing to y variables on the *right*. The strength of the relationship is represented by the weight of the *arrow*. *Solid lines* are significant at the $p < 0.005$ level; *dashed lines* are significant at $p < 0.10$. In Atlantic Coastal Plain longleaf-pine communities, sulfur and iron were significant at all scales. At the three coarser scales, *p*H and nitrogen have significant loadings

important at the 1 and 10 m^2 scales (Fig. 4). Florida longleaf-pine diversity is best predicted by pH, iron, manganese, and silt across all scales (Fig. 5). The predictability of diversity decreased with increasingly finer scale in Atlantic Coastal Plain and Florida longleaf-pine (Figs. 3 and 5), but the Sandhill longleaf-pine path models showed the opposite relationship, with increasing predictability at increasingly finer scale (Fig. 4).

The refined conceptual model (Fig. 2) was supported when measures of soil texture would not load on the same latent variable as soil nutrients. Therefore, silt (and sand in the Florida longleaf pine) was modeled with a separate influence on diversity. Confirmatory factor analysis with soil nutrients as a latent variable and separate measured variables for soil texture produced an adequate fit. This base model was used to build an initial structural equation model based on soil nutrients, texture, and diversity.

The structural equation models for longleaf pine had moderate fit values (Table 5, longleaf pine SEM). In the Atlantic Coastal Plain, diversity in longleaf stands was modeled with soil nutrients having a stronger effect on diversity than silt. Iron, organic matter, pH, sulfur and nitrogen were all strong predictors of soil

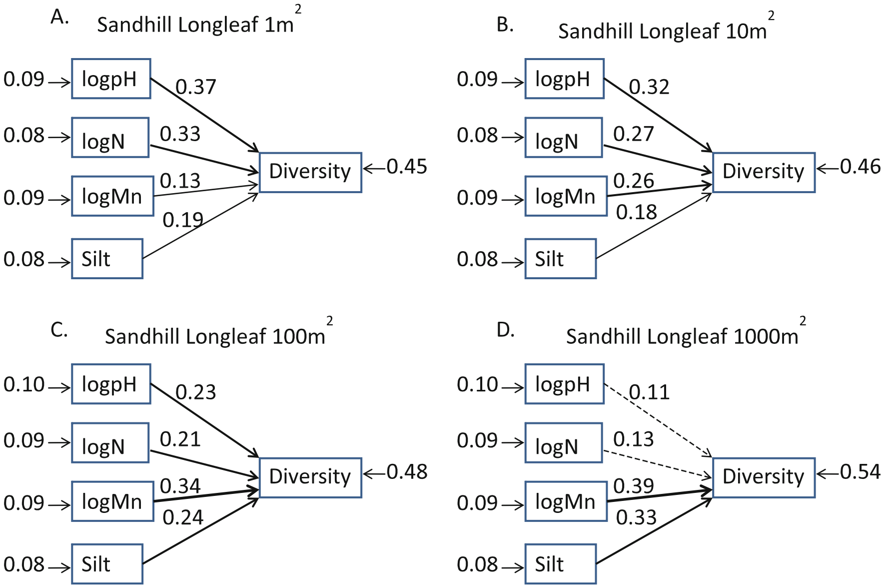

Fig. 4 Path models of diversity in longleaf-pine stands in the Sandhills of North and South Carolina and soil nutrients at the 1, 10, 100, and 1000 m^2 scales. The paths show standardized model estimates. The direction of the *arrow* represents the direction of the regression. The strength of the relationship is represented by the weight of the *arrow*. *Solid lines* are significant at the $p < 0.05$ level; *dashed lines* are significant at $p < 0.30$. In Sandhill longleaf-pine communities, *p*H, nitrogen, manganese, and silt have significant loadings at all scales. However, at the 1000 m^2 scale, soil *p*H and nitrogen were not significant

nutrients (Fig. 6). In the Sandhills, soil nutrients and silt also had strong positive loadings on diversity, but the influence of silt was stronger. Manganese, nitrogen, and pH were the best indicators of soil nutrients (Fig. 7). Diversity in Florida longleaf stands was also influenced positively by silt and soil nutrients. Sand was a very weak indicator of diversity in this model, and iron, calcium, manganese, and phosphorous were important predictors of soil nutrients (Fig. 8).

Southern Appalachian Mountain Vegetation

The strongest soil correlates of diversity for the mountain plots are summarized in Table 1. The mountain data demonstrate that pH, manganese, and calcium are strong correlates of diversity, regardless of the scale of observation, and soil texture has only a weak correlation with diversity at any given scale (Table 6). Soil cation exchange capacity (CEC) is also an important correlate at the finer scales. At the 1000 m^2 scale, iron, and sulfur were the other notable correlates.

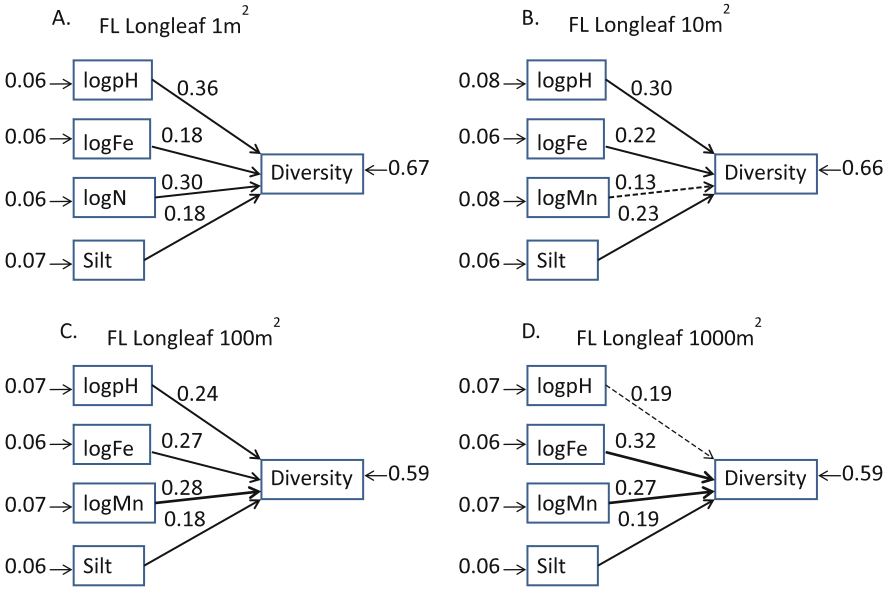

Fig. 5 Path models of Floridalongleaf-pine communitydiversity and soil nutrients at the 1, 10, 100, and 1000 m^2 scales, showing standardized model estimates. The direction of the *arrow* represents the direction of the regression. The strength of the relationship is represented by the weight of the *arrow*. *Solid lines* are significant at the $p < 0.005$ level; *dashed lines* are significant at $p < 0.10$. In Florida longleaf-pine communities, silt, *p*H, and iron have significant loadings at all scales. Nitrogen is a significant measured variable at the 1 m^2 scale, and manganese is significant at the three coarser scales

Path models using the strongest correlates of diversity (Table 1) generated models with good fit values. Both iron and calcium had insignificant or very small factor loadings at several scales. The final path models (Fig. 9) have excellent model fit values based on CFI, SRMR, and RMSEA (Table 5). The path models suggest that manganese, calcium, and pH are the strongest indicators of diversity at the 1 m^2 scale. At the full-plot scale, manganese and pH were the best measures for predicting diversity (Fig. 9).

Confirmatory factor analysis using the single-latent-variable model (Fig. 1) failed to converge. However, confirmatory factor analysis with pH as an independent indicator and the other nutrients loading onto a latent variable showed an adequate fit. This model was then used as the basis of a structural equation model for soil nutrients, pH, and diversity (Fig. 10). The mountain structural equation model has a moderate model fit (Table 5, Mountain SEM), accounting for 39 % of the variation in diversity (Fig. 10). Soil pH loads positively onto diversity, but it is a strong negative indicator for soil minerals. Soil minerals influence diversity negatively, driven by strong negative indicators (pH, Ca, Mn).

Within-plot variance was calculated for all plots with four soil samples (Table 7). Soil organic matter, cation exchange capacity, calcium, sulfur, magnesium, and

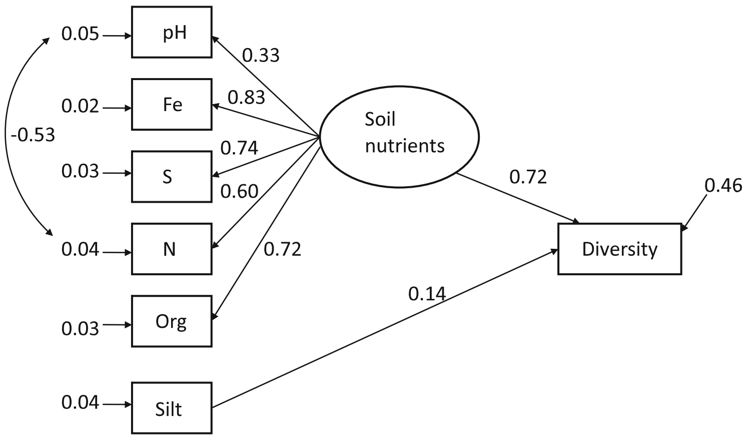

Fig. 6 Structural equation model for Atlantic Coastal Plain longleaf-pine diversity and soil nutrients (1000 m^2 scale). The direction of the *arrows* from the latent variable (Soil nutrients) indicates that this construct is determining the measured values in the field. All other *arrows* represent the direction of the regression and influence on other variables. *Short arrows* into the measured variables indicate the measurement error. All loadings are standardized and significant at $p < 0.001$. Iron, sulfur, and organic matter were the strongest indicators of soil nutrients. Silt had a separate affect on diversity. Soil nutrients had a greater influence on diversity than silt. The model explained 54 % of the variance in diversity

manganese have variances that are, on average, an order of magnitude larger in the mountains than in the longleaf-pine plots. The variances of soil pH and base saturation were the soil variables with the most similar level of within-plot variance across all regions.

Discussion

The path models indicate that there are consistent indicators of diversity across scale in both the mountain forests and longleaf-pine woodlands. The path models of soil and diversity illustrate that soil nutrient indicators differ across scale within 1000 m^2 nested plots, but only slightly. In the mountains, sulfur was important at the intermediate scales (10, 100 m^2). In the Atlantic Coastal Plain pine systems, nitrogen was a strong predictor only at the 1 m^2 scale, and pH became insignificant at this finer scale. It was also difficult to fit a path model with an adequate model fit at the finest scale (1 m^2). This variation in indicators at the 1 m^2 scale is probably

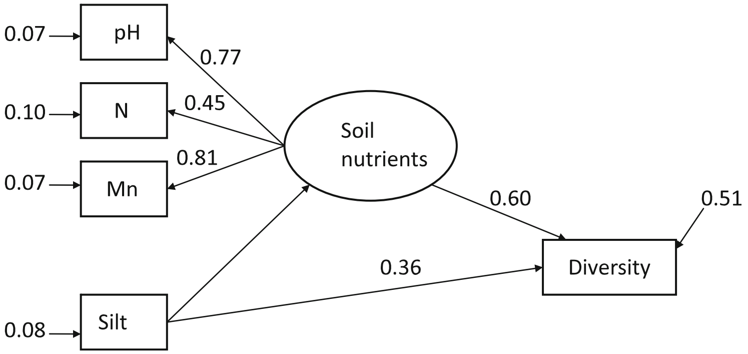

Fig. 7 Structural equation model for diversity and soil nutrients in longleaf-pine communities in the Sandhills of the Carolinas (1000 m^2 scale). The direction of the *arrows* from the latent variable (Soil nutrients) indicates that this construct is determining the measured values in the field. All other *arrows* represent the direction of the regression and influence on other variables. *Short arrows* into the measured variables indicate the measurement error. All loadings are standardized and significant at $p < 0.001$. Manganese and soil pH were the strongest indicators of soil nutrients. Silt had a separate effect on diversity, which was roughly half the influence of Soil nutrients on diversity. The model explained 49 % of the variance in diversity

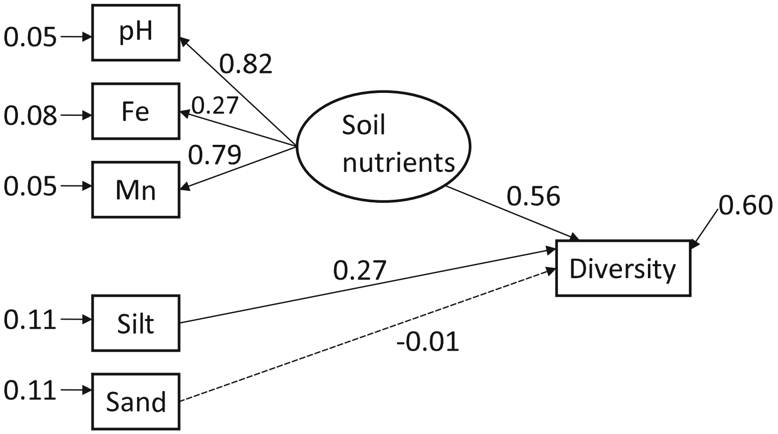

Fig. 8 Structural equation model for diversity and soil nutrients in Florida longleaf-pine communities (1000 m^2 scale). The direction of the *arrows* from the latent variable (Soil nutrients) indicates that this construct is determining the measured values in the field. All other *arrows* represent the direction of the regression and influence on other variables. *Short arrows* into the measured variables indicate the measurement error. All loadings are standardized and significant at $p < 0.001$, except for the *dotted line*, which is significant at $p < 0.9$. Manganese and soil *p*H were the strongest indicators of soil nutrients. Silt and sand had separate effects on diversity; however the loading for sand was both insignificant ($p < 0.9$) and a small number. The model explained 40 % of the variance in diversity

Table 6 Correlations between plant species richness across six scales and soil nutrients in southern Appalachian Mountain communities

Mountain	0.01 m^2	0.1 m^2	1 m^2	10 m^2	100 m^2	1000 m^2	logCEC	logpH	logOrg	logN	logS	logP	logCa	logFe	logMn	Clay	Silt	Sand
0.01 m^2	1.00																	
0.1 m^2	0.86	1.00																
1 m^2	0.66	0.87	1.00															
10 m^2	0.48	0.71	0.92	1.00														
100 m^2	0.37	0.60	0.83	0.95	1.00													
1000 m^2	0.33	0.54	0.75	0.88	0.96	1.00												
logCEC	**0.24**	**0.24**	**0.24**	0.21	0.19	0.17	1.00											
logpH	**0.25**	**0.36**	**0.46**	**0.51**	**0.55**	**0.54**	0.22	1.00										
logOrg	0.00	−0.04	−0.08	−0.13	−0.19	−0.22	0.34	−0.44	1.00									
logN	0.05	0.07	0.07	0.02	−0.04	−0.09	0.17	−0.31	0.81	1.00								
logS	−0.12	−0.18	−0.22	**−0.23**	**−0.24**	**−0.25**	0.24	−0.26	0.20	0.07	1.00							
logP	−0.09	−0.13	−0.17	−0.16	−0.15	−0.12	0.41	−0.19	0.21	−0.06	0.50	1.00						
logCa	**0.28**	**0.35**	**0.40**	**0.41**	**0.41**	**0.39**	0.86	0.55	0.13	0.08	−0.08	0.28	1.00					
logFe	−0.01	−0.14	**−0.26**	**−0.32**	**−0.35**	**−0.34**	−0.12	−0.53	0.09	0.09	0.35	0.05	−0.38	1.00				
logMn	**0.23**	**0.34**	**0.45**	**0.51**	**0.52**	**0.52**	0.40	0.50	0.00	0.13	0.02	0.16	0.57	−0.29	1.00			
Clay	−0.13	−0.11	−0.06	−0.03	−0.02	−0.05	−0.31	0.00	−0.24	−0.05	−0.01	−0.22	−0.25	0.06	0.00	1.00		
Silt	−0.20	−0.21	−0.21	−0.20	−0.21	−0.22	−0.05	−0.35	0.33	0.27	0.21	0.12	−0.17	0.14	0.01	0.18	1.00	
Sand	0.22	0.22	0.21	0.19	0.20	0.21	0.13	0.32	−0.22	−0.23	−0.19	−0.04	0.23	−0.15	−0.01	−0.47	−0.95	1.00

Correlations greater than 0.23 are in bold (see first 7 columns). Both manganese and calcium are strong correlates across all scales. Soil pH and iron are strong correlates across several scales. Cation exchange capacity and sulfur are strongly correlated at some scales

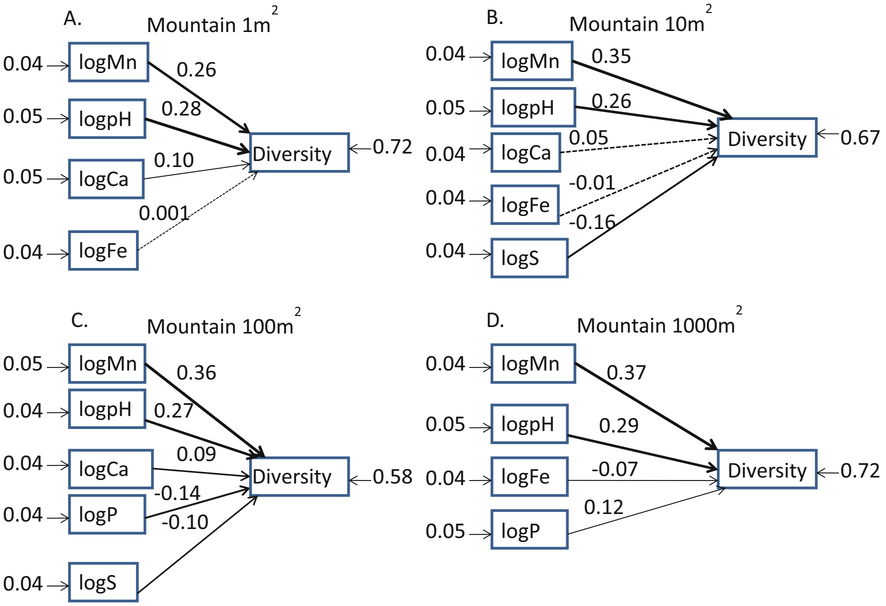

Fig. 9 Path models of southern Appalachian Mountain community soil nutrients and diversity at the 1 m^2, 10 m^2, 100 m^2, and 1000 m^2 scales showing standardized model estimates. The direction of the *arrow* represents the direction of the regression. The strength of the relationship is represented by the weight of the *arrow*. *Solid lines* are significant at the $p < 0.001$ level; *dashed lines* are for loadings with $p < 0.1$. In mountain communities, Manganese and pH are the strongest indicators for diversity at all scales

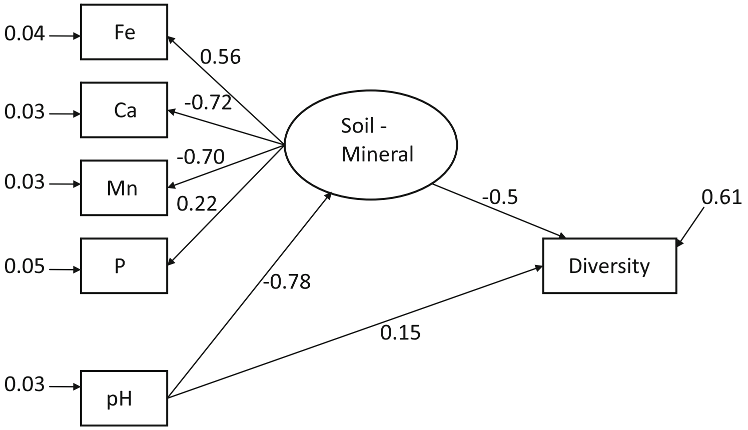

Fig. 10 Structural equation model for diversity and soil nutrients in southern Appalachian Mountain communities (1000 m^2 scale). The direction of the *arrows* from the latent variable (Soil nutrients) indicates that this construct is determining the measured values in the field. All other *arrows* represent the direction of the regression and influence on other variables. *Short arrows* into the measured variables indicate the measurement error. All loadings are standardized and significant at $p < 0.001$. Manganese, calcium and iron were the strongest indicators of soil nutrients. Soil pH had a separate effect on diversity. The model explained 39 % of the variance in diversity

Table 7 Average within-plot variance of soil characteristics by region

Region	Organic	soilPH	CEC	BaseSat	S	P	Ca_ppm	Mg_ppm	K_ppm	Na_ppm
ACP longleaf	4.73	0.08	6.10	33.34	24.50	192.36	27851.49	308.86	133.10	66.99
SH longleaf	5.00	0.05	1.71	25.48	27.83	7.13	7628.92	141.20	81.47	3.78
FL longleaf	5.28	0.06	3.52	35.42	13.68	181.17	29015.19	298.08	49.15	153.42
Mountain	79.42	0.08	18.47	39.03	106.32	77.83	121685.68	3161.65	782.07	8.59
Region	**%Ca**	**%Mg**	**%K**	**%Na**	**%Other**	**Fe_ppm**	**Mn_ppm**			
ACP longleaf	29.30	2.09	0.42	0.61	0.29	1765.20	35.60			
SH longleaf	20.74	2.35	0.38	0.15	0.20	1485.51	352.72			
FL longleaf	31.41	3.57	0.49	1.05	0.22	1824.24	201.82			
Mountain	33.47	6.03	1.32	0.20	0.29	3330.06	1463.71			

This table depicts the variance in soil characteristics within Atlantic Coastal Plain longleaf-pine plots (ACP longleaf), longleaf pine in the Sandhills of the Carolinas (SH longleaf), Florida longleaf pine (FL longleaf), and southern Appalachian Mountains (Mountain) plots. Soil characteristics include organic matter (Organic), soil pH (soilPH), soil cation exchange capacity (CEC), base saturation (BaseSat), and nutrients in either parts per million (ppm) or percentages. The variance in organic matter, cation exchange capacity, sulfur, calcium (ppm), magnesium (ppm), and manganese (ppm) are an order of magnitude larger in the mountains than in each of the longleaf regions. The variances of soil pH, and base saturation, were the variables with the most similar level of within-plot variance across all regions due to the lack of nesting of the soil samples at this finer scale, which is consistent with the results that the models using 0.1 and 0.01 m^2 measures of richness had poor fit or did not converge. However, in the longleaf-pine communities, this may also be due to fine-scale variation in soil nutrients and plant mortality caused by frequent fire. Fire is inherently patchy, resulting in fine-scale variation in intensity and nutrient availability across the landscape from place to place and year to year. Binkley et al. (1992) pointed out the high level of variability in mineral soils in longleaf-pine systems and called for more precise soil measurements within plots. In addition, our data lack a good indicator of soil moisture, but iron, organic matter and nitrogen may track the moisture gradient collectively (Peet et al. 2014).

As anticipated, texture was significant consistently across scales in the longleaf systems. Silt was a strong indicator at most scales. Clay was a weak indicator across all scales and systems, perhaps because few longleaf sites have soils with high clay content, thereby reducing the range of variation. Silt has been used previously to classify longleaf-pine communities (Peet 2006; FGDC 2013), suggesting that it is important in these systems. Silt and sand also had inverse relationships with species richness, with sand negatively correlated with diversity and silt positively related to diversity. When modeling species diversity in longleaf-pine woodlands, the conceptual model with separate texture and nutrient variables (Fig. 2) was more effective at capturing the relationship than was a simple soil-characteristics model (Fig. 1). Subsequent work analyzing herbaceous diversity in longleaf systems indicated that principle component analysis axes of environmental variables corresponding to soil moisture and soil texture are important in determining richness of the herbaceous layer (Peet et al. 2014). The key variables loading on these axes were bulk density, sulfur, organic matter aluminum, iron, clay, sand, and silt. With the exception of bulk density and the inclusion of only silt and/or sand as a proxy for soil texture, these variables were all key indicators in at least one of the longleaf structural equation models. However, the structural equation models produced here indicate that the soil variables that predict diversity most closely vary with the specific physiographic regions of longleaf pine.

The results from the mountain models match our expectations. Manganese, pH and calcium were consistently strong predictors, as observed by Peet et al. (2003) and Newell and Peet (1998). This also matches closely the results of the principle components analysis for the herbaceous species richness in southern Appalachian forests by Peet et al. (2014), in which base cation availability, including soil pH, cation exchange capacity, calcium, magnesium, and manganese, was the primary correlate of diversity. Texture does not seem to be an important indicator of diversity in this region. Because the variance of calcium and cation exchange capacity within plots in the mountains was higher than in the longleaf-pine plots (Table 7), the higher within-plot variation in calcium is probably adding to the importance of these variables in the mountains.

The initial soil structural equation models predict diversity well in both the longleaf-pine and mountain communities. Soil nutrients, modeled by calcium, manganese, iron, and phosphorous, along with pH, are the key predictors of diversity in mountain communities. A similar model is effective in all longleaf-pine communities: both soil nutrients and silt influenced diversity positively. Soil pH is a key indicator in both longleaf-pine communities and the southern Appalachian Mountains. Silt modeled the influence of soil texture effectively across all longleaf pine regions. However, a more detailed examination of the soil nutrient variation within plots, including fully nested soil samples, would add to our understanding of the influence of soil on diversity and the effect of scale of observation.

The structural equation models for both longleaf-pine and mountain communities suggest that this modeling approach and conceptual model could be applied effectively to other regions in order to further understanding of the influence of soil attributes on diversity. Specifically, this methodology could be applied: (1) to generate and test theoretical models of how soil attributes influence diversity and whether those impacts are direct or indirect; and (2) to confirm regional or community classifications that are based in part on soil attributes.

These findings demonstrate that soil characteristics vary closely with plant species richness. Further study of the within-plot variation in soil nutrients and texture would add to our understanding of how particular soil characteristics influence diversity. Manganese is a particularly strong but unexplained predictor and may be a surrogate for soil weathering or for phosphorous availability. In Atlantic Coastal Plain longleaf-pine communities, it is likely that iron and sulfur function as surrogates for water availability. Future research should focus on why these variables are meaningful and how soil nutrient availability influences diversity.

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Part V
Applied Vegetation Science

Fallopia japonica (Japanese Knotweed) in Japan: Why Is It Not a Pest for Japanese People?

Michiko Shimoda and Norifumi Yamasaki

Abstract *Fallopia japonica* is native to Japan, Taiwan and Korea. It is now widely naturalized in Europe and North America, and is regarded as one of the worst invasive alien species. For Japanese people, *F. japonica* has been one of the most familiar and useful wild plants for centuries. It is rare to regard the plant as a harmful weed in Japan. *Fallopia japonica* has many ethnobotanical uses as an edible and medicinal plant. Therefore it was recorded in many historical documents, by different names. A dictionary of local plant names recorded 689 words for *F. japonica*, and it was the plant with the most names among all plants listed. As a case study of *F. japonica*, we conducted surveys on its habitats and growth from the foot to the alpine belt of Mt. Fuji, the highest mountain in Japan. *Fallopia japonica* was found widely in man-made and natural habitats but was restricted to open, sunny sites. The plant was smaller in the habitats where the vegetation is cut repeatedly. Japanese phytosociological studies regarded *F. japonica* as the character species of an Artemisietea principis and as a constituent species of diverse herbaceous, shrub and open woodland communities. In Japan, vegetation is controlled by cutting or mowing near habitations and other infrastructure. In meadows, tall grasses dominate the vegetation. In mountainous areas, trees are dominant and open areas are limited. It is difficult for *F. japonica* to overgrow a wide area and to form a large stand. In addition, the plant has been regarded as useful plant. These matters seem to make *F. japonica* a common and familiar plant, not a pest, for Japanese people.

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Introduction

Japanese knotweed, *Fallopia japonica* (Houtt.) Ronse Decr. (synonyms: *Reynoutria japonica* Houtt., *Polygonum cuspidatum* Siebold et Zucc.) is a large rhizomatous perennial herb native to Japan, Taiwan and South Korea (Iwatsuki et al. 2006). It was introduced to Europe and North America as an ornamental in the nineteenth century and is widely naturalized in both areas (e.g., Beerling et al. 1994; Barney et al. 2006). It is now listed in "100 of the world's worst invasive alien species" (Lowe et al. 2000).

In Japan, *F. japonica* occurs widely from Hokkaido (the northernmost main island) to Kyushu (the southernmost main island). It is a very common plant from lowlands to alpine areas and from natural habitats to man-made habitats close to residential and cultivated lands. Studies of volcanic vegetation recorded it as a constituent species of plant communities in primary succession (Yoshioka 1974; Uto and Suzuki 2002; Hattori et al. 2012). *Fallopia japonica* and *Miscanthus sinensis* occur together with high frequency on the lava flows of Mt. Sakurajima on Kyushu Island. It also grows at the solfataras of Mt. Hakone, in central Honshu, where soil pH values are 3.6–3.8 (Yoshioka 1974).

Fallopia japonica was also recorded as a constituent species of grasslandvegetation. *Miscanthus sinensis*-type grassland is a mowngrassland and the most representative of tall grassland types in Japan. Numata (1974) showed the floristic composition of *Miscanthus* grassland in Miyagi Prefecture (northern Honshu) as an example of Japanese grassland vegetation (Numata 1974, Table 4). The stand was dominated by *M. sinensis* and composed of 26 species, including *F. japonica*.

Ito et al. (1982) listed *F. japonica* as one of the troublesome, dominant weeds of railroad right-of-ways. Nashiki et al. (1986) regarded it as one of the noxious weeds of pastures. On the contrary, it has been well known as a wild plant edible in spring. Therefore, it is generally rare for Japanese people to regard *F. japonica* as a harmful weed.

In this paper, we introduce the relationship between *F. japonica* and the Japanese people from an ethnobotanical point of view. Next, we show the habitats and growth of *F. japonica* on Mt. Fuji, from its base to the timber line. Finally we show the vegetation in which *F. japonica* occurs, as described by phytosociological studies. Based on these results, we discuss why *F. japonica* has not been a pest for the Japanese people.

Relationship Between Japanese People and *Fallopia japonica:* Viewed Ethnobotanically

Fallopia japonica was recorded in numerous historical documents under various names. The descriptions are valuable and interesting for us in order to know how people understood and used the plant in old days. Diverse local names of

F. japonica also show how aptly the local people expressed its characteristics and habitats. This section introduces local names and descriptions of *F. japonica* in historical documents of the eighth–nineteenth centuries.

Fallopia japonica in Old Documents: From the Eighth to the Tenth Centuries

Fallopia japonica has been one of the most familiar and useful wild plants for the Japanese people for centuries. This section introduces three examples from the eighth to the tenth centuries.

The first example is from the *Nihon Shoki* (Chronicles of Japan), which is Japan's old history book of the eighth century. It consists of 30 volumes and was submitted to the Imperial court in 720. Volume 12 of this book includes a short story of Emperor Mizuhawake as follows. "At his birth, his appearance was beautiful. There was a well from which water was drawn to wash the crown prince. A flower of "tajihi" (*F. japonica)* had fallen into this well and it was accordingly made the name of the prince. The tajihi flower is now the "itadori" flower. Therefore he was styled the Emperor Tajihi-no Mizuhawake." This story shows that the name "tajihi" was older than the name "itadori", which is the common Japanese name of *F. japonica* today.

The second example is from the *Engi Shiki* (Regulations and Laws of the Engi era). It is a 50-volume work and a management manual of the Imperial Court, compiled in 927. Its volume 39 includes a description for the office of emperor's meals. It listed *F. japonica* as one of the edible spring plants and described how to preserve it with salt: 54 l of *F. japonica* with 2.16 l of salt.

The third example is from the *Makura-no Sōshi* (The pillow book), which is a famous essay recorded by a court lady named Sei Shonagon in the 990s. She listed several things for which written names are exaggerated from the real things. She listed "itadori" (*F. japonica*) as the typical example, mentioning that the name of *F. japonica* in Chinese letters was much more spectacular than the plant itself, because its Chinese letters mean 'tiger stick'.

These three examples were recorded more than 1000 years ago and were written for people of high standing, including the Imperial Family. These records suggest that *F. japonica* was known widely by the Japanese people as a familiar plant since very old days.

Fallopia japonica in Records of the Edo Era (1603–1867)

In the Edo era, *F. japonica* was described in many records, including encyclopedias and plant dictionaries. The records include information about traditional uses of plants.

Wakan Sansai Zue (Illustrated Japanese-Chinese Encyclopedia) is an encyclopedia compiled by Ryoan Terajima, published in 1712 and consisting of 105 volumes. It includes descriptions and illustrations of many plants and animals. *Fallopia japonica* was described in volume 94 (Shimada et al. 1991), which stated that the plant grows in fields and grasslands. The description includes *Fallopia*'s life cycle and shape. It said that the plant flowers in August and fruits in October, but some *Fallopia* plants do not bear fruit. The book also described *Fallopia*'s medical uses and quoted the descriptions from the *Nihon Shoki* and *Makura-no Sōshi*, which were mentioned above.

Honzō Kōmoku Keimō (Notes on Japanese Plants) by Ranzan Ono consists of 48 volumes, published in 1803 and revised in 1847. Its description of *F. japonica* is similar to that of *Wakan Sansai Zue* (1712) but in addition to the plant's shape also gives three old names and 10 local names of the plant (Ono 1991).

Honzō Zufu (Illustrations of Japanese Plants) by Kanen Iwasaki was published in the first half of the nineteenth century and consists of 96 volumes. *Fallopia japonica* was shown in volume 20 with an illustration and a brief description (Fig. 1). The first (right) line shows *Fallopia*'s Chinese letters (tiger stick) and their pronunciation (kojō). The second and third lines show another name, saitatsuma. The six following lines, in smaller letters, are the plant description, as follows. "It is also called itatori, grows in the wilderness, and emerges from old roots in spring. The young stems have joints like bamboo sprouts, are cooked and eaten. Little children eat them raw, and they taste sour. Leaves resemble those of *F. multiflora*, lower surfaces are not purple. In autumn stems are about 1.2–1.5 m high; it bears short inflorescences between the leaves, produces small white flowers, and later bears small fruit, which also resemble those of *F. multiflora*."

Fallopia japonica and Local People in the Edo Era

The three documents mentioned above were authoritative books nationwide. *Fallopia japonica* was also recorded in local documents in the Edo era.

Geibi Dosan Zufu (Illustrations of the Products of Geibi) recorded the products of the Geibi area in western Japan near Hiroshima. The document is owned by the Graduate School of Letters of Hiroshima University and is thought to be a copy of the product report submitted by the Hiroshima Domain to the government in 1737. It includes illustrations and explanations of 74 plants and 45 animals, including *F. japonica* (Fig. 2). The plant was called 'tajina' in the explanation, and its description said, "It sprouts in February and March (March and April according to the present calendar), leaves and stems die in autumn and winter, it does not bear flower nor fruit. I do not hear that the plant is used for food or medicinal purposes." This description reveals that the writer's knowledge of the plant was limited. The description may suggest that *F. japonica* without flowers was familiar to the local people because the plant grew often in frequently mown habitats.

The first author joined the compilation of the "History of Kurose Town", of Higashi-Hiroshima City (Fig. 3), in 2000–2008. As an example of more local

Fig. 1 *Fallopia japonica* in *Honzō Zufu*. Courtesy of the National Diet Library

documents, we will show the documents of the Edo era found in Kurose Town. Figure 4 shows the documents of 1780–1829, which recorded the products of 18 villages for the local government. *Fallopia japonica* was listed as an edible plant in Kanesawa village and as a wild herbaceous plant with beautiful flowers in Kanehiro village (Committee for Compilation of History of Kurose Town 2004). In Kurose we found four textbooks of flower arrangement from the nineteenth century (Shimoda 2006). These books include many pictures of diverse garden plants and wild plants as the material for flower arrangement. Figure 5 is a picture from one of the books. The materials are young shoots of *F. japonica* and *Calendula officinalis*, suggesting that *F. japonica* was one of the popular materials at that time.

Fig. 2 Illustration and explanation of *F. japonica* in *Geibi Dosan Zufu*. Courtesy of committee for compilation of history of Kurose Town

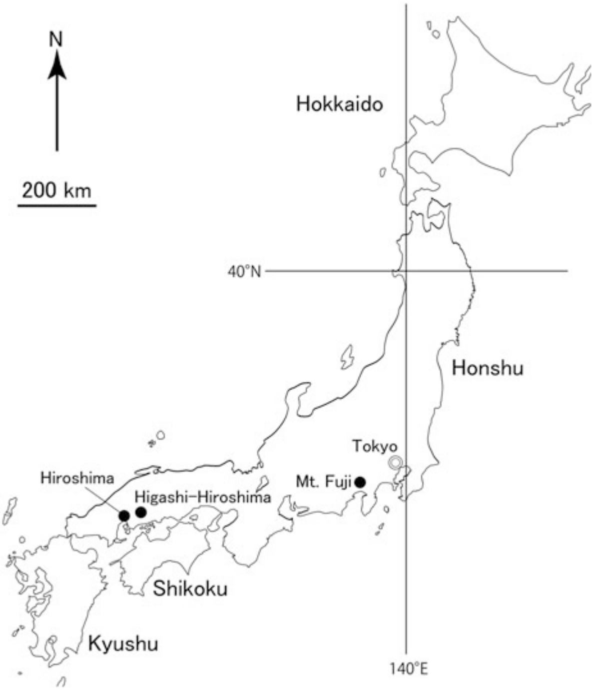


Fig. 3 Map of Japan and locations of main places mentioned in the text

Fig. 4 Documents in the Edo era found in Kurose Town, Higashi-Hiroshima City, western Japan. Courtesy of committee for compilation of history of Kurose Town

Documents of the Edo era, mentioned in this section, show that *F. japonica* was a well-known plant and regarded as a product of local areas. Probably the plant was known widely, not only by intellectuals but also by common people in rural areas.

Fallopia japonica Has Been a Useful Plant for Japanese People

As shown in the previous sections, *F. japonica* has many ethnobotanical uses. Kimura (1988) stated that *F. japonica* was used as food (young shoots), as a medicinal plant (rhizomes), as a substitute for tobacco (young leaves) and for dye. He also showed that the plant had been described as an emergency plant during famine in eight documents of the eighteenth–twentieth centuries and as one material for flower arrangement in seven documents of the fifteenth–twentieth

Fig. 5 A picture of flower arrangement in the nineteenth century. Chinese letters mean *F. japonica* and *Calendula officinalis*. Courtesy of committee for compilation of history of Kurose Town

centuries. Today the plant is still regarded as useful (e.g., Hotta et al. 1989; Shibata 2001). It is still a popular edible wild plant in spring and is always included in the books of edible wild plants. Its dried rhizomes have been used in traditional medicine. Books on medical plants show that its rhizomes are effective for excretion of urine, evacuation of the bowels, menstrual irregularity, coughing and as a sedative (e.g., Kimura and Kimura 1964; Mitsuhashi 1988).

For children, young stems used to be a snack, as for the children in the Edo era (Figs. 1 and 6a), and were a material for making water wheels (Fig. 6b). When the first author was a child, if she found a young *Fallopia* plant in the field, she snapped it and ate its stem like the girl in Fig. 6a. At present, however, children are not as interested in wild plants as in the past.

Fig. 6 *Fallopia japonica* has been a friend of children. (**a**) sour snack in the field, (**b**) water wheel

Numerous Local Names of *F. japonica*

The standard Japanese name of *F. japonica* today is *itadori*, but there are also numerous local names. For example, Watanabe (2001) recorded 128 local names in Hiroshima Prefecture and Umemoto (2002) recorded 45 names in Wakayama Prefecture, both in western Japan. A dictionary of local names of Japanese plants (Yasaka Shobo 2001) listed the names of ca. 2000 plants. The dictionary recorded 689 words for *F. japonica*, the most for any plant listed. The second most names belong to *Equisetum arvense* (654 names: 482 for fertile stem, 172 for sterile stem) and the third most are for *Lycoris radiata* (555 names). These three species are widespread, common, well-known plants found on roadsides and around cultivated fields and inhabited lands. Their numerous names suggest that local people have recognized and utilized these plants in many places.

As shown above, various old names of *F. japonica* were recorded in old documents. In *Honzō Kōmoku Keimō* (Notes on the Japanese Plants), published in 1803, *F. japonica* was described as “itadori” (Ono 1991), the standard name at present. In the book, in addition to ‘itadori’, three old names and 10 local names are listed. All of the 10 local names are included in the dictionary of local plant names

Table 1 Patterns of local names of *F. japonica* recorded in a dictionary of local plant names (Yasaka Shobo 2001)

Characteristics of *F. japonica* for its names	Number of names	Example of names
Shape	92	Like bamboo, tall plant, phallus
Snapping sound of young stem	85	Po, poko, pon, itan-po, tan-poko, kappon
Taste	68	Sour taste, sour plant, sour leaf
Taste and snapping sound	37	Sour + po (pon)
Shape and snapping sound	26	Bamboo + po (pon), standing stem + po
Taste and shape	22	Sour bamboo, sour tall plant
Habitat and shape	13	Mountain + *Fallopia*, river + *Fallopia*, river + bamboo, riverbed + bamboo
Shape, taste and sound	6	Bamboo + sour + po (pon)
Habitat and taste	3	Mountain + sour plant, river + sour plant
Edible herb	22	Green leaf, tall edible herb
Medicinal plant	5	Pain remover
Toy plant	2	Water wheel
Total number of names	381	

(Yasaka Shobo 2001), showing that local names of the nineteenth century are still being used in recent times.

Among the 689 collected names in the dictionary of local plant names (Yasaka Shobo 2001) we could understand the meanings of 381 names (Table 1). We could not know the meanings of nearly half of the names recorded because the names were highly local. The numerous names of *F. japonica* describe characteristics of the plant, such as shapes of matured stem and young shoot, snapping sound of young stem and sour taste. The names also refer to the plant's habitats, such as along rivers, in riverbeds and in mountains. There are also many combinations of taste, snapping sound and habitat (Table 1). The diverse names show that local people had abundant botanical and ecological knowledge of *F. japonica* for a long time.

Fallopia japonica of Mt. Fuji

Mount Fuji is the highest mountain in Japan, with an altitude of 3776 m (Fig. 7). *Fallopia japonica* occurs from the mouth of the Fuji River to about 2500 m on the mountain slope, which is the upper distributional limit of *F. japonica*. Its habitats are diverse, from natural to anthropogenic environments. Therefore Mt. Fuji is suitable for the ecological study of *F. japonica*.

There are many studies on the ecology of *F. japonica* as a primary colonizer of lava flows at higher altitudes of the alpine and subalpine areas of Mt. Fuji (e.g., Maruta 1976, 1983, 1994; Masuzawa and Suzuki 1991; Adachi et al. 1996; Minami

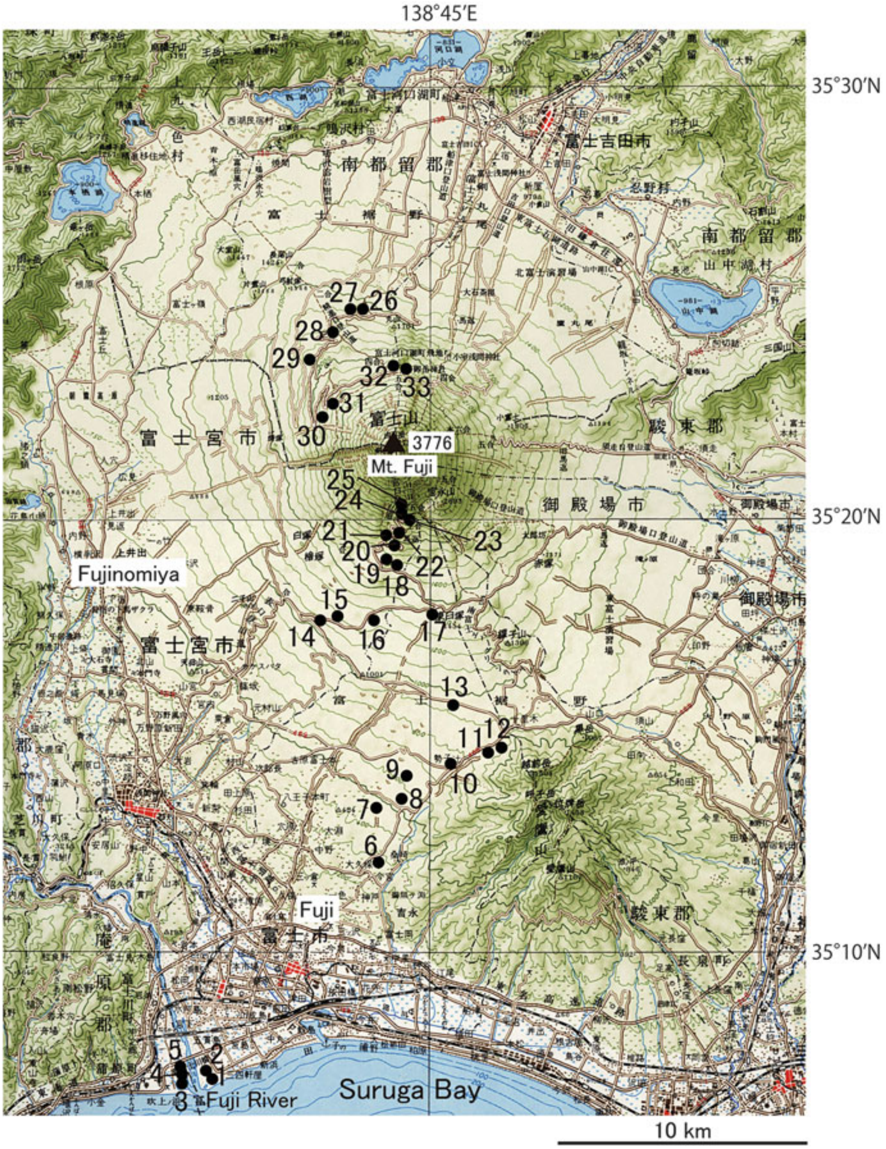


Fig. 7 Mount Fuji and study sites based on 1:200,000 topographic maps issued by the Geographical Survey Institute of Japan in 2005

and Watanabe 2007). Odaki et al. (1971) investigated the flora of artificially disturbed places above 1000 m and reported that *F. japonica* was the most widely occurring plant up to 2540 m. Although *F. japonica* has been best studied in Japan on high-altitude slopes of Mt. Fuji, there was little information on the plant growing in man-made habitats at lower altitudes. In this section, we describe the habitats and growth conditions of *F. japonica* at the base and on the slopes of Mt. Fuji, based on field research conducted in 2008.

Mount Fuji

Mount Fuji is a conical volcano located in central Japan (Figs. 3 and 7). It has erupted repeatedly in the past, and the last eruption took place in 1707, on the southeastern slope at 2500 m. The explosive eruption created three craters and formed a huge volcanic ash field on the eastern slope.

The vegetation of Mt. Fuji is a good example of the vertical distribution of vegetation (e.g., Ishizuka 1974). The natural vegetation of the hilly zone up to about 500 m is assumed to be warm-temperate evergreen forest, but most of the original forests in this area have been destroyed and transformed by anthropogenic disturbance. The montane belt, between about 500 and 1500 m, is dominated by cool-temperate deciduous forest. The subalpine belt, between about 1500 and 2500 m is characterized by evergreen coniferous forests, and the alpine belt extends upward from the forest limit. In general, the timberline on Mt. Fuji occurs at 2400–2500 m (Masuzawa and Suzuki 1991). Part of the southeastern slope is a volcanic desert covered by a scoria layer formed by the eruption of 1707.

Mount Fuji has long been revered as a sacred mountain. As it was known for the devout to climb it, several mountain trails were opened. The trails were equipped with quarters which acted as lodging for the devout climbers. Today Mt. Fuji is a famous tourist site, and many climbers, hikers and tourists visit the mountain and its surrounding area especially in summer. Paved roads reach up to 2000–2400 m on the mountain slopes.

Field Research

We conducted surveys on the habitats and growth of *F. japonica* on Mt. Fuji in September and October 2008, from the river mouth (2 m above sea level) to the volcanic desert (2415 m), mostly along paved roads on the southern and northern slopes (Fig. 7). There are 25 study sites on the southern slope and 8 sites on the northern slope. The study sites were covered with pure stands of *F. japonica* or stands dominated with *F. japonica*. We recorded the habitat environment and growth conditions of *F. japonica* and associated species of the stands. We measured the height of 10 stems of *F. japonica* at each study site, or all stems if there were fewer than 10.

Fig. 8 Man-made habitats of *F. japonica*. (**a**) site 6 at 278 m, (**b**) site 11 at 843 m, (**c**) site 18 at 1660 m, (**d**) site 32 at 2288 m. Site numbers are shown in Fig. 7. October 2008

Habitats and Stands of *F. japonica*

Fallopia japonica was found in various man-made habitats, such as road verges and parking lots, roadside embankments, forest edges and other disturbed ground (Fig. 8). It was also found in the Fuji River floodplain at its mouth and in the volcanic desert above timberline (Fig. 9).

Its habitats were on ground ranging from horizontal to slopes up to 32°. It grew in a wide range of soil types, including sand, gravel, rock and forest soil with litter. It grew on dry soil to slightly wet soil but was never found on waterlogged soil. All its habitats were restricted to open, sunny sites.

Fallopia japonica occurred mostly in pure stands (Fig. 8a) or nearly pure stands (Fig. 8c, d). Species often found with *F. japonica* were *Miscanthus sinensis* (Figs. 8b and 10), *Pueraria lobata* (Fig. 10) and several Compositae species, including *Artemisa princeps*, *Anaphalis margaritacea, Cirsium nipponicum* var. *incomptum* (Fig. 11), *Senecio nemorensis* and *Solidago altissima*. The plants grew densely in most of the stands. *Fallopia japonica* formed sparse stands only on the volcanic deserts at its upper distributional limit (Fig. 9). The shapes of the stands were varied, some long and narrow around forest margins and along roadsides, such as site 6, which was 19.7 m long and 3.3 m wide (Fig. 8a). Elliptic and round stands were also found, such as site 11 (Fig. 8b).

Figure 12 shows the altitude and the average height of *F. japonica* at each study site. Plant height was sometimes over 2 m at low altitude (2–12 m at sites 1–5 in Fig. 7). These stands were along an unpaved road in the floodplain and along a

Fig. 9 *Fallopia japonica* on volcanic desert at site 25 (2415 m). 9 October 2008

Fig. 10 *Fallopia japonica* growing on forest edge with *Miscanthus sinensis* and *Pueraria lobata* at site 7 (457 m). 16 October 2008

paved road near the river mouth. From 200 to 2000 m there was not a clear relationship between altitude and plant height, but the plant was shorter on roadsides and forest edges where the vegetation is cut repeatedly. For example, the average plant height was 63.8 cm at site 18 on the verge of a parking lot (Fig. 8c). The average plant height was up to 1 m above 2000 m. Plants on slopes above 2400 m (sites 24 and 25) are strictly protected and are never cut, but the plants were small, less than 50 cm high (Fig. 9). Our research shows that the plants were shorter at high altitude > 2000 m and that the frequency and time of cutting had a great effect on plant height at lower altitude < 2000 m.

Fig. 11 *Fallopia japonica* growing on the verge of parking lot with *Cirsium nipponicum* var. *incomptum* at site 20 (1989 m). 28 September 2008

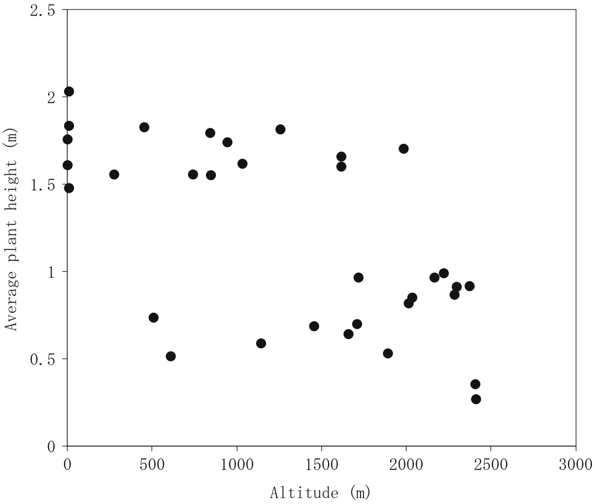


Fig. 12 The altitude and the average height of *F. japonica* at each study site of Fig. 7

Fallopia japonica as a Constituent of Plant Communities: Phytosociological Studies

In the previous sections we showed that *F. japonica* grows in diverse habitats and that it has been a plant familiar to Japanese people since old days. Finally, we will show in which vegetation *F. japonica* grows, based on phytosociological studies.

Fallopia japonica in the Vegetation of Mt. Fuji

Miyawaki (1971), Okutomi and Matsuzaki (1974), Miyawaki and Murakami (1982, 1987) and Miyawaki et al. (1984) conducted phytosociological studies on the vegetation of Mt. Fuji and described numerous plant communities. Table 2 shows the associations and communities from the above-mentioned studies that include *F. japonica* as a constituent species.

Miyawaki (1971) studied the vegetation at elevations above 800 m and reported the natural and anthropogenic vegetation in detail. *Fallopia japonica* was recorded in the sparse herbaceous vegetation of the volcanic desert and in open tree and shrub vegetation on lava flows. It was also recorded in the anthropogenic vegetation, including *Miscanthus* grassland and forest edge communities. *Fallopia japonica* was not recorded in the evergreen coniferous forest or the deciduous broad-leaved forests, which have dark conditions on the forest floor.

Okutomi and Matsuzaki (1974) and Miyawaki et al. (1984) reported the vegetation of Fuji City, on the southern slope and at the foot of Mt. Fuji. Miyawaki and Murakami (1982, 1987) reported the vegetation of Fujinomiya City, on the western slope and at the foot of Mt. Fuji. In these four studies the plant communities with *F. japonica* were herbaceous or shrub communities found on forest edges, in grasslands, on roadside slopes and embankments, on deforested areas, on abandoned fields and on riversides. Most of these communities occurred up to 1500 m and were affected by various human influences.

Relevés with cover-abundance values of *F. japonica* more than two (>25 % cover) involved only three plant communities: the Arabido-Polygonetum weyrichii alpinae and Cirsio-Campanuletum hondoensis on the volcanic desert and a *Senecio nemorensis*-*Artemisia montana* community on roadside forest edges (Table 2). The most common cover-abundance entry in the relevés listed in Table 2 was "+" (present but with very small total cover).

According to the phytosociological studies of Mt. Fuji, the plant communities with *F. japonica* occur over wide ranges of altitude and habitat type. Abundant growth of *F. japonica* was limited, however, to the herbaceous communities of the volcanic desert and to roadside forest edges. These results were consistent with the distribution of *F. japonica* stands in our study.

Vegetation Units with *F. japonica*

In the phytosociological studies of Japanese vegetation there were numerous plant communities that include *F. japonica* as a constituent species. Okuda (1978), in his study of the river vegetation of Kantō (the area around Tokyo), regarded *F. japonica* as the character species of Artemisietalia principis and Artemisietea principis. Ohba and Sugawara (1982), in their study on the class, also regarded *F. japonica* as the character species of Artemisietea principis.

Table 2 Plant communities of Mt. Fuji with *Falopia japonica*

Association and community with *F. japonica*	Class	Habitat	Altitude (m)	C-A[a]	Source
Natural vegetation					
Communities on volcanic ash and lava					
Arabido-Polygonetum weyrichii alpinae	–[b]	Volcanic ash	2000–3300	+-5	Miyawaki (1971)
Cirsio-Campanuletum hondoensis	–	Volcanic ash	1600–2880	+-4	Miyawaki (1971)
Saussureo-Betuletum ermanii	Betulo-Ranunculetea	Volcanic ash	2300–2600	+-1	Miyawaki (1971)
Rhodoreto-Betuletum platyphyllae	–	Lava	1500–1600	+-2	Miyawaki (1971)
Rhodoreto-Pinetum densiflorae	–	Lava	800–1200	+	Miyawaki (1971)
Riverside community					
Rumicetum crispo-japonici	–	Riverside	2–10	+-1	Miyawaki et al. (1984)
Anthropogenic vegetation					
Grassland communities					
Rosa wichuraina-Miscanthus sinensis community	–	*Miscanthus* Grassland	900–980	+	Miyawaki (1971)
Miscanthus sinensis-Galium verum v. *asiaticum* f. *nikkoense* community	–	*Miscanthus* Grassland	840–1330	+-2	Okutomi and Matsuzaki (1974)
Pueraria lobata-Miscanthus sinensis community	Miscanthetea sinensis	Abandoned field	340–400	+	Miyawaki and Murakami (1982)
Arundinello-Miscanthetum sinensis	Miscanthetea sinensis	*Miscanthus* Grassland	580–600	+	Miyawaki and Murakami (1982)
Sasa nipponica community	Miscanthetea sinensis	Deforestation site	990	+	Miyawaki et al. (1984)
Mantle and forest edge communities					
Boehmeria longispica-Gonostegia hirta community	Artemisietea principis	Forest edge	40	+	Miyawaki et al. (1984)
Boehmeria gracilis-Leucosceptrum japonicum f. *barbinerve* community	Artemisietea principis	Forest edge	600–890	+	Miyawaki et al. (1984)
Fagario nipponici-Polygonetum cuspidati	–	Forest edge	1310–1320	+-1	Miyawaki and Murakami (1987)

(continued)

Table 2 (continued)

Association and community with *F. japonica*	Class	Habitat	Altitude (m)	C-A[a]	Source
Cirsio-Campanuletum hondoensis	–	Roadside	1480	+	Miyawaki and Murakami (1987)
Youngio-Macleayetum cordatae	–	Roadside slope	870–1160	+-2	Miyawaki and Murakami (1987)
Sedum kamtschaticum-Youngia denticulata community	–	Forest-margin	880–1500	+-2	Miyawaki (1971)
Leucosceptrum japonicum-Cirsium nipponicum community	–	Forest-margin	1400–2000	+-2	Miyawaki (1971)
Senecio nemorensis-Artemisiamontana community	–	Forest-margin	1700–2000	+-3	Miyawaki (1971)
Lycium rhombifolium community	Rosetea multiflorae	River embankment	10	+	Miyawaki et al. (1984)
Weigelo fujisanense-Prunetum incisae	Rosetea multiflorae	Forest edge	930–1050	+	Miyawaki et al. (1984)
Clematis apiifolia-Deutzia crenata community	Rosetea multiflorae	Forest edge	630–680	+	Miyawaki et al. (1984)
Clematis apiifolia-Deutzia crenata community	Rosetea multiflorae	Forest edge	270–1080	+	Miyawaki and Murakami (1987)
Stephanandro tanakae-Rubetum coptophylii	Rosetea multiflorae	Forest edge	540–950	+	Miyawaki and Murakami (1987)
Clematido stantis-Kerrietum japonicae	Rosetea multiflorae	Forest edge	770	+	Miyawaki and Murakami (1987)
Pioneer forest communities					
Prunusincisa-Astilbe thunbergii community	–	Deforestation site	900–1500	+	Okutomi and Matsuzaki (1974)
Weigelo fujisanense-Prunetum incisae	Salicetea sachalinensis	*Miscanthus* Grassland	670–1280	+-2	Miyawaki and Murakami (1987)
Saussureo-Alnetum firmae hirtellae	Salicetea sachalinensis	Forest edge	1750	+	Miyawaki and Murakami (1987)
Quercus dentata community	Salicetea sachalinensis	*Miscanthus* Grassland	880–890	+	Miyawaki and Murakami (1987)

[a] C-A, Cover-abundance of *F. japonica* in the relevés

[b] Undetermined

Vegetation units with *F. japonica* as a character species are limited, but the plant was recorded as a companion species of various communities (Table 3). Miyawaki and Okuda (1972) and Okuda (1978) described many communities, including herbaceous communities of Bidentetea tripartitae, Artemisietea principis and Phragmitetea, and woodland communities of Salicetea sachalinensis from Kanto floodplains. Abe and Okuda (1998) studied the *Alnus firma* communities of mountain floodplains and described Calamagrostio-Alnetum firmae, in which *F. japonica* occurred with high frequency. So *F. japonica* was recorded in many vegetation units in phytosociological studies along rivers and streams.

Ohba and Sugawara (1979) studied pioneer shrub communities of landslide slopes and grouped them into the order Weigelo-Alnetalia firmae. In the synoptic table of this order (Ohba and Sugawara 1979, Table 1), *F. japonica* was listed as a companion species. In the syntaxonomical studies of mantle communities in Japan (Murakami 2004), the communities in most of the area were grouped in the class Rosetea multiflorae, which includes the shrub and climber communities at forest edges, maintained by human activities such as cutting. In the synoptic table (Murakami 2004, Table 15) of 39 associations and 11 communities, *F. japonica* was regarded as a companion species and occurred in 22 associations and 7 communities.

Fallopia japonica occurs also in the Miscanthetea sinensis, which includes grassland communities maintained by mowing, grazing and burning. In the study of grassland vegetation by Itow (1974), *F. japonica* occurred in mown grasslands (Arundinario-Miscanthetum sinensis and Saussureo-Miscanthetum sinensis) and grazed grassland (Geranio-Zoysietum japonicae). Nozaki et al. (1998) described a Eulalio speciosae-Miscanthetum sinensis on bald hills and irrigation-pond embankments, in the association table of which *F. japonica* was listed as a companion species (Nozaki et al. 1998, Table 1). Asami et al. (1998) described an Erigeronto-Imperatetum cylindricae dominated by *Imperata cylindrica* and maintained by weeding two or three times per year. *Fallopia japonica* was recorded as a differential species of the lower unit of the association (Asami et al. 1998, Appendix 2).

These phytosociological studies showed that *F. japonica* grows as a constituent species in diverse plant communities, from natural to anthropogenic vegetation, and from herbaceous to woodland vegetation.

What Is the Most Familiar Plant Community with *F. japonica* for Japanese People?

Among the plant communities with *F. japonica* mentioned above, which community has been the most familiar for common Japanese people? Which community has occurred in the sphere of daily life of the people? Alpine vegetation and mountain floodplain vegetation occur in remote areas. Grass and forb communities maintained by mowing are more likely to be familiar communities for rural people.

Table 3 Associations with *Fallopia japonica*

Association	Alliance	Order	Class	Source
Setario-Bidentetum pilosae	Panico-Bidention frondosae	Bidentetalia tripartiti	Bidentetea tripartiti	Miyawaki and Okuda (1972), Okuda (1978)
Kalimerio-Artemisietum princeps	Penniseto-Artemision princeps	Artemisietalia princeps	Artemisietea princeps	Okuda (1978)
Kummerovio-Asteretum kantoensis	Anaphalido-Artemision princeps	Artemisietalia princeps	Artemisietea princeps	Miyawaki and Okuda (1972), Okuda (1978)
Artemisio-Potentilletum chinensis	Anaphalido-Artemision princeps	Artemisietalia princeps	Artemisietea princeps	Miyawaki and Okuda (1972), Okuda (1978)
Mosletum punctulato-diantherae	Moslo-Microstegion	Oplismenetalia	Artemisietea principis	Murakami (2006)
Oplismeno undulatifolii-Microstegietum japonici	Moslo-Microstegion	Oplismenetalia	Artemisietea principis	Murakami (2006)
Cirsio-Campanuletum hondoensis	Cirsio-Campanulion	–[a]	–	Ohba (1969)
Geranio-Zoysietum japonicae	Zoysion japonicae	Caricetalia nervatae	Miscanthetea sinensis	Itow (1974)
Erigeronto-Imperatetum cylindricae	Zoysion japonicae	Caricetalia nervatae	Miscanthetea sinensis	Asami et al. (1998)
Arundinario-Miscanthetum sinensis	Miscanthion sinensis	–	Miscanthetea sinensis	Itow (1974)
Saussureo-Miscanthetum sinensis	Miscanthion sinensis	–	Miscanthetea sinensis	Itow (1974)
Eulalio speciosae-Miscanthetum sinensis	Arundinello-Miscanthion sinensis	Miscanthetalia sinensis	Miscanthetea sinensis	Nozaki et al. (1998)
Miscanthetum sacchariflori	–	–	Phragmitetea	Miyawaki and Okuda (1972)
Galio dahuricae-Miscanthetum sacchariflori	Miscantho sacchariflori-Phragmition	Phragmitetalia	Phragmitetea	Okuda (1978)
Arabido-Polygonetum weyrichii alpinae	Stellariion nipponicae	Minuartetalia vernae japonicae	Dicentro-Stellarietea nipponicae	Ohba (1969)

(continued)

Table 3 (continued)

Association	Alliance	Order	Class	Source
Pleioblastetum simonii	Viti ficifoliae-Clematidion terniflorae	Lonicero japonicae-Paederietalia mairei	Rosetea multiflorae	Murakami and Miyawaki (1995)
Clematidetum terniflorae	Viti ficifoliae-Clematidion terniflorae	Lonicero japonicae-Paederietalia mairei	Rosetea multiflorae	Murakami and Miyawaki (1995)
Hydrangeo-Iteetum japonicae	Clematido apiifoliae-Rubion palmati	Lonicero japonicae-Paederietalia mairei	Rosetea multiflorae	Murakami (2000)
Deutzio maximowiczianae-Boehmerietum spicatae	Clematido apiifoliae-Rubion palmati	Lonicero japonicae-Paederietalia mairei	Rosetea multiflorae	Murakami (2000)
Clematido apiifoliae-Deutzietumm crenatae	Clematido apiifoliae-Rubion palmati	Lonicero japonicae-Paederietalia mairei	Rosetea multiflorae	Murakami (2000)
Caesalpinietum japonicae	Clematido apiifoliae-Rubion palmati	Lonicero japonicae-Paederietalia mairei	Rosetea multiflorae	Murakami (2000)
Clematido stantis-Kerrietum japonicae	Clematido apiifoliae-Rubion palmati	Lonicero japonicae-Paederietalia mairei	Rosetea multiflorae	Murakami (2000)
Ampelopso leeoidis-Uncarietum rhynchophyllae	Clematido apiifoliae-Rubion palmati	Lonicero japonicae-Paederietalia mairei	Rosetea multiflorae	Murakami (2000)
Sinomenio acuti-Actinidietum polygamae	Clematido apiifoliae-Rubion palmati	Lonicero japonicae-Paederietalia mairei	Rosetea multiflorae	Murakami (2000)
Wisterio floribundae-Actinidietum polygamae	Clematido apiifoliae-Rubion palmati	Lonicero japonicae-Paederietalia mairei	Rosetea multiflorae	Murakami (2000)
Rhododendro-Maletum japonicae	Actinidio-Vition coignetiae	Actinidio kolomiktae-Vitietalia coignetiae	Rosetea multiflorae	Murakami (2004)
Tripterygio-Hydrangeetum paniculatae	Actinidio-Vition coignetiae	Actinidio kolomiktae-Vitietalia coignetiae	Rosetea multiflorae	Murakami (2004)

(continued)

Table 3 (continued)

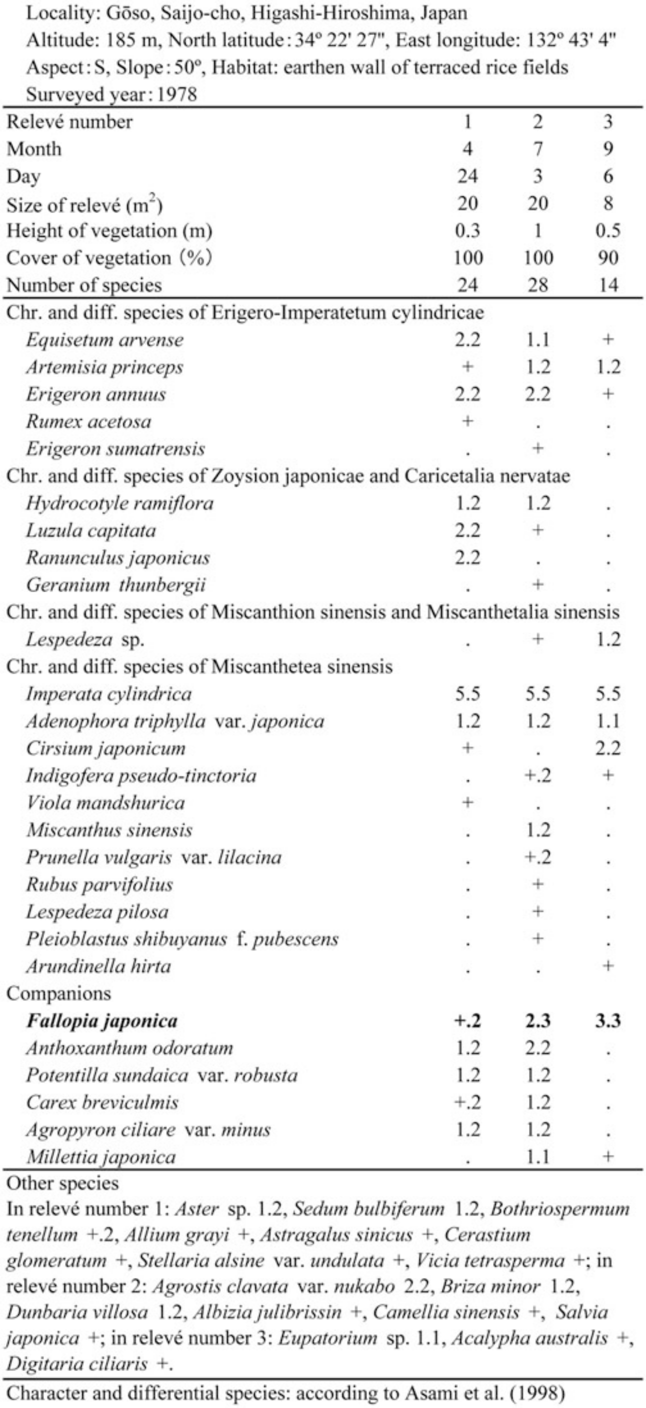
Association	Alliance	Order	Class	Source
Dioscoreo-Vitietum coignetiae	Actinidio-Vition coignetiae	Actinidio kolomiktae-Vitietalia coignetiae	Rosetea multiflorae	Murakami (2004)
Ribesetum japonici	Actinidio-Vition coignetiae	Actinidio kolomiktae-Vitietalia coignetiae	Rosetea multiflorae	Murakami (2004)
Rubetum pseudoaceris	Actinidio-Vition coignetiae	Actinidio kolomiktae-Vitietalia coignetiae	Rosetea multiflorae	Murakami (2004)
Salicetum integrae	Salicion integrae	–	–	Miyawaki and Okuda (1972)
Salicetum serissaefoliae	Salicion jessoensis-serissaefoliae	Alno-Salicetalia serissaefoliae	Salicetea sachalinensis	Okuda (1978)
Calamagrostio-Alnetum firmae	Weigelo-Alnion firmae	–	–	Abe and Okuda (1998)

[a] Undetermined

Grasslands dominated by *Miscanthus sinensis* (Miscanthion sinensis) are maintained by mowing or burning at one-to-several-year intervals (Itow 1974) and occurred widely on mountainous and hilly areas. Another type of grassland is dominated by *Imperata cylindrica*, such as the Erigeronto-Imperatetum cylindricae (Asami et al. 1998), and is common on roadsides, levee slopes and embankments of rivers, ditches and irrigation ponds. The *Imperata* grasslands around houses and farmland are mown more frequently than the grasslands of remote areas. *Imperata* grassland is likely to have been maintained as one of the most familiar grasslands for rural people.

As an example of *Imperata* grassland with *F. japonica*, we show the relevés of grassland from Higashi-Hiroshima City (see Fig. 3) in Table 4. The relevés were recorded in 1978, by the first author, on the sunny slopes of earthen walls of terraced rice fields (Fig. 13) and are identified as the Erigero-Imperatetum cylindricae described by Asami et al. (1998). The first author confirmed that the vegetation on the slope was mown in July, September and November. *Fallopia japonica* grew with various other plants and was in flower in September. The historical documents (Fig. 4) mentioned above from Kurose Town were from south of the study site of Table 4. The documents of two villages in the early nineteenth century recorded *F. japonica* as a village product. It is probable that the village people picked *Fallopia*'s young shoots on mown grasslands like Fig. 13 and at river sides, and used them for food.

Table 4 *Imperata* grassland with *Fallopia japonica*



Locality: Gōso, Saijo-cho, Higashi-Hiroshima, Japan
Altitude: 185 m, North latitude: 34° 22' 27", East longitude: 132° 43' 4"
Aspect: S, Slope: 50°, Habitat: earthen wall of terraced rice fields
Surveyed year: 1978

Relevé number	1	2	3
Month	4	7	9
Day	24	3	6
Size of relevé (m^2)	20	20	8
Height of vegetation (m)	0.3	1	0.5
Cover of vegetation (%)	100	100	90
Number of species	24	28	14
Chr. and diff. species of Erigero-Imperatetum cylindricae			
Equisetum arvense	2.2	1.1	+
Artemisia princeps	+	1.2	1.2
Erigeron annuus	2.2	2.2	+
Rumex acetosa	+	.	.
Erigeron sumatrensis	.	+	.
Chr. and diff. species of Zoysion japonicae and Caricetalia nervatae			
Hydrocotyle ramiflora	1.2	1.2	.
Luzula capitata	2.2	+	.
Ranunculus japonicus	2.2	.	.
Geranium thunbergii	.	+	.
Chr. and diff. species of Miscanthion sinensis and Miscanthetalia sinensis			
Lespedeza sp.	.	+	1.2
Chr. and diff. species of Miscanthetea sinensis			
Imperata cylindrica	5.5	5.5	5.5
Adenophora triphylla var. *japonica*	1.2	1.2	1.1
Cirsium japonicum	+	.	2.2
Indigofera pseudo-tinctoria	.	+.2	+
Viola mandshurica	+	.	.
Miscanthus sinensis	.	1.2	.
Prunella vulgaris var. *lilacina*	.	+.2	.
Rubus parvifolius	.	+	.
Lespedeza pilosa	.	+	.
Pleioblastus shibuyanus f. *pubescens*	.	+	.
Arundinella hirta	.	.	+
Companions			
Fallopia japonica	**+.2**	**2.3**	**3.3**
Anthoxanthum odoratum	1.2	2.2	.
Potentilla sundaica var. *robusta*	1.2	1.2	.
Carex breviculmis	+.2	1.2	.
Agropyron ciliare var. *minus*	1.2	1.2	.
Millettia japonica	.	1.1	+

Other species

In relevé number 1: *Aster* sp. 1.2, *Sedum bulbiferum* 1.2, *Bothriospermum tenellum* +.2, *Allium grayi* +, *Astragalus sinicus* +, *Cerastium glomeratum* +, *Stellaria alsine* var. *undulata* +, *Vicia tetrasperma* +; in relevé number 2: *Agrostis clavata* var. *nukabo* 2.2, *Briza minor* 1.2, *Dunbaria villosa* 1.2, *Albizia julibrissin* +, *Camellia sinensis* +, *Salvia japonica* +; in relevé number 3: *Eupatorium* sp. 1.1, *Acalypha australis* +, *Digitaria ciliaris* +.

Character and differential species: according to Asami et al. (1998)

Fig. 13 Earthen wall of terraced rice fields dominated by *Imperatacylindrica* (Table 4). Higashi-Hiroshima. 3 July 1978

Conclusions: Why Has *Fallopia japonica* Not Been a Pest in Japan?

We have shown that *F. japonica* grows in diverse habitats but is limited to sunny places, and that it grows with various other plants as a constituent species of herbaceous, shrub and open woodland communities. In Japan vegetation is cut or mown near habitations and other infrastructure, which controls the overgrowth of *F. japonica*. In meadows, tall grasses such as *Miscanthus sinensis* and forbs dominate the vegetation, while in hilly and mountainous areas, trees are dominant and open areas are limited. Therefore, it is difficult for *F. japonica* to overgrow a wide area and to form very large stands. The friendly relationship between the Japanese people and *F. japonica* suggests that these ecological limitations prevent *F. japonica* from growing very tall and occupying wide areas.

Fallopia's suitable habitats are limited in Japan, and the plant has been controlled mostly by mowing as a part of daily life. In addition, the plant has been regarded as a useful plant. These matters seem to make *F. japonica* a common and familiar plant for Japanese people and not regarded as a pest species, as in some other countries.

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Iberian Atlantic Forest Restoration: An Experiment Based in Vegetation Succession

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Abstract Restoration of European Atlantic forest has been taking place in the Basque Country since 1994. For this study three plots were selected, each for restoration of one of the three main types of natural forest common in the area: Mesophytic Oak Forest, Eutrophic Beech Forest and Oligotrophic Beech Forest. In order to find the most appropriate method for successful restoration, the plots were planted with three different densities and three species combinations of indigenous trees and shrubs. In the species selection, mature forest and seral-stage trees and shrubs were chosen, as it was intended to investigate whether planting seral-stage species was a better option than planting mature-forest tree species directly. The results after 14 years of monitoring show that, in spite of the low overall survival rate, using seral-stages shrubs improves the biodiversity of the restored forests and accelerates succession by controlling the invasion of some shrubs, such as *Rubus* and *Ulex*, which have inhibitory effects on secondary succession in degraded lands. A selection of saplings with good root systems contributes effectively to higher survival rates and to more successful results. As a general rule, a combination of trees and shrubs is recommended for ecological restorations, and in any case, it is recommended to improve soil conditions before initiating the restoration.

Introduction

Human-induced ecosystem and habitat degradation is a widespread phenomenon throughout the world; and "Restoration Ecology", which studies all the issues of repairing, renewing and restoring ecosystems to a more natural or more sustainable situation, is an actively unfolding field in ecology. The Society for Ecological Restoration (SER) defines ecological restoration as an "intentional activity that

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initiates or accelerates the recovery of an ecosystem with respect to its health, integrity and sustainability" (SER 2004). The practice of ecological restoration includes several activities such as: erosion control, reforestation, use of native species collected locally, removal of alien species and weeds, revegetation of disturbed areas, etc. The inexorable growth of human population worldwide, empowered by technological changes and the rise in commodity demands, causes ecosystem destruction at a pace that outraces natural recovery and current restoration activities. Our work is within the frame of the global necessity of gathering efforts to restore ecosystems for our health and well being. Ecosystems have a remarkable potential for self-repair. Given enough time, under stable conditions without human-induced severe disturbance, most degraded ecosystems can restore themselves. This self-healing capacity is an important and valuable attribute (Bradshaw 1987), but most frequently the time needed to reach a mature and complex stage is so long that active restoration can be a valuable option. Restoration, in this sense, would be a means to accelerate the natural recovery process of a degraded ecosystem.

Exact reproduction of the original community is generally impossible because some site conditions will have been altered irreversibly and some species cannot survive in them any longer or have become locally extinct (Balaguer 2002). Thus, when reflecting on the aims and intention of starting such a project, we assumed that restoration of a forest ecosystem, particularly when starting from a severely degraded stage, is not a perfect reconstruction but only an imitation of the natural forest. We can create a system that is not identical but which can be similar in essential aspects and can function in the same way (Jordan et al. 1987).

Among the different aspects of restoration, the reconstruction of natural forests is of growing importance in many areas of the world (Jordan et al. 1987) and has been considered an increasingly important activity for environmental sustainability (Miyawaki and Box 2006). In our case, we have performed a forest reconstruction experiment, i.e., an attempt to restore several types of natural forests using only woody species of the native flora. The importance and utility of acquiring knowledge for restoring natural forests is strategic in the context of the conservation policy of any country, and particularly in the European Union, where the Habitats Directive (92/43/EEC) focuses much attention in forests ecosystems (Loidi 1999).

The principles of ecological restoration are based on succession theory. This means that restoration should follow the steps accepted by the geobotanical survey for succession. Precise descriptions of vegetation succession in the past may enable us to make accurate predictions about the nature of future succession (Harper 1987). This has lead to the practice of making chronosequences (space-for-time substitutions), which have certain flaws in their predictive power (Chiarucci et al. 2010). In the absence of a better approach supported sufficiently by scientific documentation, Clementsian climax theory adapted to the concept of potential natural vegetation (PNV, Tüxen 1956) has provided the fundamental conceptual basis describing succession and the basic guidelines for restoration programs (Loidi and Fernández-González 2012). In this sense, mapping PNV types is essential for guiding the spatial aspects of restoration, and some countries have worked on this extensively (Rivas-Martínez 1987, 2007; Miyawaki 1980–1989; Blasi 2010, etc.). PNV analysis and cartography provide the models to be tested in the practice of ecological restoration and can also be useful tools in the field of land management (Biondi 2011). Intensive research on PNV units in the Basque area has been carried out in previous years (Loidi et al. 2005, 2011; Loidi and Báscones 1995) and has described the forest types existing in the area at the moment of project design.

Forest planting in the Basque Country throughout most of the twentieth century was done almost entirely using exotic tree species: *Pinus radiata*, *Eucalyptus globulus*, *Pseudotsuga menziesii*, *Chamaecyparis lawsoniana*, *Larix kaempferi*, *Quercus rubra*, *Robinia pseudoacacia*, etc. Those plantations were extensive and nowadays cover nearly 30 % of the total area (Inventario Forestal CAE 2005). This intense planting activity has been taking place from the 1930s onwards, because before that the territory had been deforested severely by intensive land use for animal husbandry and agriculture. Such exotic tree plantations cannot be considered ecological restorations in any case, since they ignored completely the essential requirement that native species be used.

When planning the restoration project, we decided not to follow all the successive steps described by theory based on space-for-time observations. In order to ensure relative success in forest restoration we assumed that: (1) Natural forest restoration requires a minimum area and number of components; monospecific plantations are not suitable (Kirby and Patterson 1992); and (2) Some typical stages of forest development are not essential and may be bypassed (Ashby 1987). We decided to use several native species which are components of natural forests in the area. We also wanted to test whether planting mature-stage trees directly was more or less effective than planting secondary forest trees and shrubs, as representatives of earlier stages in succession. We assumed that younger-stage species may modify site conditions favoring the establishment of mature-stage species: this is the facilitation paradigm, which can be applied to forest succession and was meant to be tested in our survey.

Ecosystem restoration has become a very important issue in the Iberian Peninsula in the last years, but most of the projects have been done in the Mediterranean area, due to the urgency created by the desertification threat characterizing that environment (Benayas et al. 2003). In the Atlantic zone of the Iberian Peninsula, such experiences are scarce, particularly those focusing on restoration of natural forests. For this reason, in 1993, we started a Project entitled *Criterios de restauración de la vegetación natural en el territorio de Bizkaia mediante la utilización de especies leñosas de la flora silvestre autóctona* (Criteria for restoration of the natural vegetation in the territory of the Basque Country using woody species of the native wild flora). We established a network of plots to plant forest tree species and monitor their long-term growth. The main aim was to gain knowledge of the criteria and techniques for re-vegetation of degraded areas with natural forests. In this paper we present the results of three of those plots after 15 years of monitoring.

The hypothesis we established for this survey were that:

1. Species from seral stages have higher survival rates than long-living trees of mature stages;
2. Growth during the first years is faster in seral-stage species than in mature-stage trees.

Material and Methods

Study Area

The survey area is located in the Basque Country (northern Spain), within the area of the Urkiola Natural Park, in the southern sector of the territory of Bizkaia (Basque Country) (Fig. 1). It is a mountainous area crossed by the Duranguesado range, with its highest elevation on the Anboto peak (1330 m); most of the Natural Park area is above 600 m. The climate is temperate-oceanic with cool winters, mild summers, abundant precipitation ranging from 1400 to 2000 mm per year, and no summer drought. In the biogeographic classification of Rivas-Martínez et al. (2007), the area is included in the Basque-Cantabrian sector of the European Atlantic province of the Euro-Siberian region.

The Urkiola Natural Park is an area of high ecological diversity, and almost all the natural forest types of the Atlantic Basque Country can be found there. For this survey we have selected three of these forest types:

- Subcantabrian Mesophytic Oak Forest (*Crataego laevigatae-Querctum roboris*)
- Eutrophic Montane Beech Forest (*Carici sylvaticae-Fagetum sylvaticae*)
- Oligotrophic Montane Beech Forest (*Saxifrago hirsutae-Fagetum sylvaticae*).

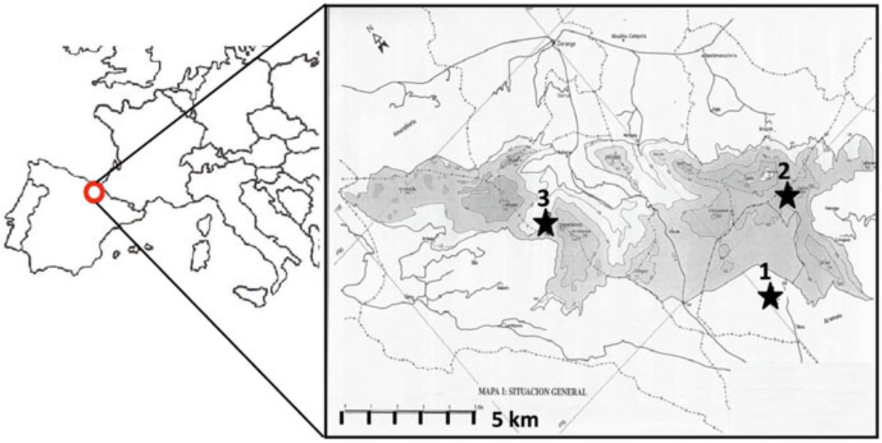


Fig. 1 Location of the three experimental plots: *1* Subcantabric Mesophytic Oak Forest; *2* Eutrophic Montane Beech Forest; *3* Oligotrophic Montane Beech Forest

Plot Design

Three plots were selected, one in each of the three forest types. The characteristics of the three plots are described in Table 1. Each plot involves two replicates of 40×40 m. Both replicates were located close to each other so that environmental conditions would be similar. Each replicate was divided into 6 subplots of 200 m^2, and different treatments (plantation density and species combination) were carried out in each subplot. There was also a control subplot for each replicate (Fig. 2).

Species Selection

Species were selected using phytosociological information about the area (Loidi et al. 1997), following the successional hypotheses of the vegetation series of the Basque Country (Loidi et al. 2011). The species are shown in Table 2.

Data Sampling

Plant survival and growth were monitored annually during the first 5 years (1994–1999) and every 5 years thereafter (1999–2008). Survival was quantified as the proportion of living saplings relative to the total number of seedlings planted in each plot. Plant growth was estimated as the absolute growth rate in height and diameter (AGRH and AGRD) and the relative growth rate in height and diameter (RGRH and RGRD) (Hunt 1982):

$$\text{Absolute growth rate in height :}\quad \mathrm{AGRH}\,(t_n - t_0) = (\mathrm{ALT}\,t_n - \mathrm{ALT}\,t_0)\,/\,t_n - t_0$$

$$\text{Absolute growth rate in diameter :}\quad \mathrm{AGRD}\,(t_n - t_0) = (\mathrm{GROS}\,t_n - \mathrm{GROS}\,t_0)\,/\,t_n - t_0$$

$$\text{Relative growth rate in height :}\quad \mathrm{RGRH}\,(t_n - t_0) = (\ln \mathrm{ALT}\,t_n - \ln \mathrm{ALT}\,t_0)/\,t_n - t_0$$

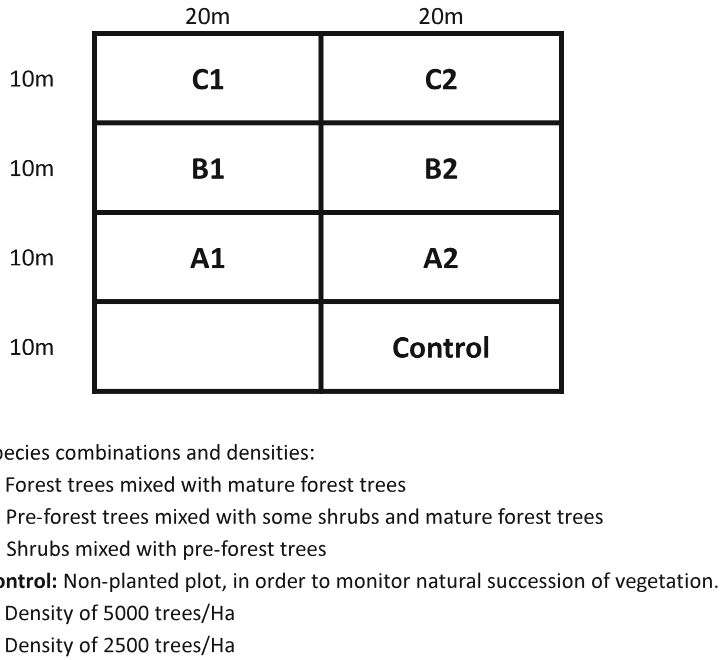
$$\text{Relative growth rate in diameter :}\quad \mathrm{RGRD}\,(t_n - t_0) = (\ln \mathrm{GROS}\,t_n, -\ln \mathrm{GROS}\,t_0)\,/\,t_n - t_0$$

Table 1 Description of the three plots

	Plot 1. Subcantabric Mesophytic Oak Forest type (*Crataego laevigatae-Querctum roboris*)	Plot 2. Eutrophic Montane Beech Forest type (*Carici sylvaticae-fagetum sylvaticae*)	Plot 3. Oligotrophic Montane Beech Forest type (*Saxifrago hirsutae-Fagetum sylvaticae*)
Location	Oleta area, municipality of Aramaio	Arridu area, municipality of Mañaria	Atxin area, municipality of Aramaio
UTM	30TWN2967	30TWN2575	30TWN3269
Altitude (m a.s.l.)	580	720	800
Steepness (%)	0	Between 16 and 35	Over 35
Orientation		NW	E
Precipitation (mm)	1583.7	2100.61	1774.8
Mean annual temperature (°C)	11.73	11.02	10.78
Soil type	Distric fluvisol	Orthic acrisol	Umbric regosol
Bedrock	Clayey lutites	Sandstone and clay	Sandstone
Vegetation at the beginning of the restoration	Grassland dominated by *Agrotis capillaris* accompanied by brambles and *Juncus* sp. and *Salix atrocinera* in the wettest places	Grassland dominated by *Agrostis capillaris*, with some shrubs such as willows, sloes and some disperse trees, mostly birches	Totally covered by gorses (*Ulex gallii*)
Surrounding vegetation	Artificial plantation of various species such as *Acer pseudoplatanus*, *Pinus sylvestris* and *Pinus pinaster*, with some *Quercus robur* specimens scattered in the canopy	Artificial plantation of *Pinus radiata*	Recent mixed plantation of rowan (*Sorbus aucuparia*), birch (*Betula pendula*) and beech (*Fagus sylvatica*)
Previous use of the area	Tree nursery of the forestry service		Tree plantation of *Chamaecyparis lawsoniana*

Analysis

Negative growth has been counted as null for the calculations of the growth indices. Normality analysis was performed by using the Kolmogorov-Smirnov test (Sokal and Rohlf 2012). To compare growth between species, an analysis of variance (ANOVA) was performed using the minimal-significant-differences test (DMS) when the distribution of residuals was distributed normally (Norušis 2012). In order to understand temporal changes in growth rate, relative growth in height and diameter were compared over two periods: 1994–2004 and 1994–2008. Pearson



Species combinations and densities:

C: Forest trees mixed with mature forest trees

B: Pre-forest trees mixed with some shrubs and mature forest trees

A: Shrubs mixed with pre-forest trees

Control: Non-planted plot, in order to monitor natural succession of vegetation.

1: Density of 5000 trees/Ha

2: Density of 2500 trees/Ha

Fig. 2 Experimental design of the plot replicates with the spatial distribution of 6 subplots plus the control. Species combinations and densities: *C*, Pre-forest trees mixed with mature forest trees; *B*, Pre-forest trees mixed with some shrubs and mature forest trees; *A*, Shrubs mixed with pre-forest trees; *Control*, Non-planted plot, in order to monitor natural succession of vegetation. *1*, Density of 5000 trees/ha; *2*, Density of 2500 trees/ha

Table 2 Species planted in each of the three plots

Plot 1. Subcantabric Mesophytic Oak Forest type (*Crataego laevigatae-Querctum roboris*)	Plot 2. Eutrophic Montane Beech Forest type (*Carici sylvaticae-fagetum sylvaticae*)	Plot 3. Oligotrophic Montane Beech Forest type (*Saxifrago hirsutae-Fagetum sylvaticae*)
Acer campestre (ACCA)	*Crataegus monogyna* (CRMO)	*Betula celtiberica* (BECE)
Corylus avellana (COAV)	*Fagus sylvatica* (FASY)	*Crataegus monogyna* (CRMO)
Crataegus monogyna (CRMO)	*Fraxinus excelsior* (FREX)	*Fagus sylvatica* (FASY)
Euonymus europaeus (EUEU)	*Populus tremula* (POTR)	*llex aquifolium* (ILAQ)
Fraxinus excelsior (FREX)	*Prunus spinosa* (PRSP)	*Salix atrocinerea* (SAAT)
Ilex aquifolium (ILAQ)	*Rosa squarrosa* (ROSQ)	*Sorbus aucuparia* (SOAU)
Ligustrum vulgare (LIVU)	*Salix atrocinerea* (SAAT)	*Sorbus aria* (SOAR)
Prunus spinosa (PRSP)	*Sorbus aria* (SOAR)	*Salix caprea* (SACA)
Quercus robur (QURO)	*Corylus avellana* (COAV)	

correlation analysis showed high correlation between absolute and relative growth rate, indicating similar tendencies. So we present only the results for relative growth in the three plots.

Survival accumulation rate was calculated as the percentage of surviving plants in each sampling, taking the first sampling as the baseline. Cumulative survival rates were calculated by the Kaplan-Meier method, and survival curves were compared using the log-rank test (Kleinbaum 1996).

Results

Sapling Survival

In the **Subcantabrian Mesophytic Oak Forest**, the survival rate was low (25.2 %) if we consider the total number of individuals planted (Table 3). Nevertheless, some species were more successful, approaching 50 % survival, such as *Quercus robur* (QURO, 48.3 %), *Corylus avellana* (COAV, 48.3 %) and *Crataegus monogyna* (CRMO, 40 %). On the other hand, other species presented a low or very low survival rate, and *Ligustrum vulgare* and *Euonymus europaeus* did not survive at all. The survival diagram (Fig. 3) shows three separate groups. The first group involves the three species (QURO, COAV and CRMO) with over 80 % survival over the first 10 years. These species suffered high mortality during the last 5 years due mainly to routine maintenance activities, such as clipping and clearing, which eliminated some of the saplings. This group shows significant differences relative to the other species planted in the plot, except *Corylus avellana* and *Ilex aquifolium*. The second group is formed by *Acer campestre*, *Ilex aquifolium*, *Fraxinus excelsior* and *Prunus spinosa*. These had high mortality between 5 and 10 years after planting, with around 50 % survival, and then suffered high mortality again during the last 5 years. Finally, there is a third group formed by two species, *Ligustrum vulgare* and *Euonymus europaeus*, which had very low survival (less than 10 %) after the first 5 years and did not survive at all by the end of the 15 years. Average seedling life extended from 54.95 months for *Euonymus europaeus* to 167.6 months for *Crataegus monogyna* (Table 4).

A good survival rate (59.3 %) was observed in the **Eutrophic Montane Beech Forest**. Some species showed a survival rate of ca. 90 %, i.e., *Crataegus monogyna* (91 %), *Salix atrocinerea* (87.93 %) and *Corylus avellana* (86.6 %). The rest had a survival rate over 50 % except for *Sorbus aria*, with only 24.6 % (Table 5).

The survival-curve analysis (Fig. 4) showed three groups of species with significant differences among them. The first group is that with the highest survival during the monitoring time, including *Crataegus monogyna*, *Salix atrocinerea*, *Corylus avellana* and *Rosa squarrosa* (ROSQ). These species had a slight decline during the period 2004–2008, especially *Rosa*. The second group showed gradual mortality through the entire period, with over 50 % survival except for *Prunus spinosa* (36 %); it includes *Prunus spinosa*, *Populus tremula*, *Fraxinus*

Table 3 Total number of seedlings of each species planted and percentage of survival in the Subcantabric Mesophytic Oak Forest

Species	Seedling	% Seedling	Surv08	% surv08	Pos.gr	% pos.gr
QURO	236	26.50	114	48.30	111	97.4
FREX	148	16.60	20	13.50	11	55.0
LIVU	86	9.68	0	0.00	0	0.0
COAV	60	6.75	29	48.30	16	55.2
PRSP	88	10.20	9	10.20	4	44.4
ILAQ	60	6.75	13	21.60	1	7.7
CRMO	60	6.75	24	40. 00	20	83.3
ACCA	90	10.10	15	16.60	8	53.3
EUEU	60	6.75	0	0.00	0	0.0
Total	888	100 %	224	25.20 %	171	76.3

Surv08, Number of specimens surviving in 2008; *% surv08*, Survival percentage in 2008; *Pos.gr*, Number of specimens with positive growth in 2008; *% pos.gr*, Percentage of specimens with positive growth with respect to the surviving specimens in 2008 for each of these species

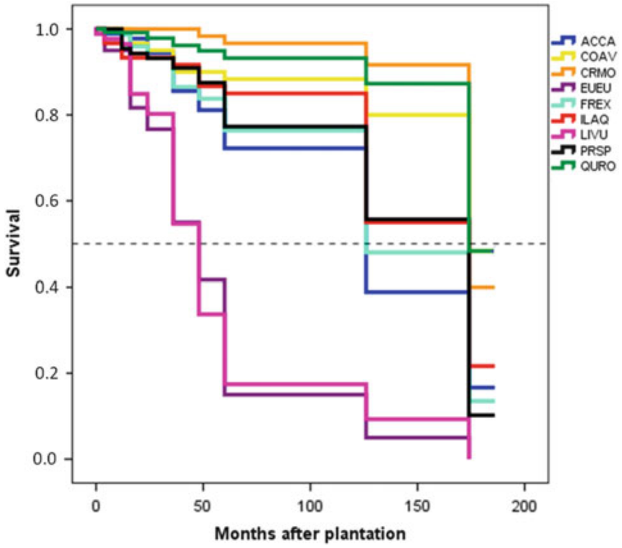


Fig. 3 Accumulated survival curves for each of the species planted in the Subcantabric Mesophytic Oak Forest, the *dotted line* indicates 50 % survival

excelsior and *Fagus sylvatica*. The third group involves only *Sorbus aria*, which suffered high mortality during the second year after planting. Average seedling life extended from 83.36 months for *Sorbus aria* to 172.4 months for *Rosa squarrosa* (Table 6).

The **Oligotrophic Montane Beech Forest** showed very low survival in general (17.5 %), and only one species, *Sorbus aucuparia* (77 %), had over 50 % survival. The next highest survival rate was that of *Sorbus aria* at 35.7 %. Other species, such as *Betula celtiberica* (17.9 %), *Ilex aquifolium* (15 %), *Fagus sylvatica* (8.60 %)

Table 4 Mean survival times (months) and log rank test results for the planted species in the Subcantabric Mesophytic Oak Forest

	Survival means (S.E.)	ACCA	COAV	CRMO	EUEU	FREX	ILAQ	LIVU	PRSP
ACCA	121.36 (5.71)								
COAV	153.43 (6.03)	22.29***							
CRMO	167.6 (3.09)	28.02***	0.02						
EUEU	54.95 (5.43)	51.47***	79.79***	105.25***					
FREX	128.61 (4.47)	0.25	26.74***	31.64***	76.21***				
ILAQ	133.03 (6.61)	2.8	10.59**	13.46***	57.77***	2.22			
LIVU	58.63 (5.01)	52.88***	84.27***	106.53***	0.063	79.83***	58.10***		
PRSP	133.68 (5.73)	0.59	23.16***	28.75***	65.73***	0.12	1.3	66.99***	
QURO	161.93 (2.33)	66.46***	0.2	0.48	245.03***	81.22***	27.81***	255.67***	60.32***

S.E. = Standard error
**P < 0.01
***P < 0.001

Table 5 Total number of seedlings of each species planted and percentage of survival in the Eutrophic Montane *Beech Forest* type

Species	Seedling	% Seedling	Surv08	% surv08	Pos.gr	% pos.gr
FASY	236	26.50	140	59.30	84	60.0
POTR	148	16.60	86	58.10	75	87.2
PRSP	30	3.37	11	36.60	1	0.09
FREX	90	10.13	45	50.00	21	46.7
SOAR	150	16.89	37	24.60	0	0.0
ROSQ	30	3.37	22	73.30	1	0.05
CRMO	116	13.06	105	91.00	48	45.7
COAV	30	3.37	26	86.60	17	65.4
SAAT	58	6.50	51	87.93	41	80.4
Total	888	100	527	59.30	286	54.3

Surv08, Number of specimens surviving in 2008; *% surv08*, Survival percentage in 2008; *Pos.gr*, Number of specimens with positive growth in 2008; *% pos.gr*, Percentage of specimens with positive growth with respect to the surviving individuals in 2008 for each of these species

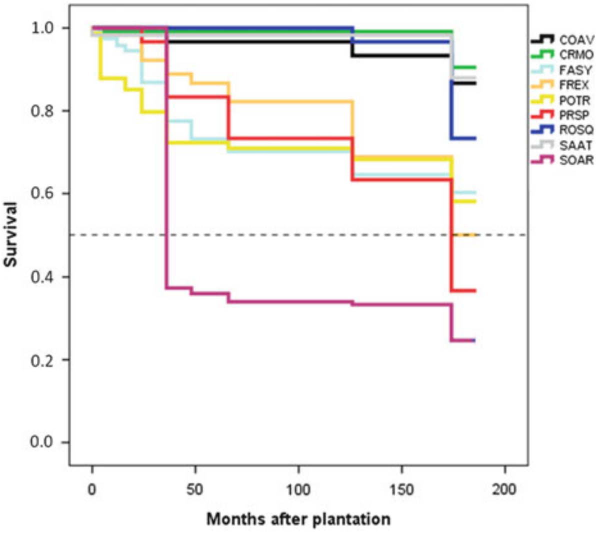


Fig. 4 Accumulated survival curves for the species planted in the Eutrophic Montane Beech Forest type, the *dotted line* indicates 50 % survival

and *Salix atrocinerea* (1.90 %) presented very low survival rates. *Crataegus monogyna* and *Salix caprea* did not survive at all (Table 7).

Survival curves (Fig. 5) showed that all the planted species suffered high, gradual mortality throughout the monitoring period and that most seedlings, except *Sorbus aucuparia*, died during the first 5 years. Three groups with significant differences between them can be distinguished. The first group was formed by only *Sorbus aucuparia*, with the highest survival scores and significant differences from all the other taxa. The second group was formed by *Sorbus aria* (SOAR),

Table 6 Mean survival times (months) and log rank test results for the planted species in the Eutrophic Montane Beech Forest type

	Survival means (S.E.)	COAV	CRMO	FASY	FREX	POTR	PRSP	ROSQ	SAAT
COAV	167.8 (5.47)								
CRMO	170.36 (2.18)	0.14							
FASY	117.87 (4.52)	11.44**	45.26***						
FREX	141.13 (5.63)	12.65***	45.17***	0.10					
POTR	127.88 (5.82)	8.40**	32.57***	0.87	0.62				
PRSP	135 (10.55)	15.82***	47.38***	0.47	0.89	2.08			
ROSQ	172.4 (1.68)	1.36	4.41*	6.10*	7.33**	3.59	10.62**		
SAAT	163.41 (4.16)	0.01	0.25	20.66***	22.41***	14.88***	25.80***	2.01	
SOAR	83.36 (5.30)	36.32***	116.20***	17.19***	18.31***	20.94***	3.67	27.00***	60.94***

S.E. = Standard error

*$P < 0.05$

**$P < 0.01$

***$P < 0.001$

Table 7 Total number of seedlings of each species planted and percentage of survival in the Oligotrophic Montane Beech Forest type

Species	Seedling	% Seedling	Surv08	% surv08	Pos.gr	% pos.gr
FASY	256	25.90	22	8.60	12	54.5
ILAQ	100	10.12	15	15	1	6.7
CRMO	100	10.12	0	0.0	0	0.0
SAAT	154	15.58	3	1.90	1	33.3
SOAU	122	12.36	94	77.0	68	72.3
SACA	30	3.03	0	0.0	0	0.0
SOAR	14	1.41	5	35.7	0	0.0
BECE	212	21.40	38	17.90	38	100.0
TOTAL	988	100	177	17.50	120	67.8

Surv08, Number of specimens surviving in 2008; *% surv08*, Survival percentage in 2008; *Pos.gr*, Number of specimens with positive growth in 2008; *% pos.gr*, Percentage of specimens with positive growth with respect to the surviving individuals in 2008 for each of these species

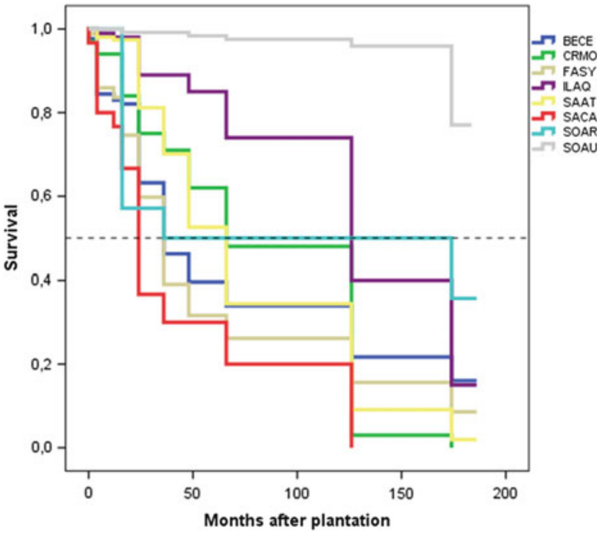


Fig. 5 Accumulated survival curves for the species planted in the Oligotrophic Montane Beech Forest type, the *dotted line* indicates 50 % survival

Betula celtiberica, *llex aquifolium*, *Fagus sylvatica* and *Salix atrocinerea*; in this group, *llex aquifolium* deviates slightly because it is the only species presenting significant differences from all the other taxa. The third group was formed by *Crataegus monogyna* and *Salix caprea*, with no survival. Average seedling life extended from 44.07 months for *Salix caprea* to 170 months for *Sorbus aucuparia* (Table 8).

Table 8 Mean survival times (months) and log rank test results for the planted species in the Oligotrophic Montane Beech Forest type

	Survival means (S.E.)	BECE	CRMO	FASY	ILAQ	SAAT	SACA	SOAR
BECE	71.61 (4.42)							
CRMO	80.8 (5.00)	0.09						
FASY	60.9 (3.70)	5.14*	2.75					
ILAQ	123.94 (5.30)	16.27***	40.43***	40.51***				
SAAT	76.17 (3.96)	0.17	0.21	4.17*	46.50***			
SACA	44.07 (8.22)	9.22**	13.65***	4.53*	53.62***	15.68***		
SOAR	96.43 (22.03)	1.49	6.62*	4.58*	0.13	6.15*	7.71**	
SO AU	170 (1.96)	145.91***	208.52***	200.22***	107.23***	222.91***	195.60***	22.18***

S.E. = Standard error
$^*P < 0.05$
$^{**}P < 0.01$
$^{***}P < 0.001$

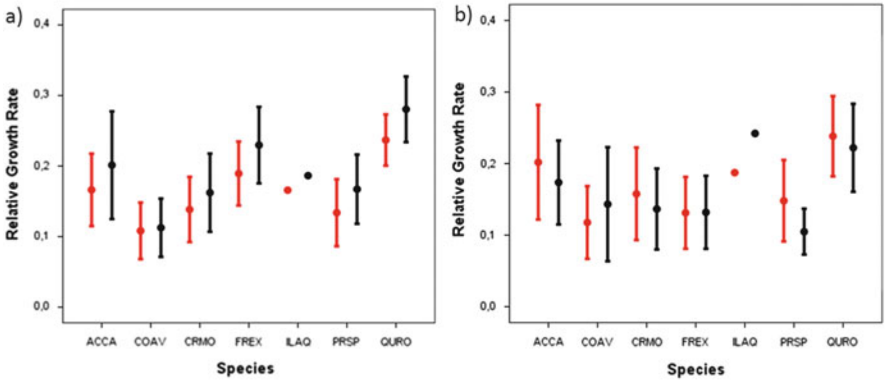


Fig. 6 Mean and standard deviation for (**a**) relative growth rate in height and (**b**) relative growth rate in diameter in Subcantabric Mesophytic Oak Forest type**.** *Red bars*: 1994–2004 and *black bars*: 1994–2008

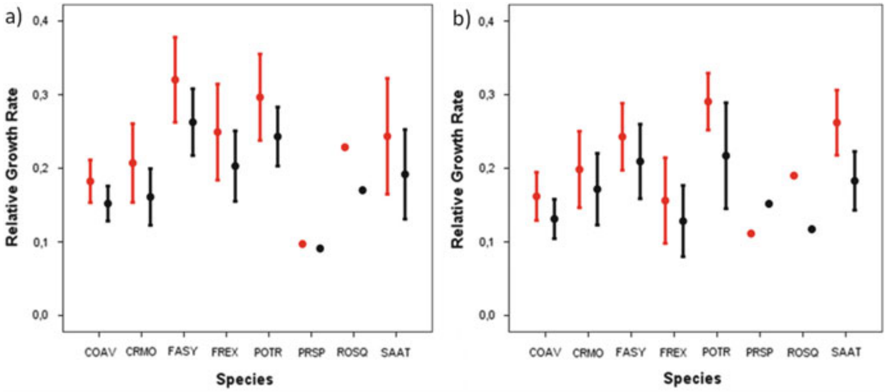


Fig. 7 Mean and standard deviation for (**a**) relative growth rate in height and (**b**) relative growth rate in diameter in Eutrophic Montane Beech Forest type**.** *Red bars*: 1994–2004 and *black bars*: 1994–2008

Sapling Growth

Plant growth was analyzed by combining all the data for height and diameter increases by the different species for the two periods monitored (1994–2008 and 1994–2004). The standard deviation was very high, due to the high variation in growth rate among individuals (Figs. 6, 7 and 8).

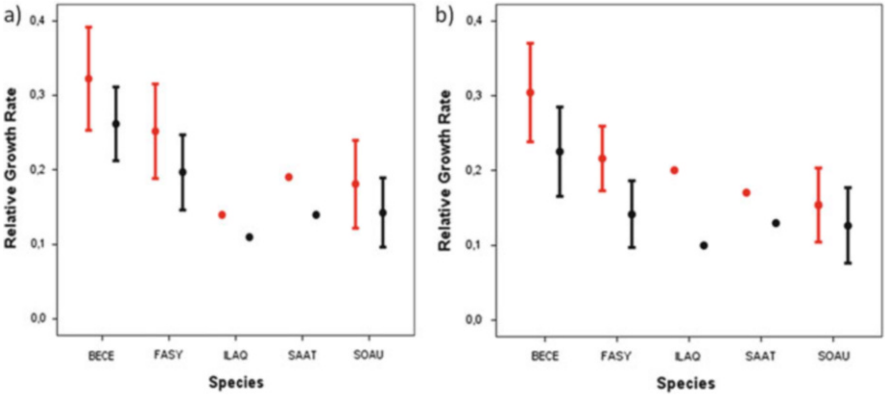


Fig. 8 Mean and standard deviation for (**a**) relative growth rate in height and (**b**) relative growth rate in diameter in Oligotrophic Montane Beech Forest type. *Red bars*: 1994–2004 and *black bars*: 1994–2008

Subcantabrian Mesophytic Oak Forest Type (*Crataego laevigatae-Querctum roboris*)

In all, more than 75 % of the surviving plants had positive growth. *Quercus robur* had the best result, with almost all surviving seedlings showing positive growth (97.4 %); this was followed by *Crataegus monogyna* (83.3 %). The relative rate of height growth was greater for the 15 years than for the first period in all species, but the opposite was true for diameter growth, except for *Corylus avellana*.

Over the 15 years of monitoring, the species with the highest growth rate in height was *Quercus robur* ($\mathrm{RGRH}_{1994\text{–}2004} = 0.24$ and $\mathrm{RGRH}_{1994\text{–}2008} = 0.28$) and *Acer campestre* had the second fastest growth per year. On the other hand, the lowest rates of height growth were by *Corylus avellana* ($\mathrm{RGRH}_{1994\text{–}2004} = 0.11$ and $\mathrm{RGRH}_{1994\text{–}2008} = 0.11$), followed by *Crataegus monogyna* and *Prunus spinosa* (Fig. 5a). *Quercus robur* ($\mathrm{RGRD}_{1994\text{–}2004} = 0.24$ and $\mathrm{RGRD}_{1994\text{–}2008} = 0.22$) and *Acer campestre* were the two species with the fastest relative rates of diameter growth, while *Prunus spinosa* ($\mathrm{RGRD}_{1994\text{–}2004} = 0.15$ and $\mathrm{RGRD}_{1994\text{–}2008} = 0.10$) was the slowest, followed by *Fraxinus excelsior* (Table 9, Fig. 6b).

Eutrophic Montane Beech Forest (*Carici sylvaticae-Fagetum sylvaticae*)

In spite of having the highest survival rates (59.3 %), only 54 % of the surviving seedlings in this forest type had positive growth. The highest growth percentages were by *Populus tremula* (87.21 %) and *Salix atrocinerea* (80.39 %).

Relative rates of height and diameter growth were higher in all species during 1994–2004 than during 1994–2008. This suggests a tendency for growth to slow down during later years.

Table 9 Results of Fisher LSD post-hoc tests for ANOVA between relative growth rate for planted species in Subcantabric Mesophytic Oak Forest type

		1994–2004					1994–2008				
		ACCA	COAV	CRMO	FREX	PRSP	ACCA	COAV	CRMO	FREX	PRSP
RGRH	COAV	0.06**					0.09***				
	CRMO	0.03	0.03**				0.04	0.05**			
	FREX	0.02	0.08***	0.05**			0.03	0.12***	0.07***		
	PRSP	0.03	0.03	0.01	0.06*		0.03	0.05*	0.01	0.06*	
	QURO	0.07***	0.13***	0.10***	0.05***	0.10***	0.08***	0.18***	0.12***	0.05**	0.11***
RGRD	COAV	0.08**					0.03				
	CRMO	0.04	0.04*				0.04	0.01			
	FREX	0.07**	0.01	0.03			0.04	0.01	0.01		
	PRSP	0.05	0.03	0.01	0.02		0.07	0.04	0.04	0.03	
	QURO	0.04	0.12***	0.08***	0.11 ***	0.09**	0.05*	0.08***	0.09***	0.09***	0.12***

*P < 0.05
**P < 0.01
***P < 0.001

Table 10 Results of Fisher LSD post-hoc tests for ANOVA between relative growth rate for planted species in Eutrophic Montane Beech Forest type

		1994–2004					1994–2008				
		COAV	CRMO	FASY	FREX	POTR	COAV	CRMO	FASY	FREX	POTR
RGRH	CRMO	0.02					0.01				
	FASY	0.14***	0.11***				0.10***	0.10***			
	FREX	0.07**	0.04**	0.07***			0.05**	0.04***	0.06 ***		
	POTR	0.11 ***	0.09***	0.02*	0.05**		0.09***	0.08***	0.02**	0.04***	
	SAAT	0.06 ***	0.04**	0.08***	0.01	0.05***	0.04**	0.03**	0.07 ***	0.01	0.05***
RGRD	CRMO	0.04**					0.04**				
	FASY	0.08***	0.04***				0.08***	0.04***			
	FREX	0.01	0.04**	0.09***			0.01	0.04**	0.08 ***		
	POTR	0.13***	0.09***	0.05***	0.13***		0.09***	0.05***	0.01	0.09***	
	SAAT	0.10***	0.06***	0.02*	0.11***	0.03**	0.05**	0.01	0.03*	0.05***	0.03**

*$P < 0.05$
**$P < 0.01$
***$P < 0.001$

Table 11 Results of Fisher LSD post-hoc tests for ANOVA between relative growth rate for planted species in Oligotrophic Montane Beech Forest type

		1994–2004		1994–2008	
		BECE	FASY	BECE	FASY
RGRH	FASY	0.07**		0.06***	
	SOAU	0.14***	0.07**	0.12***	0.05***
RGRD	FASY	0.09***		0.08**	
	SOAU	0.15***	0.06***	0.10***	0.02

**$P < 0.01$
***$P < 0.001$

The highest rate of height growth over the whole 15 years of monitoring was by *Fagus sylvatica* ($RGRH_{1994–2004} = 0.32$ and $RGRH_{1994–2008} = 0.26$), followed by *Populus tremula* and *Salix atrocinerea*; the lowest rate corresponded was by *Corylus avellana* ($RGRH_{1994–2004} = 0.18$ and $RGRH_{1994–2008} = 0.15$) (Fig. 7a).

For relative rate of diameter growth, *Populus tremula* ($RGRD_{1994–2004} = 0.29$ and $RGRD_{1994–2008} = 0.22$) had the highest values, followed by *Fagus sylvatica* and *Salix atrocinerea* (Fig. 6b); *Corylus avellana* ($RGRD_{1994–2004} = 0.16$ and $RGRD_{1994–2008} = 0.13$) had the slowest growth. Differences in growth between most of the species pairs declined over time, not only for relative height growth but also for relative diameter growth (Table 10).

Oligotrophic Montane Beech Forest Type (*Saxifrago hirsutae-Fagetum sylvaticae*)

Although survival was very low (17.5 %), the proportion of seedlings with positive growth reached 67.8 % and *Betula celtiberica* stood out with 100 % survival, followed by *Sorbus aucuparia* with 72.3 % (Table 7).

Relative rates of height and diameter growth were higher in the period 1994–2004 in all the species, indicating a slowing-down in their growth rate.

Over the 15 years of monitoring, the species with the highest rates of height and diameter growth was *Betula celtiberica* ($RGRH_{1994–2004} = 0.32$; $RGRH_{1994–2008} = 0.26$; $RGRD_{1994–2004} = 0.30$ and $RGRD_{1994–2008} = 0.23$), followed by *Fagus sylvatica*; lower rates were showed by *Sorbus aucuparia* ($RGRH_{1994–2004} = 0.18$; $RGRH_{1994–2008} = 0.14$; $RGRD_{1994–2004} = 0.15$ and $RGRD_{1994–2008} = 0.13$) (Fig. 8a, b). Differences in growth between all the species pairs declined with time, not only for relative height growth but also for relative diameter growth (Table 11).

Discussion

Seeding survival can be attributed to the combined effects of human disturbance and microclimatic conditions (Ramírez-Marcial 2003) and also to the quality of the seedlings, in terms of their survival capacity (Grossnickle 2012). The high survival (almost 60 %) among seedlings in the Eutrophic Montane Beech Forest (EMBF), as compared to the Oligotrophic Montane Beech Forest (OMBF, less than 20 %), is related to soil and climatic conditions where the plots are located. The Oligotrophic beech forest, besides having poorer nutrient availability, is located on a steeper slope that experiences high runoff, thus captures less water, and consequently is drier. In addition, the sandstone substrate facilitates water loss and the southeast orientation confers greater summer drought. The better soil conditions in the Eutrophic beech plot and its northwest orientation, which promotes higher humidity especially in summer, has led to better plant survival. On the other hand, the poor quality of the seedlings of several species, such as *Sorbus aria*, *Ligustrum vulgare*, *Euonymus europaeus* and *Prunus spinosa*, caused high mortality during the first years (Grossnickle 2012). Another factor was the action of herbivores that affected some species, such as *Ilex aquifolium*.

Already in 2004 it was observed that a high proportion of the trees showed very little growth; by 2008 high mortality was recorded. Root-system size is proportional to the diameters of the above-ground main stem (Mexal and Landis 1990), and the ability to grow roots has a significant effect on survival (Grossnickle 2012). Thus, the low growth rate could indicate a small root system that leads to plant death. Moreover, the routine maintenance work conducted in the plots increased the mortality, especially in the Subcantabrian Mesophytic Oak Forest, where about 30 % of the seedlings were cut.

There was some variation in survival between different functional groups. In general, shrubby species showed better survival than species of mature stages in later succession. Thus, the hypothesis that species of seral stages (secondary forests and shrubland) have higher survival rate than mature-stage species seems to be confirmed. This is to be expected for beech, since it is well known that it has lower survival rates under high light intensity (Petritan et al. 2007; Jarcuska 2009). This was not the case with oak (*Quercus robur*), however, which had a survival rate similar to that of *Corylus avellana* or *Crataegus monogyna*.

Relative rate of height growth has been greater in the last 5 years than in the previous period in mesic oak forest (SMOF), but in the beech forest plots growth in the first 10 years was greater than in the last period. Even the species planted in both the mesic oak forest and eutrophic beech forest, such as *Corylus avellana*, *Crataegus monogyna* and *Fraxinus excelsior*, showed this tendency. This suggests that greater water availability in deeper soil layers of the flat ground, where the plots are located, could induce more growth in the last period, once the tree roots had reached these more moist levels. The different relative growth rates of *Fagus sylvatica* in the eutrophic versus oligotrophic beech forest can be explained by the worse soil and microclimatic conditions at the Oligotrophic Montane Beech Forest plot.

There are also some other differences between the functional groups of plants. Trees of mature and secondary stages (*Quercus robur*, *Fagus sylvatica*, *Populus tremula* and *Acer campestre*) tend to show greater rates of height and diameter growth than do shrubs of successional stages (*Crataegus monogyna*, *Prunus spinosa* and *Corylus avellana*). The higher growth rate of the mature-forest species is a phenomenon that has also been observed in tropical forests by Shono et al. (2006), where a number of primary forest species had better growth rates than did secondary-forest species.

In summary, the results have proved that the initial topographic and soil conditions of the plots determine the afforestation success to a great extent, which was already evident and reported by the second year of monitoring (Sesma et al. 1997). The Eutrophic Montane Beech Forest plot, with more structured soil and humid conditions, especially in summer, had better survival and growth rates, probably due to the orientation of the plot. On the other hand, the steeper slope and sandy soil of the Oligotrophic Montane Beech Forest plot, together with its SW orientation, resulted in worse conditions for seedling establishment, increasing mortality and reducing growth rates. In fact, water stress related to high temperatures and lower moisture availability in pastures was reported as one of the main factors causing mortality in several reforestation attempts (Hooper et al. 2002, Doñobeytia et al. 2007). Finally, in the Mesic Oak Forest plot, there were some areas with very compacted soil due to the presence of paths; this resulted in high plant mortality in the first years. Another factor that caused a remarkable decline in the survival of all species was the weeding and clearing work carried out in the plots, especially in the oak forest. Although weeding has been documented to have a strong positive effect on seedling and sapling growth (Löf and Welander 2004), it must be done by hand or very carefully, in order to avoid cutting the plants.

Despite low overall survival, the general growth rate of the surviving seedlings allows us to conclude that the study results were positive, accelerating the natural forest successional processes and controlling invasion by shrub species like *Rubus* and *Ulex*, which limit natural succession in degraded lands (cf Shono et al. 2006). Tree-planting strategies should include improving the soil conditions before afforestation and selecting seedlings with good root systems that contribute to better survival. With regards to species selection, even though growth rates were higher in trees than in shrubs, we recommend using shrubs also in order to improve the biodiversity of the restored forests.

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Carbon-Stock Measurement in Community Forests in Lampung Province, Sumatra

Nobukazu Nakagoshi, Anjar Yogie Supriatna, and Hadi Susilo Arifin

Abstract The question is how to estimate carbon stock in community forests in Indonesia. Field carbon stocks were estimated, in Lampung Province (southern Sumatra), using allometric methods based on measurements in 20 m × 100 m plots. A non-destructive method was applied to individual trees with breast-height diameter (DBH) more than 30 cm, and a destructive method was used for trees with DBH below 30 cm. Landsat images (path 123 and row 64) were used to calculate the carbon stock in community forests for two different years (2006 and 2009). According to the GIS analysis, this study covers 1853 ha, which include four land-cover types: selectively cut woods, shrub-mixed dryland farm, shrub-bush land, and bare land. Carbon measurement in the community forest suggested that the most carbon was in trees of DBH 5–30 cm and the least was in the shrubs of the research area. Field measurements showed that, in general, the average carbon stock in the selectively cut area was 32 t/ha, which was higher than in the other cover types, i.e., 22 t/ha for shrub-mixed dryland farm, 14 t/ha for the bush/shrub cover, and 5.8 t/ha for the bare land. This study is limited in that it does not include soil carbon, due to the time and technological constraints involved in estimating soil carbon. Future studies, though, should include soil carbon data for a whole-ecosystem analysis of community forests.

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Introduction

Natural forest stores more carbon than agricultural land. Therefore, natural forest with many species of long-lived trees and much surface litter has shown the highest carbon storage among different land covers. When a forest is changed into agricultural land, plantation or pasture, the amount of stored carbon decreases. The amount of carbon stored by these various land-cover types varies depending on the diversity and density of the existing vegetation, the soil type, and how the land is managed. Increasing levels of atmospheric greenhouse gases are believed to be a main cause of global warming, and studies have shown that this is changing the Earth's weather patterns and could raise ocean levels substantially in the next 100 years (Schimel et al. 1994; Watson et al. 1996).

These climatic changes will affect current environmental conditions and human populations, causing serious detrimental disturbances to the global economy. As international concern over greenhouse-gas emissions and global warming finds common ground in industrial, political, and social spheres, it appears that carbon will become an internationally tradable commodity. Forest-based land use systems of natural forests, forest-like tree plantations and agroforestry systems sequester carbon dioxide, a major greenhouse gas, by storing carbon in living biomass.

Changing land use practices can increase or decrease the amount of carbon stored by a given land use system. The most significant increases in carbon storage can be achieved, and the rate of global warming slowed the most, by moving from lower-biomass land-use systems such as grassland, agricultural fallows and permanent shrublands, to tree-based systems. Forest-based carbon storage projects are a feasible option for utilities and industries interested in investing in carbon sequestration in order to offset a percentage of the carbon released by their use of fossil fuels. This investment is essential for these projects to be user friendly and a cost-effective method for monitoring carbon sequestration (MacDicken 1997).

Indonesia provides an attractive environment for carbon investment. There are over 8.5 million hectares of *Imperata* grassland, cyclical fallows and shrubland which are acknowledged to be underutilized. There is clear interest, at both governmental and smallholder farmer levels, to convert some of these lands into more productive land uses, including tree-based use systems (Garrity et al. 1997). Home gardens are a type of smallholder agroforestry system common to many parts of Indonesia. These species-rich tree-based systems occupy land near houses and produce a diverse array of food and other products. Traditionally intended to produce well mainly for home consumption, home gardens have become more commercially oriented with the arrival of rural infrastructure and market economies. Home-garden production now commonly serves both household and market demand, providing families with much needed income (Michon and Mary 1994; Krol 1992).

This study attempts to estimate the carbon stock in community forests, in Lampung Province (Sumatra) of Indonesia, over 3 years between 2006 and 2009. This study has two main objectives: to obtain population distributions of species trees in the community forests, and to estimate the amount of carbon stored in community forests at Tanggamus, Lampung Province.

Methodology

Study Area

The Tanggamus District is located at 104°18′00″–105°12′00″E and 5°05′00″–5°56′00″S, at the southern end of Sumatra, in Indonesia (Fig. 1). The west side of the Tanggamus District tends to follow the Bukit Barisan slope. Tanggamus District has a land area of 3335.61 km^2 and a sea area of 1799.50 km^2, with a coastline of 210 km. There are various topography types, from low land to high land.

Land-Use and Land-Cover Classification

Land Use and Land Cover (LULC) maps for 2006 and 2009 produced by the Ministry of Forestry of Indonesia (MoF) were used in this study. Based on the MoF definition, however, the secondary forest in the Tanggamus district, which is located within the community forest, is classified as a primary logged-over area (LOA). In order to avoid conflict with international terminology, LOA in this study is called Selective Cutting (SC) area.

GIS analysis estimated the total extent of the research area as 1853 ha. Based on satellite imagery, field surveys and combinations with GIS analysis, land cover in this research area was classified into two main categories, forest and non-forest

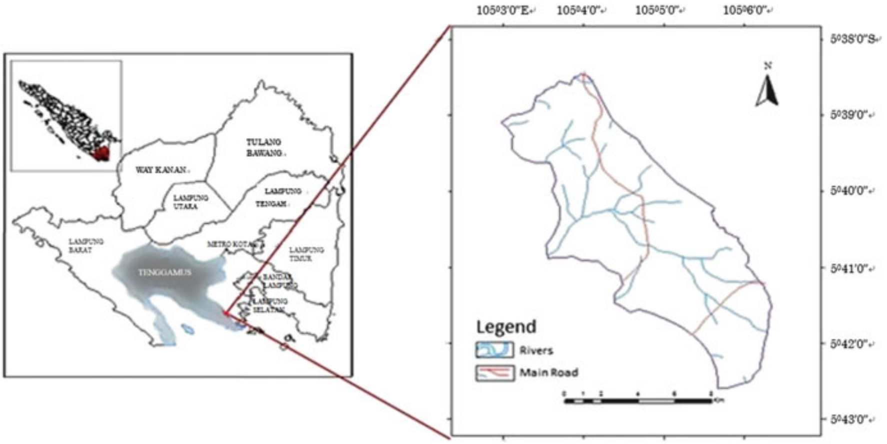


Fig. 1 Location map of Klumbayan, Lampung province, Indonesia

area. Forest includes selectively cut areas and shrub-mixed dryland farmland, while non-forest consists of shrub-bush landscapes and bare land, as explained in more detail below.

1. Bareland
   This type of land cover refers to areas without any vegetation, generally open areas created after severe degradation had occurred in the area.
2. Bush/Shrub
   This type refers to areas dominated by herbaceous species, ferns or grass. Woody vegetation is also found sporadically, with very low total cover. The term ‘shrub’ in this cover refers to areas dominated by woody species, mixed with ferns, grass and climbers. Any trees are relatively small and are mainly pioneer species.
3. Selective Cutting/Logged-Over Area
   This type of land cover refers to secondary forest that has been cut selectively and has recovered (somewhat) either naturally or artificially.
4. Shrub-Mixed Dryland Farm
   This type of land cover refers to gardens owned by local people. Vegetation found in these gardens includes woody species and plants producing fruits and vegetables.

Carbon Measurement

Above-Ground Carbon

The carbon stock of a land-use system is determined by its vegetation. A land use system involving tree species with a high density will have higher carbon storage in biomass than land with low tree density, even with similar tree diameters. Tree biomass, in dry weight, is estimated using allometric equations based on stem diameter at breast height (DBH), 1.3 m above the ground.

The amount of dry-weight biomass in a community forest is calculated using allometric equations that have been developed by researchers in Indonesia. By this method, trees do not need to be destroyed but are measured at breast height, for diameter directly, using a diameter tape. Several equations used to estimate dry-weight biomass in this study are explained in the following section (Table 1).

This study adopts allometric equations used commonly in biomass studies in Indonesia, as follows:

$W = 0.11\ \rho D^{2.62}$ (Ketterings et al. 2001)

where:

W = dry-weight biomass of the tree (kg dw/tree)
ρ = wood density
D or DBH = tree diameter at breast height (cm)

Table 1 Above-ground parameters and methods used in carbon-stock measurement

No.	Parameter	Methods
1.	Living trees with a stem diameter of • 30 cm in standard sample plot (20 m × 100 m) • 5 < ··· <30 cm in large area (5 m × 40 m)	Non-destructive measurement of stem diameter, with allometric equations applied on the basis of stem diameter
2.	Understorey vegetation (including trees < 5 cm in diameter) sample plot (0.5 m × 0.5 m)	Destructive
3.	Litter: • Coarse/standing litter • Fine litter • Surface roots	Destructive
4.	Ash	Destructive
5.	Dead standing trees	Non-destructive, using allometric or cylindric equation (for branched and unbranched remains, respectively)
6.	Dead felled trees	Non-destructive, using cylindric (or allometric) equation
7.	Stump (trunk) remains in forest	Non-destructive, using cylindric equation

After the dry biomass of the tree is known, the amount of carbon (50 % of the dry biomass) can be estimated using the following equation, developed by Murdiyarso et al. (1999):

$$C = 0.5\ W$$

where:

W = Biomass dry weight of a tree (Kg)
0.5 = estimated amount of organic carbon, i.e., 50 % of W

Litter

The following formula is used to estimate biomass dry weight for litter and undergrowth:

$$\text{Total DW} = (\text{Sub-sample DW}/\text{Sub-sample WW}) \times \text{Total WW}$$

where:

Total DW = total biomass dry weight (g)
Sub-sample DW = sub-sample dry weight (g)
Sub-sample WW = Sub-sample wet weight (g)
Total WW = Total wet weight (g)

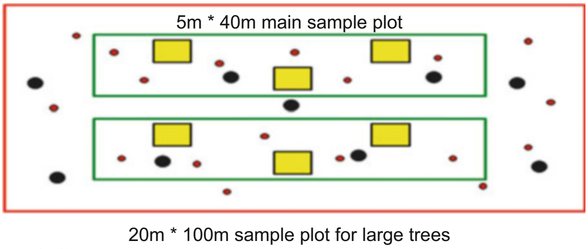
Design of Sampling Plots

This non-destructive method is rapid, and a much larger area and number of trees can be covered within limited sampling time, reducing the number of sampling errors that may be introduced by the destructive method. According to several reports (Henry et al. 2010; Hairiah et al. 2011; Cole and Ewel 2006, etc.), half the biomass of a natural forest can be estimated by calculating only a few trees with diameters above 50 cm. The accuracy can be improved if trees with DBH above 30 cm are sampled, in a 20 m × 100 m sampling area. Sample plots of 5 m × 20 m were used for trees 5–30 cm in diameter, and sample plots of 0.5 m × 0.5 m were used for the understorey. Under specific conditions, such as where large trees occurring at densities of 10 trees/ha or less can be a substantial part of total carbon, further adjustments of sample size may be needed. The total number of sample plots made on the research area was 81, of which 3 were large plots, 6 were medium-sized plots, and 18 were small plots on selectively cut areas. On the bush-shrub areas, there were 2 large plots, 4 medium plots and 12 small plots. On the shrub-mixed dryland farm areas there were 3 large plots, 6 medium plots and 18 small plots. On the bare land there was 1 large plot, 2 medium plots and 6 small plots (Fig. 2).

Allometric Equations

The ‘scaling’ relationships, by which the ratios between different aspects of tree size change when small and large trees of the same species are compared, are generally known as ‘allometric’. Allometric equations can be developed locally by

Fig. 2 Nested plot design for sampling various carbon pools at appropriate scales



Symbolism:

□ Big Plot (20m x 100m)

□ Medium Plot (5m x 40m)

🟨 Small Plot (Understorey & litter layer sample plot) 0.5 m x 0.5 m

● Trees DBH > 30 cm, inside or outside of plot

🔴 5cm < tree DBH< 30 cm, inside or outside plot destructive sampling, derived from the literature for supposedly comparable forest types, or estimated from fractal branching analysis. Such equations normally use the tree diameter at breast height (DBH, measured 1.3 m above the ground) as a basis. Empirical equations for total biomass W, based on the diameter D, have a polynomial form.

The allometric equation for *Theobrama cacao* is taken from other research in Central Sulawesi Province, which was done for calibration using destructive sampling based on the Ketterings method (Smiley and Kroschel 2008). The allometric equation for this is

$$\mathrm{W} = 0.202 \times \mathrm{D}^{2.112}$$

The equation for *Swietenia mahagoni* is based on the Ketterings method (Krisnawati et al. 2011) and is

$$\mathrm{W} = 0.0048 \times \mathrm{D}^{2.68}$$

In both equations, W (dry-weight biomass of the tree) is in the units kg dw/tree, and D (DBH) is in cm.

Results

Land Cover

Based on GIS analysis of land cover from the year 2006, it appears that the bush/shrub category was occupying the largest portion of the research area, i.e., 930 ha or 50.2 % of the total area. The selective-cutting category ranked second, with 434 ha or 23.4 % of the total area. Shrub-mixed dryland farm was third, with 290 ha or 15.6 % of the area. Bareland had the lowest coverage, at 199 ha or 10.8 % (see Fig. 3; Table 2).

For the year 2009, land cover was estimated in combination with interpreted data from the Ministry of Forestry. In 2009, bush/shrub was occupying the largest portion of the research area, at 1006 ha or 54.4 % of the total area. Selective cutting ranked second, with 442 ha or 23.8 % of the total. Shrub-mixed dryland farm was third, with 326 ha or 17.6 % of the area; and bare land showed the lowest coverage, with 79 ha or 4.2 % of the total area. Figure 4 depicts the general land-cover condition in 2009.

As shown in Table 2, the most significant change in land cover from 2006 to 2009 was due mainly to an increase in the shrub-mixed dryland farm category, from 930 ha in 2006 to 1006 ha in 2009, an increase of about 4.1 %. On the contrary, the area of bare land decreased from 199 ha in 2006 to 79 ha in 2009. There was no oil-palm plantation in the research area. GIS analysis identified that approximately

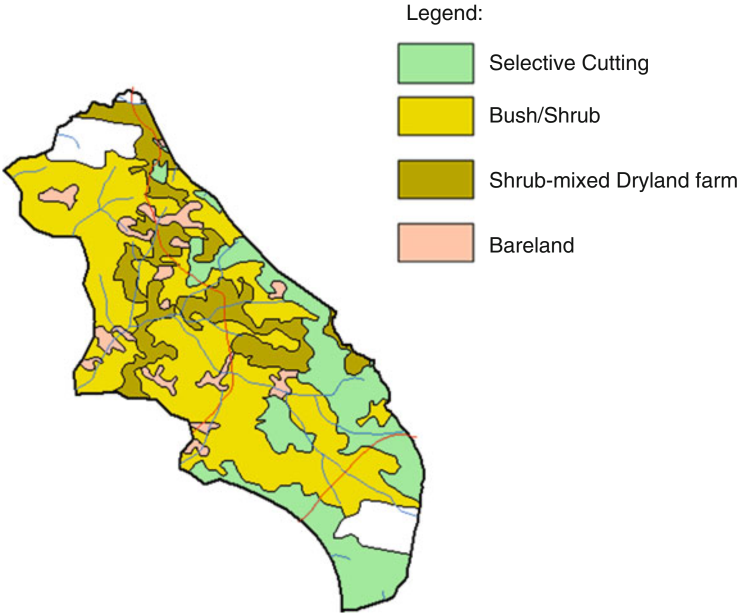


Fig. 3 Land cover map for 2006 for the research area at Klumbayan

Table 2 Areas of land-cover types in 2006 and 2009, for the research area at Klumbayan

		2006		2009	
No.	Land cover type	ha	%	ha	%
1.	Selective cutting	434	23.4	442	23.8
2.	Bush/shrub	930	50.2	1006	54.4
3.	Shrub-mixed dryland farm	290	15.6	326	17.6
4.	Bare land	199	10.8	79	4.2
Total		1853	100	1853	100

160 ha of bare land changed to bush/shrub and shrub-mixed dryland farm over the period 2006–2009.

Carbon

Allometric modeling was applied to estimate biomass and carbon stocks, for each individual tree in the plots. Based on the specific area factors for plot and subplot sizes, the total C stock per unit area (hectares) can be estimated for each individual tree in a plot. Several allometric equations have been derived from past studies for various tropical tree species. Some of these equations consider tree diameter, height

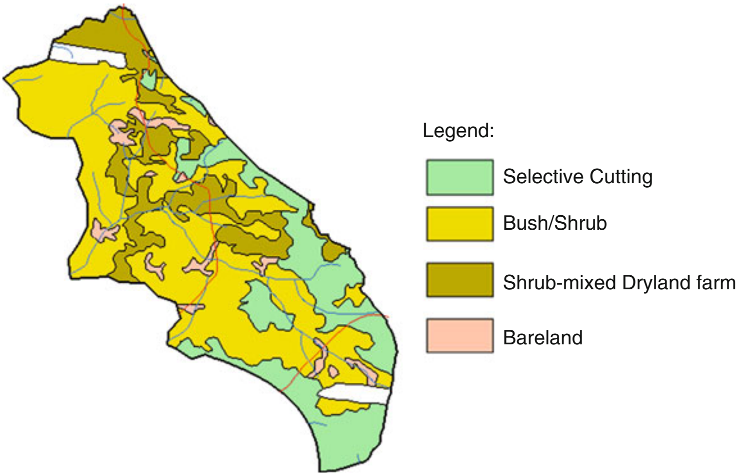


Fig. 4 Land cover map for 2009 for the research area at Klumbayan

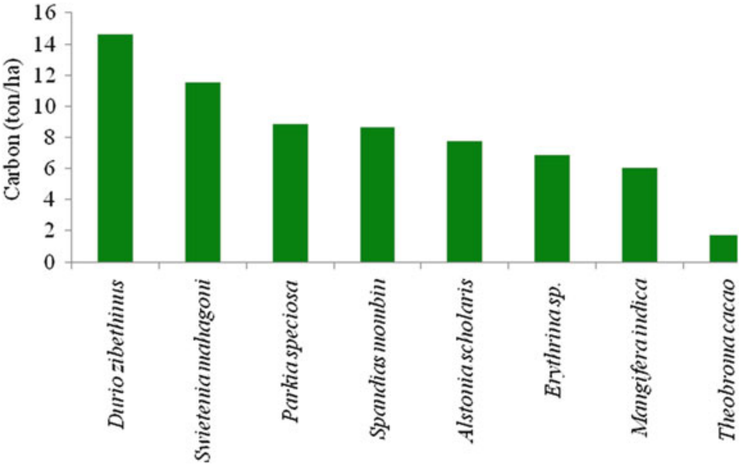


Fig. 5 Carbon stock for trees species in the selective-cutting area

and wood density, and some involve subsets of the three variables. Some equations were developed specifically for particular climatic zones.

Figure 5 presents the carbon stock for species in the selective-cutting area of the sample plots, including the species *Theobroma cacao, Parkia speciosa, Swietenia mahagoni, Durio zibethinus, Pithecelobium jiringa, Mangifera indica, Spondias mombin, Alstonia scholaris and Erythrina* sp. For species with diameter 5–30 cm, the highest carbon stock was in *Durio zibethinus* (14.95 t/ha) and *Swietenia mahagoni* (11.56 t/ha), because these two species have the largest diameters.

Figure 6 presents the carbon stock for species in the shurb-mixed dryland farm area of the sample plots. The species include *Theobroma cacao, Lansium domesticum, Swietenia mahagoni, Durio zibethinus, Pithecelobium jiringa, Alstonia scholaris and Erythrina* sp. For species with diameter 5–30 cm, the highest carbon stock was again in *Durio zibethinus* (6.07 t/ha) and *Swietenia mahagoni* (4.94 t/ha), because these two species have the largest diameters.

Figure 7 presents the carbon stock for species in the bush/shrub area of the sample plots, with values for *Theobroma cacao, Parkia speciosa, Swietenia mahagoni, Durio zibethinus, Pithecelobium jiringa, Mangifera indica and Spondias mombin.* For species with diameter 5–30 cm, the highest carbon stocks

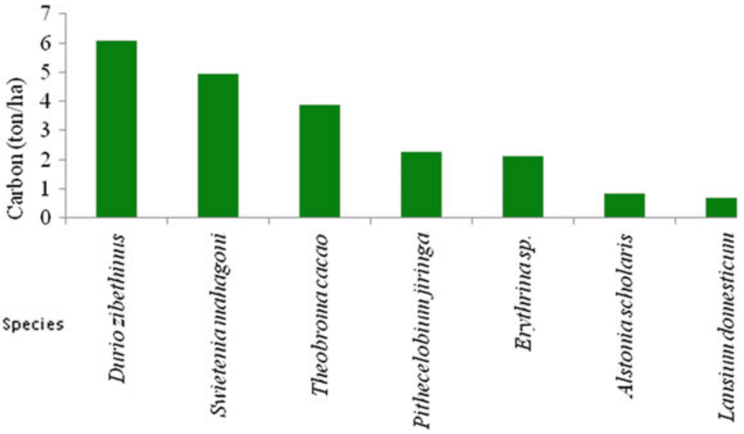


Fig. 6 Carbon stock for tree species in the shrub-mixed dryland farm area

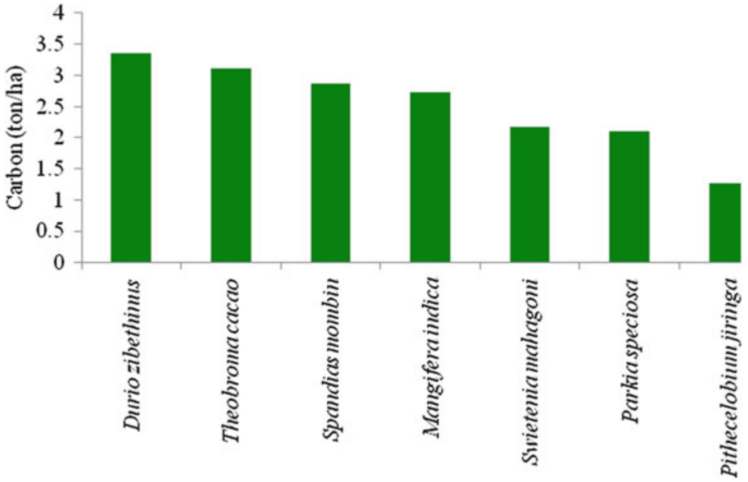


Fig. 7 Carbon stock from tree species in the bush/shrub area

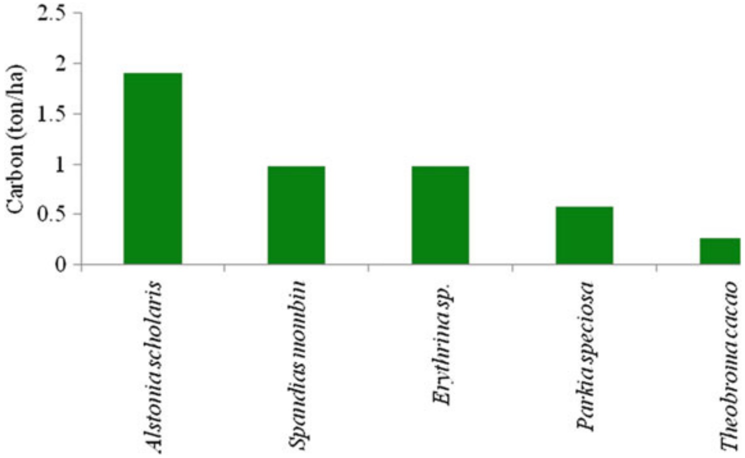


Fig. 8 Carbon stock from tree species in the bare-land area

were in *Durio zibethinus* (3.13 t/ha) and *Theobroma cacao* (3.11 t/ha), because these two species have the largest diameters.

Figure 8 presents the carbon stock from species in bare land area within the sample plots, including *Theobroma cacao, Spondias mombin, Parkia speciosa, Alstonia scholaris and Erythrina* sp. For species with diameter 5–30 cm, the highest carbon stocks were in *Alstonia scholaris* (1.91 t/ha) and the *Erythrina* sp. (0.98 t/ha), because these two had the largest diameters.

Three size classes were recognized for the study of the community forest: trees with DBH > 30 cm, trees of DBH 5–30 cm, and understorey. The most carbon was in trees of the 5–30 cm diameter class, and the lowest coverage belonged to the understorey of the research area (Table 3).

The highest average C stock was in trees with DBH 5–30 cm in the selective-cutting area. Trees with DBH 5–30 cm contributed more than 50 % of the average C stock in the selective-cutting, bush/shrub, shrub-mixed dryland farm and bare-land areas, which was more than for trees of DBH > 30 cm or for the understorey (Fig. 9).

The carbon stocks in this study represent the organic carbon contained in the biomass of trees, shrubs and litter as well as the soil. The remote-sensing data used to build the model were from Landsat ETM years 2006 and 2009, path 123 and row 64, with spatial resolution of 30 × 30 m. Field carbon stocks were estimated using allometric methods based on measurements on 20 m × 100 m plots located in the selective-cutting, bush/shrub, shrub-mixed dryland farm, and bare-land portions of the research area. Field measurements show that, in general, the average C stock in the selectively cut area, at 32 t/ha, was far higher than in the bush/shrub (14 t/ha), shrub-mixed dryland farm (22 t/ha) or bare-land (5.8 t/ha) areas (Fig. 10).

From the 81 plots that were measured, we were not able to derive time-averaged carbon stock for each of the land use systems because, for some land use types, we

Table 3 Total carbon measured in the research area

Land cover type	Plot	Measured variables			C (t/ha)
		Tree > 30 (cm)	Tree 5–30 (cm)	Understorey	
Selective cutting	Plot VI	5.8	25.2	1.0	32.1
	Plot VII	5.6	25.7	1.0	32.3
	Plot VIII	7.6	21.6	1.0	30.1
	Average	6.3	24.2	1.0	32
Bush-shrub	Plot III	1.02	12.2	0.8	14
	Plot V	1.46	10.6	1.0	13
	Average	1.24	11.42	0.90	7
Shrub-mixed dryland farm	Plot I	10.3	12.4	0.8	23.5
	Plot II	4.7	14.6	0.8	23.5
	Plot IV	4.8	17.3	1.0	23.5
	Average	6.6	14.8	0.9	24
Bareland	Plot IX	–	4.7	1.1	5.78
	Average	–	4.7	1.1	5.8

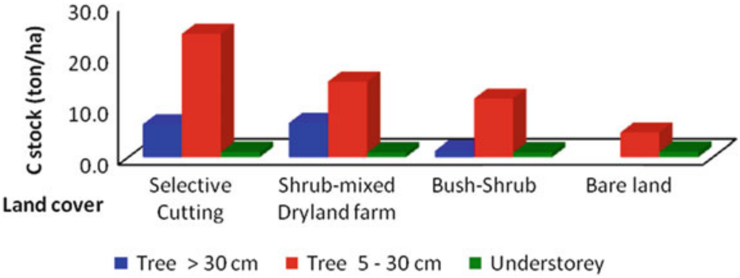


Fig. 9 Carbon stock in several land cover classification types

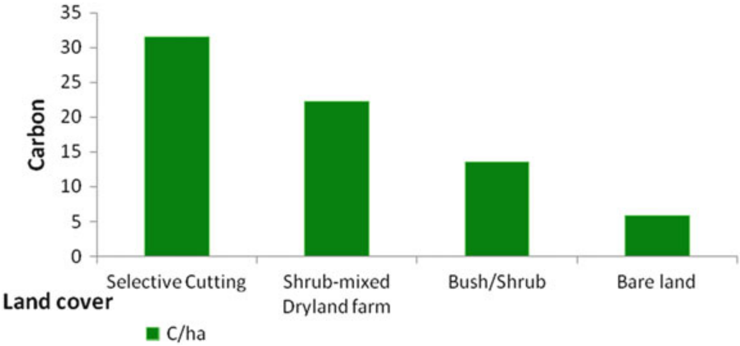


Fig. 10 Carbon stocks in the four land cover types studied

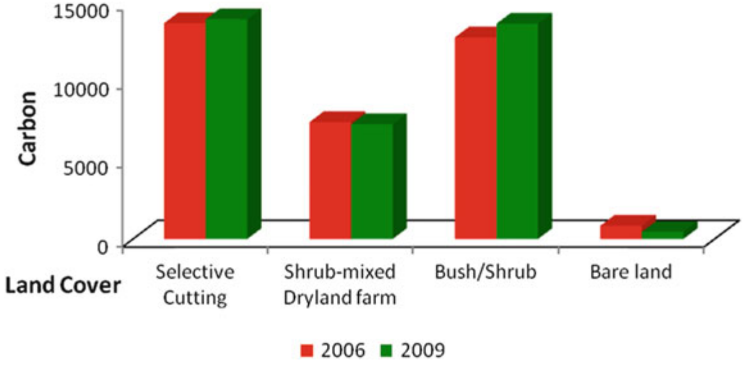


Fig. 11 Total carbon stock of 2006 and 2009 in every land cover condition

could not find plots that represented different age groups within the full cycle of a land use system. Therefore we referred to them as land-use types rather than land-use systems. We used Ketterings' allometric equation for the forest tree species (Ketterings et al. 2001). All measurements were conducted on mineral soils. Forest plots of all types have higher average carbon stock than other land use/cover types.

The estimated above-ground carbon stocks in community forest from the Landsat ETM model of year 2006 show that, in general, the carbon stock in the selective-cutting area, at 13,671 t, was far higher than in the bush/shrub (12,770 t), shrub-mixed dryland farm (7387 t) or bare land (837 t) areas. For the landsat ETM model of year 2009, the results were the same as for year 2006, with actual carbon stocks of 13,923 t for the selective-cutting area, 13,638 t for the bush/shrub area, 7257 t for the shrub-mixed dryland farm area, and 456 t for the bare land (Fig. 11).

Discussion

Allometric functions were used for estimation of carbon in above-ground biomass. Since leaf carbon accounted for less than 3 % of total above-ground carbon, the relationships between allometric variables and C stocks in stems and total above-ground biomass are likely to predict above-ground non-foliage C stocks accurately. Since wood constitutes the largest portion of total tree biomass and is concentrated in the stem, biomass and diameter are closely related. This relationship has been reported to occur in a wide range of different-sized trees (e.g., Senelwa and Sims 1998; Van et al. 2000).

On the other hand, allometric relationships for leaf and branch biomass as a function of DBH show lower correlation coefficients than for stem and total above-ground biomass. Similar results have also been reported for leaf biomass in other forest trees (e.g., Kira and Shidei 1967; Kenzo et al. 2009). Greater variation in environmental conditions, such as light, soil nutrients and water, may be reflected as variations in the leaf and branch allometric relationships (Lambers et al. 1998). In fact, significant interspecific differences for the leaf allometric equation have also been reported in early-successional tropical secondary forest trees (Kenzo et al. 2009).

Field measurements show that, in general, the C stock in the selective-cutting area was far higher than in the bush/shrub area (Fig. 8). The total average C stock under selective cutting (2009) was 13,923 t, which is much lower, however, than that found in forest at Sumber Jaya, West Lampung, i.e., 26,282 t (van Noordwijk et al. 2002).

The total carbon density (Fig. 8) derived from the land-cover classes and the typical carbon densities indicate a substantial increase over the 2006–2009 period, especially in the selective-cutting (13,671–13,923 t) and bush/shrub (12,770–13,638 t) areas. The total carbon budget for the land cover was estimated from the total area of each land-cover type, including estimates made under cloud cover.

The study did not include soil carbon, although soil carbon represents a significant amount of forest carbon, due to time and technology constraints involved in estimating soil carbon.

Community forest is a strategy likely to be adopted by other countries as part of their national REDD program. It could be carried out in all forest areas near rural settlements, particularly in those parts of the forest that are already under community management or that will be brought under community management under REDD. This may in itself provide a stimulus for involvement of local communities in REDD Carbon storage in community forest systems and its eventual consequences for global climate are fraught with a number of uncertainties. Consequently, there is still some work to be done to improve our understanding of C sequestration and mitigation of the effects of increasing amounts of greenhouse gases in the atmosphere.

Conclusion

Based on the study results, several conclusions can be made:

1. The greatest carbon content was in trees of DBH 5–30 cm, and the lowest amount was in the understorey of the research area.
2. Field measurements show that, in general, the average carbon stock on community forest in Lampung was far higher under selective cutting (32 t/ha) than in the bush/shrub (14 t/ha), shrub-mixed dryland farm (22 t/ha) or bare-land (5.8 t/ha) areas.
3. The total carbon density derived from the land cover classes and typical carbon densities indicated a substantial increase over the 2006–2009 period, especially for carbon in the selective-cutting (13,671–13,923 t) and bush/shrub (12,770–13,638 t) areas.

4. This study was limited by not including soil carbon, because of time and technological constraints. Future study should include soil carbon data for a truer picture of whole-ecosystem carbon in community forests.

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Part VI
Perspectives

Vegetation History and Dynamics in New Zealand: Future Scenarios and Improved Trajectories Towards Restoring Natural Patterns

Colin D. Meurk, Jon Sullivan, and Wendy McWilliam

Abstract New Zealand is a micro-continent that has been more isolated from mainstream (especially Northern Hemisphere) evolution than any other large, ice-free land mass. This has created a land of unusual and often unique ecology, notably lacking land mammals. Native Gondwanan elements, and others considered ancestral to major world lineages, imply some continuity back to Gondwana itself. Together, both old and new arrivals make up a largely endemic biota. These have been decimated both ecologically and socio-culturally (extinction of experience) by large numbers of recent continental imports. We examine opportunities for recovery of some of the lost integrity of natural patterns, at a range of scales, albeit in the absence of an alarmingly high number of extinct and critically endangered, keystone species. Apart from the essential pest-control programmes being carried out assiduously by Government and NGOs, our research has focused on design of landscape factors that can facilitate regeneration, recovery, and connectivity (ecologically and socio-culturally). Earlier landscape-optimising models are being combined with reserve-design theory (island-biogeography concepts) and spatial configurations based on empirical dispersal data, refined by considering the patch condition and proximity requirements of contrasting wildlife guilds. We present some preliminary data. Like the rest of the world, New Zealand is at an ecological crossroads regarding the extent to which it will retain its endemic biota and landscape legibility. We can take action even in the absence of perfect knowledge to apply the most promising strategies and restoration techniques available—or we can wait and watch the decline.

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Introduction

New Zealand is a micro-continent that has been more isolated from mainstream (especially Northern Hemisphere) evolution than any other large, ice-free land mass. Pine, willow, poplar, oak, elm, ash, maple, birch, rosaceous trees, land mammals and most large advanced reptiles are significant South Temperate Zone absentees. Glaciation had a considerable impact on tropical elements—with nowhere to go on an archipelago. This has created a land of unusual and often unique ecology (Sullivan at al. 2010). While many groups have reached New Zealand shores regardless (Goldberg et al. 2008), native Gondwanan elements (leiopelma frogs and tuatara), and others considered ancestral to major lineages (such as the New Zealand wrens, basal to the passerines), imply that there has been some continuity, albeit as archipelagic and temporal stepping stones, through the >60 million years back to Gondwana itself (Lee et al. 2001; Wilson 2004; Swaffield et al. 2009; Gibbs 2011). These ancient elements have in turn been masked somewhat by many more recent, trans-oceanic arrivals over the past 5–10 million years, which have subsequently radiated in new mountain environments or, in the absence of mammalian predators, evolved some bizarre adaptations and lost redundant functionality, such as bird flight. Together, both old and new arrivals, make up a largely endemic biota (100 % of bats, amphibians and reptiles; 90 % freshwater fish; >80 % vascular plants and invertebrates; and 70 % of land and wetland birds).

One of the most defining influences on the unique biogeography of New Zealand is the lack of land-dwelling mammals except bats (Wilson 2004; Lee et al. 2010). This is the largest ice-free land mass in the world with such a lop-sided fauna. There are bats, sea mammals and evidence of a small marsupial snuffling around in the Tertiary (Worthy et al. 2006). Furthermore, New Zealand was the last major land mass besides Antarctica to be settled by humans, with Polynesians now thought to have arrived around 1280 A.D. (Wilmshurst et al. 2008). These and later peoples brought predatory mammals which have devastated the highly endemic native fauna, totally naïve to this brand of continentally honed predation. And later mammalian herbivores, together with an avalanche of exotic plant species co-adapted to mammal grazing and browsing, and associated with widespread deforestation and land use change, created a pincer movement of defoliation from above and competition from below.

Added to these ecological circumstances is the complex social dynamic. 'Extinction of experience' (Miller 2005) has occurred because the human-co-adapted, introduced utility/amenity species, supported by centuries of plant and animal breeding from the immigrant's homelands, took over the transformed landscapes and created in New Zealand the old familiarity and sense of place that reinforces the dominance of and protectiveness towards exotic (homeland) species in the cultural landscape (Meurk and Swaffield 2000). This has put great strain on the ecological integrity of lowland biota especially. Unfortunately, the transformed landscape is familiar to northern hemisphere tourists, and so it is marketed and further reinforces

New Zealand as an ‘unspoilt’, clean, green, idyllic and romanticised Northern Hemisphere in miniature.

This short paper summarises key factors of the condition and trend of New Zealand landscapes and ecosystems, as well as opportunities for recovery of some of the lost integrity of natural patterns, albeit in the absence of an alarmingly high level of extinct and critically endangered species—some of which were keystone.

New Zealand Forest and Wetland Vegetation: Excluding Alpine, Seral and Dune Vegetation

Outside of the Southern Alps, and naturally disturbed or excessively wet environments, New Zealand was, and is potentially, forested throughout. The forests and shrublands of New Zealand comprise several broad groupings (Meurk 1995; Wiser et al. 2011; Wiser & De Caceres 2013): rainforest of kauri (*Agathis australis*) in the far north, podocarps throughout, and southern beech (*Nothofagus*) in cool or leached land; floodplain and swamp forest (podocarp-hardwood); dry forest (podocarp and hardwood woodlands); and coastal forest (hardwoods); plus quasi-climax communities of small-leaved divaricating shrubs in very dry or otherwise stressed environments. Wetlands comprise swamps (*Typha*, *Phormium*, sedges, rushes), fens (sedges and restiads), bogs (cushion plants, restiads, *Gleichenia* fern) and salt marshes (mangroves, restiads, rushes, sedges and mat plants) (Johnson & Gerbeaux 2004). These communities expanded following Polynesian fires and have contracted again in the post-European drive to drain and farm their productive soils.

Condition and Trend

Forest canopies have been stable although there is a shifting emphasis to less palatable regeneration and understorey species—due to naturalised deer, pigs, goats and possums (Forsyth et al. 2010; Stewart 2010). Native shrublands and woodlands, apart from unpalatable *kanuka* and daisy shrubs, are often regarded as ‘living dead’ due to lack of recruitment from palatable seedlings. These landscapes have also been displaced by exotic leguminous or daisy shrubs, hastened by use of herbicides or fire, which in fact favour the quickly regenerating and browse-tolerant exotic woody plants, and cause the gradual shift of dominance away from the native species. Coastal dieback, wetland drainage, and replacement of wet marshes by farmers’ ponds (often for attracting and shooting the introduced and prevalent mallard duck) are all contributing to general and widespread attrition of natural vegetation.

Critical aspects of New Zealand's forest biology are that about 75 % of native woody plants bear fleshy fruits and/or nectar (Burrows 1994; Kelly et al. 2010), are largely evergreen, and somewhat shade-tolerant. Many of these species thus depend on birds (or lizards) for dispersal. In contrast, the majority of the dominant exotic trees are dry-fruited or they are warm-temperate to subtropical evergreen broadleaved, shade-tolerant trees that have similar but more aggressive functional characteristics to the native forest species. These also get dispersed by birds and can therefore invade the evergreen indigenous forests.

All this underscores the fact that a primordial bird/lizard-driven ecosystem has been largely replaced by a naturalised mammal-bird-driven system during just 0.001 % of New Zealand's separate history. The prognosis is not good, based on current trends. Various strategies have been debated and tested over the years, though, and new technologies are providing more options, notwithstanding their publicly controversial nature. Killing anything is an ethical/moral dilemma and much conservation in New Zealand, in order to be successful, requires killing plants and animals, or even extermination of whole populations. But what the public (and animal-rights advocates) do not see is the nightly carnage of defenseless unique indigenous species meted out by the exotic carnivores. In light of this, the independent environmental commissioner for New Zealand has been unequivocal about the need for these methods of control (http://www.pce.parliament.nz/publications/all-publications/evaluating-the-use-of-1080-predators-poisons-and-silent-forests).

New Zealand's Department of Conservation and regional councils already target about 500 weedspecies, about 20 % of the naturalised vascular flora, which in total is now larger than the native vascular flora (Sullivan et al. 2004) and continually increasing. As well, there have been several concerning outbreaks of potentially transformative diseases attacking indigenous species such as the phytophthora disease in kauri.

Responses

Apart from the essential New Zealand pest-control programmes and research, we have been focusing on landscape factors that can facilitate regeneration, recovery, and connectivity (not only ecological but also socio-cultural). We are building on preliminary modeling work carried out by Meurk and Hall (2006) that endeavours to design (within practical human constraints and requirements of cultural landscapes) optimum reserve sizes, configurations, linkages, structural integrity (that facilitates regeneration) and composition (continuous fruit and nectar sources for wildlife), while avoiding biosecurity risks. This is essentially defining and implementing a re-born vegetation pattern through space and time for New Zealand's cultural landscape. Much of it is about facilitating natural regeneration (Stewart et al. 2004) along appropriate trajectories, while armies of volunteers are actively planting back the lost forests, wetlands and dune systems (Sullivan et al. 2009, http://www.dunestrust.org.nz/). In the meantime, those government departments responsible for conservation, biodiversity and biosecurity are developing systems to work smarter with declining budgets by prioritising targets with more quantified indicators.

Our Research Contribution

We have looked to extend the earlier landscape-optimising modeling work through combining reserve-design theory (based on island-biogeography concepts) and spatial configuration based on empirical dispersal data (Meurk and Hall 2006), literature (Walker et al. 2008), personal observation, and refined by considering contrasting guilds of wildlife with different habitats, food requirements, size and likely foraging distances. We already know a substantial amount about receptivity of landscape elements to seedling establishment. Most native forest trees and shrubs in New Zealand are evergreen, bird-dispersed, shade-tolerant and palatable, but are also weak competitors in dense, exotic grass swards (as opposed to the more open bunch-grass natural grasslands). These species generally require a woody canopy that has been through an initial dense phase and suppressed the grass, then matured, opened and let in enough light for woody plant seed to germinate and grow. In New Zealand this “goldilocks zone” can be provided by some early successional species in the families Myrtaceae, Rubiaceae or the genus *Pittosporum*, but also by short-lived, exotic leguminous shrubs, willows, eucalypts and conifers. Thus restoration of habitats and landscapes is now often managed through pre-existing cover, because, as it turns out, removal of this is counter-productive and usually just creates a bigger and endless (new) weed problem. Many naturalised exotics are better and faster at exploiting these disturbances than indigenous species. Indicative guidelines that meet landscape requirements for various indigenous wildlife are shown in Table 1.

To reiterate, predator control is imperative, not just for the ferocious predators like mustelids, rodents, cats and dogs, but the vacuum cleaner-like mice, hedgehogs, possums and pigs—for full ecosystem restoration. Some shade-tolerant exotic trees, shrubs and ferns will need to be managed, and dense herbaceous growth has to be controlled for open ground native species to co-exist (see below). Diseases also threaten at times, as mentioned. While exotic polyphagous pest insects can be an issue for some native plants at some locations; hitherto this has been unusual (Brockerhoff et al. 2010).

The particular innovation that is springing up around the country is the predator-proofed eco-sanctuary (see Fig. 1). This is perhaps the cornerstone of an even more ambitious goal of a pest-free New Zealand (now dubbed the Callaghan concept). Basically, this involves fenced or systematically poisoned sanctuaries in both mainland islands (http://sanctuariesnz.org) (and yes this seems full of paradoxes) and real oceanic islands, where the line is drawn creating a starting point for rolling back the predator wall from pressing against these bulwarks. The widely used

Table 1 Working hypotheses for modeling (ecologically and socially) optimum spatial configuration and other metrics of habitat and patches for a range of different wildlife guilds in New Zealand cultural landscapes (based on sources indicated in text)

Guild	Indicator species	% Habitat cover	Minimum patch or matrix* area (ha)	Maximum interpatch gap (km)
Bush bird—herbivore	NZ Wood pigeon	10–15	5–10	25
Bush bird—omnivore	Bellbird and Tui	10–15	5–10	10
Bush bird—insectivore	Grey Warbler and Fantail	5	0.5–1	1
Wetland bird	Fernbird and Pukeko	5	25–50	50
Forest/scrub lizards and sedentary inverts	Gecko and Leaf Vein Slug	5	5–10	0.005
Open ground lizards and mobile inverts	Skink and Large Moth	5	1	0.05

*Note: the maximum inter-patch gap compatible with effective dispersal of berry fruits is only about 2–3 km from source to receptive sink.

Fig. 1 A uniquely New Zealand 'landscape sculpture' (otherwise known as a scientifically tested, predator-proof fence) is a concept particularly resonant of New Zealand's battle to save its unique wildlife

mammalian pest-targeted pesticide 1080, along with cocktails of other poisons, does mean killing many organisms, and there are some side-effects and by-kill. But, unfortunately, much of New Zealand's native wildlife has near zero-tolerance of exotic mammals and just cannot coexist with them.

One celebrated example is Zealandia (http://www.visitzealandia.com) in Wellington, where local communities operate and various recording systems are being used to monitor the 'halo effect' which is the spread of vulnerable wildlife out from the fenced sanctuary into the surrounding residential and even commercial property (http://naturewatch.org.nz/projects/enhancing-the-halo). It is helped by the fact that Wellington is a hilly, moist place with gully remnants of native bush. The question is whether these birds that explore the great wide world are just easy meat for cats, rodents and mustelids, or whether we can control the urban domestic and feral animals to effectively establish the halo.

Regardless of how effective removal of invasive and predatory species is, New Zealand will always have more exotic plants, birds, and mammals than indigenous species. Acceptance of this requires a new analysis of the possible vegetation patterns and objectives—what we will end up with are sometimes referred to as 'recombinant' ecosystems (Meurk 2011). A new type of management will also be required to balance the species and ensure survival of all our remaining biota. An approach to this is what we have referred to as 'gradient management' (Meurk et al. 2003).

This is really a scaled-up version of J. P. Grime's stress-disturbance matrix for interpreting and managing herbaceous vegetation especially (Grime 1977; 2002; Meurk 2004). It proposes that different permutations and combinations of plant composition will exist under every conceivable management regime (lying somewhere along the continuum of a stress x disturbance matrix). Some positions on the spectrum will be more or less favourable to indigenous and less so to exotic species. But every species will have a different optimum position, so no single management will suffice to ensure survival of all our biota (particularly that of the lowlands). Generally, indigenous species will do best when conditions are less hospitable, as competition from exotics will be reduced (Moen & Meurk 2001). Accordingly, many levels of stress (e.g. from temperature, drought, fertility) and disturbance (e.g. from natural land and soil disruptions, wind, and grazing) please remove this phrase, I can't seem to - thanks need to be applied in an adaptive management context to generate fully representative spatial and temporal patterns of indigenous species' distributions, environments and successional stages.

The implementation of these concepts to forest, wetland and seral habitats across New Zealand is being achieved in a somewhat *ad hoc* fashion through natural regeneration, numerous planting and pest control guides, and through hundreds of community groups across the country (Sullivan et al. 2009). These groups volunteer their time to restore lost habitats, often in partnership with government departments, businesses and local government. Dozens of native-specialist plant nurseries are also supplying millions of indigenous plants every few years. How well these plants are being selected, propagated, planted and managed, and how well the wildlife is being protected, remains to be seen.

All players are striving to attain a more professional and efficient approach to this urgent task, often in the face of shrinking resources that sometimes seem to be unproductively used for competitive fund raising and administration. They are out there fixing up degraded habitats. They are removing weeds and replanting lost species. Other groups focus on predator trapping and creation of pest-free sanctuaries (Fig. 1). While still others are deliberately planning wider landscape configurations that follow the theoretical pattern devised by Meurk and Hall (2006) that addresses the issues of critical mass of core habitat, minimizing negative edge effects, reserve spacing, and connectivity—both ecological and social (Figs. 2, 3 and 4) (e.g. http://www.kakariki.org.nz/).

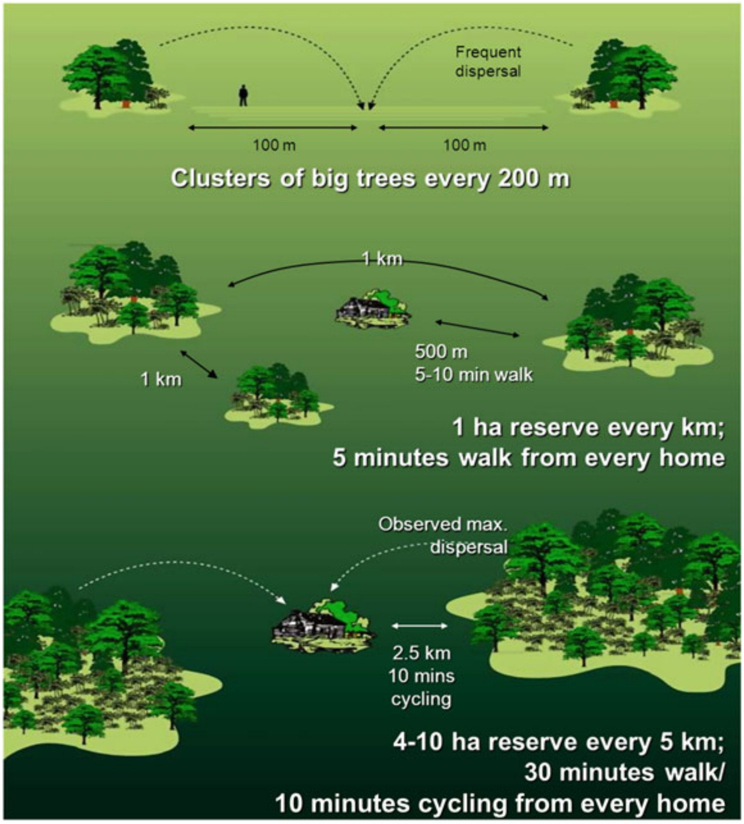

Fig. 2 An optimised configuration of habitat patches, connectivity (within stepping-stone distances)—complemented by continuous habitat corridors, protection for different guilds, and community visibility, identity, and acceptability within the context of cultural landscapes

The intention of all these intiatives is to achieve landscapes with ecological integrity (that function correctly), and natural character with 'the New Zealand look.' This can be described as evergreen broadleaved bushy and emergent trees (early botanists saw an almost tropical appearance), juvenile forms, divaricating shrubs, tussock grasses, and weird wildlife (Gibbs 2011). These landscapes resonate with the 'meaning' of these species to the indigenous people and later immigrants. This is about the landscape concept of 'legibility'—being able to read the stories in the visible patterns of the land that are understandable or interpretable. They may be recombinant systems, but the indigenous component is strong and visible in its own right, not reduced to subordinate 'green fluff'. Only then can we look the world straight in the eye and say we are 100 % pure and clean and green, and legitimately invite tourists here to see an authentic, unique environment. The highway network is the shop window of the country, and this will be a good place to start to repair the

Fig. 3 A real-world example of patch configuration (different-sized forest patches) with varying degrees of separation within a pastoral farmland context. Such a landscape can be said to have natural character (the tree components are predominantly indigenous). The ecological integrity of the patches and corridors are dependent on predator control or extermination

Fig. 4 A landscape topographically similar to the previous (Fig. 3) but biologically depauperate, demonstrating the need and opportunity for restoration of habitats and linkages

damage (Meurk et al. 2012). The recombinant nature of the landscape poses problems for herbaceous systems, but the Gradient management approach (Meurk & Greenep 2003) is one way to overcome this. Still more knowledge and experience are required to understand the best ways to manage these novel combinations.

As part of these recombinant rearrangements (Norton 2009), we also have to consider the staging of manipulation. Are some predators useful as an interim solution, e.g., the meso-predators (cats) that in turn prey on and keep in check the more vicious predators (rodents and mustelids)? And are some exotic nectar-producing plants to be encouraged in the short term, such as Australian Myrtaceae and Proteaceae (which, after all, were here in the Tertiary), providing that they do not themselves become weeds?

The key need is to hold the line on biodiversity, i.e., to retain all remaining species in self-sustaining populations that also contribute to the visual landscape. We can do better with our production forestry (currently dominated by Californian pines), such as by storing more carbon by increasing the use of slow-growing, heartwood-dense native trees in managed continuous-canopy forestry. This also reduces the need for toxic wood preservatives, necessary for utilizing the fast-growing exotic soft-wood trees in construction timber. Eco-tourism is one of the primary products we have to offer, but we also need to be aware that the cost of international travel is likely to increase in the future. Many trees need to be grown in order to offset the carbon emissions and New Zealand has many areas of young regenerating scrub where this is possible.

There will be major ecological barriers to recovery that still must be overcome, and the fact that New Zealand has insular idiosyncrasies makes this more difficult ecologically. Relative scientific illiteracy and the extinction of experience make this even more challenging. Nevertheless, there is hope for positive change, to some extent by stealth (native plants are a bit like the tortoise in the famous 'tortoise and hare' parable), and through the choices of a younger, and more educated generation of New Zealanders. Our unique New Zealand experiences may yet be brought back from extinction. We can also be smarter and more creative in design, so that we increase the wilderness without raising people's suspicion and fear of losing control over their environment (Nassauer 1995). Just communicating what is possible and establishing demonstrations of the innovative ways for using indigenous species in almost every conceivable urban context, will help (Ignatieva et al. 2008).

Conclusions

Vegetation patterns in New Zealand are complicated by the importation of continental species into an endemic biota that is essentially 'other-worldly' in terms of the global mainstream. This is fundamentally different to typical oceanic islands, which are also vulnerable to invasion but where the biota has a low level of endemism, with completely different drivers. Predator control is the key, but the patterns are dynamic, evolutionary, and can now be directed towards a take-off point for nature to become the principal determinant of those patterns. We can assist by providing the infrastructure of appropriate patch arrangements, and quality of patches to facilitate recovery. Humanity took away the self-determination of nature in New Zealand and now it is in our power to give it back—a little. It is important, not just to the intrinsic value of life, but also for somewhat utilitarian purposes, to our identity as humans, not to mention pure survival. But it takes us past purely material survival to some deeper engagement with the universe and the miracle of existence—however it happened to be. Like the rest of the world, New Zealand is at a crucial crossroad. There are choices we have to make. We can't wait for perfect knowledge, or we will be watching the decline. We must apply the best information we have now to make the best decisions we can. Informed leadership and champions will be needed at all levels to implement a cultural shift.

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Fundamentals and Perspectives of Geobotanical Research in the Twenty-First Century

Richard Pott

Abstract Geobotany or Vegetation Science is the discipline that attempts to document and understand spatial and temporal patterns of diversity in the world of plants and vegetation. Diversity has evolved into a key word in ecological but also geobotanical research, and so the introductory part draws attention to some aspects of biodiversity: The present-day biodiversity of the earth is reflected from a palaeoecological viewpoint. The natural diversity of climate, geodiversity and biodiversity constitute the treasures of the present global ecosystems. So, biodiversity is a concept of different aspects: Structural biodiversity of life forms, functional biodiversity of ecosystems and production, and evolutionary diversity of long-term and short-term evolution. We share our planet Earth with countless other creatures—today about 1.75 million species of animals, plants and microorganisms are registered, and we know that many more species exist: perhaps between 10 and 100 million species. However, a portion will go extinct before even being discovered.

We use uncountable services of nature in our daily lives: air, water, soil, food and energy for our existence—absolutely for free. By the destruction and overexploitation of natural habitats by human activity, the number of today's known species on earth decreased by about 40 % between 1970 and 2000: a decline of nearly a half in just 30 years! This led to the creation of the term "The Sixth Extinction" to describe the crisis on our planet. With that background, some aspects of global problems in the twenty-first century are discussed and, finally, the role that Geobotanical research could play at the beginning of this new century is outlined.

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Biodiversity: Treasures in the Earth's Ecosystems

Living things are incredibly diverse. The number of known species of organisms, including all living plants, animals and microorganisms, is estimated to be 1.75 million (Wilson 1994). This number does not include many hundreds of thousands of, as yet, poorly defined species in particular groups of organisms (e.g., microbes), which are not readily accessible in the general literature relating to biodiversity. In addition, there are also many species still waiting to be discovered and described scientifically.

This contribution is dedicated to the 70th anniversary of my colleague and friend, Professor Dr. Kazue Fujiwara. She did, during all her scientific life, great fundamental geobotanical research all over the world in nearly all important ecosystems, especially in mires and different forests from the boreal zone to tropical biomes. This manuscript follows a previous one from Pott et al. (2003a), with additions and new aspects for this twenty-first century (Pott 1998).

In addition to present-day species, many more species—almost certainly some millions and perhaps billions—lived at some time in the past but are now extinct; only a small fraction of them have been preserved as fossils. The full geological history of life extends back perhaps 4 billion years, when the first single-celled and hence microscopic Cyanobacteria organisms appeared. These formed stromatolite ecosystems (Fig. 1).

The origin of eucaryotic organisms—the so-called "higher organisms"—dates to about 1.8 billion years ago. Their DNA was enveloped in membranes, and the first eucaryotes resembled modern protozoans and the simpler forms of algae. The rapid increase in biodiversity that took place in the Cambrian, 540–500 million years ago, marked a great step forward in the evolutionary process. New macroscopic plants and animals evolved in a radiative pattern to create the major adaptive types that exist today, and the supply of free oxygen in the atmosphere was close to the present-day 21 % level. The "big bang" in plant and animal evolution at that time created a new, microscopic world of pathogens, symbionts and decomposers. By the late Ordovician period, 450 million years ago, the first plants *Cooksonia* (Fig. 2), *Rhynia* and *Psilophyton* succeeded in colonising dry land (Kerp and Haas 2009). Within 50 or 60 million years, i.e., early in the Devonian, these pioneer terrestrial plants constituted thick mats and low shrub cover over all continents. During the Carboniferous period, i.e., approximately 340 million years ago, this pioneer vegetation had given away to the coal forests, which were dominated to towering lycophyte trees, seed ferns and a great variety of ferns in general. By late Palaeozoic and early Mesozoic time, close to 240 million years ago, many of the carboniferous species were extinct but ferns, conifers, cycads and cycadeoids survived (Fig. 3).

During the course of the last 600 million years, the thrust of biodiversity, mass extinction episodes notwithstanding, has been generally upward. The question arises why the trend in biodiversity has been constantly upward, in spite of major and minor temporary declines along the way and the nearly complete turnover of

Fig. 1 Stromatolites are biogenically layered accretionary structures in shallow marine benthic biotopes, formed by the trapping, binding and cementation of sedimentary grains by biofilms of cyanobacteria, which produce oxygen. The earliest stromatolite on earth is confirmed from 2.7 billion years ago. The modern columnar types from Lake Thetis in Western Australia look like thick calcium carbonate crusts and have been dated to about 3300 years old (Cervantes, Western Australia, 2008)

species, genera and families that has occurred repeatedly. Part of the answer is that the continental land masses have changed in a way that has favoured speciation (Bennett 1998; Pott 2005).

During late Palaeozoic times, the earth's land surface was composed of the single supercontinent Pangaea. By the Middle Eocene 50 million years ago, Pangaea had split into two great fragments, Laurasia to the north and Gondwana to the south; India had broken off as a smaller fragment and was crawling northward to form the Himalayan arc (Fig. 4). Around 10 million years ago, the modern continents were in place, with the oceans between them widening progressively. Major faunal and floristic assemblages evolved in the context of increasing isolation and adapted to new habitats. This resulted in new assemblages of organisms and new ecosystems, which included the phenomena of vicariance and convergence, and so the present-day different faunal and floristic provinces came into being (Comes and Kadereit 1998).

Present-day global biodiversity owes its origin partly to this fragmentation of the land masses (Fig. 5). The map of global diversity of vascular plants, published by Barthlott et al. (1996, 1999), indicates the six areas of highest diversity, which are located in the humid tropics and subtropics. Other centers occur in Mediterranean-type regions with an Etesian climate, for instance in South Africa, Australia and on some Archipelagos in the Atlantic Ocean (Box et al. 1998; Fujiwara and Box 1999;

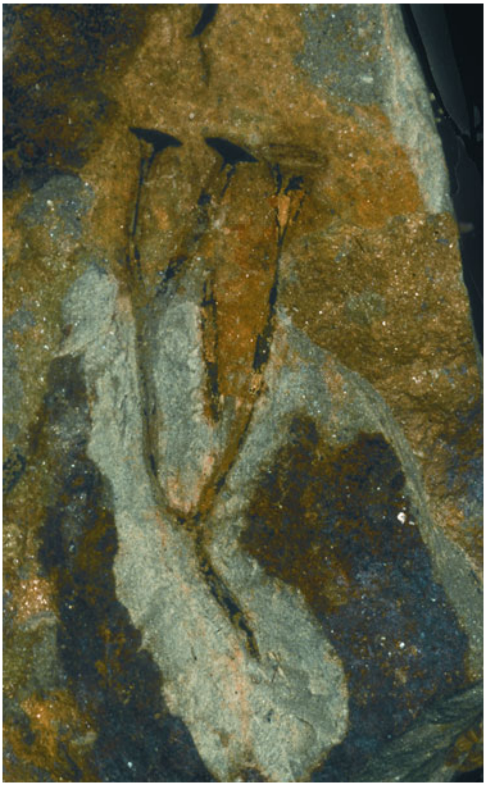

Fig. 2 *Cooksonia pertonii* was a vascular plant from the Devonian and had anatomical features more advanced than those of the bryophytes [Photo: H. Kerp, from Pott (2005)]

Fig. 3 *Cycas revoluta* (Cycadaceae) is native to southern Japan. Its roots are called coralloid, with *Anabaena* symbiosis allowing nitrogen fixation. This dioecious plant occurs widely throughout the Ryukyu Islands, with natural habitats on steep stony sites near the coast (Iriomote, Japan, 2009)

Pott et al. 2003b). Comparatively high species numbers can be found especially in non-arctic mountain regions, such as the Andes in South America or in the Himalaya, showing that high geodiversity increases biodiversity (Pott 2012).

Apart from species richness, other criteria of quality play a role, especially when assessing the value of the biodiversity within a particular region. The proportion of

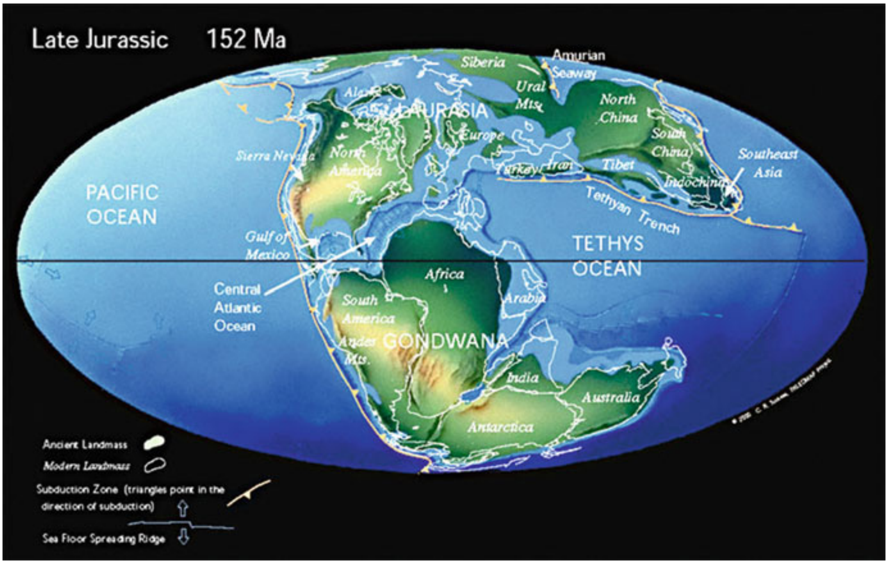

Fig. 4 The supercontinent Pangaea began to break apart in the Middle Jurassic. By the Late Jurassic the central Atlantic Ocean was a narrow sea separating Africa from eastern North America. Eastern Gondwana had begun to separate from Western Gondwana (http://www.scotese.com/late1.htm)

allophytes is a criterion of the quality of habitats which has been receiving increasing attention. It is a manifestation of growing biological globalization, which changes natural habitats and may result in the displacement of indigenous species. It is therefore not surprising that biodiversity and potential changes in biodiversity are playing an increasingly important role in geobotanical research and public discussions.

The Sixth Mass Extinction

The dinosaurs went extinct in slow motion, during the Fifth Extinction some 65.5 million years ago. We expect between 70 and 100 animal and plant species to disappear from planet Earth every single day, and we do not even have an idea what value for biotechnology, medicine or the nourishment of humanity is irretrievably lost. It is a matter of fact that our unprecedented overexploitation of nature endangers our own base of existence in the middle to long term (e.g., Lovejoy 1980; Körner 2012; Tollefson 2013). By the destruction and overexploitation of natural habitats by human activity, the number of today's known species and ecosystems on earth decreased about 40 % between 1970 and 2000—a decline of nearly half in just 30 years! This led to creation of the term "The Sixth Extinction" to describe the crisis on our planet (Barnosky et al. 2011).

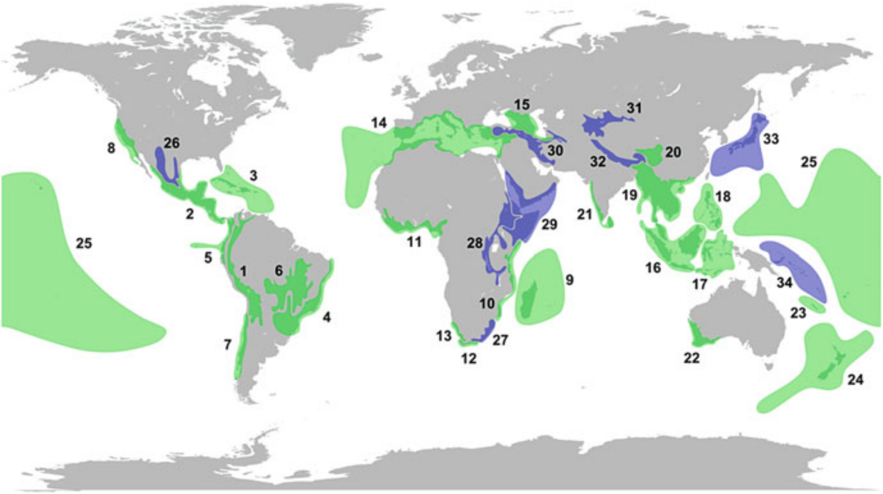

Fig. 5 Biodiversity hotspots (*green*) as indicated in Myers et al. (2000) and Mittermeier et al. (2005): *1* Tropical Andes, *2* Mesoamerica, *3* Caribbean Islands, *4* Atlantic Forest, *5* Tumbes-Chocó-Magdalena, *6* Cerrado, *7* Chilean Winter-Rainfall Valdivian Forests, *8* California Floristic Province, *9* Madagascar and the Indian Ocean Islands, *10* Coastal Forests of Eastern Africa, *11* Guinean Forests of West Africa, *12* Cape Floristic Region, *13* Succulent Karoo, *14* Mediterranean Basin, *15* Caucasus, *16* Sundaland, *17* Wallacea, *18* Philippines, *19* Indo-Burma, *20* Mountains of Southwestern China, *21* Western Ghats and Sri Lanka, *22* Southwest Australia, *23* New Caledonia, *24* New Zealand, *25* Polynesia and Micronesia, *26* Madrean Pine-Oak Woodlands, *27* Maputaland-Pondoland-Albany, *28* Eastern Afromontane, *29* Horn of Africa, *30* Irano-Anatolia, *31* Mountains of Central Asia, *32* Eastern Himalaya, *33* Japan, *34* East Melanesian Islands

A solution for the future is to conserve sufficient amounts of pristine nature and the web of life in all climate-related major biomes and the oceans of the biosphere in order to ensure the required services of global ecosystems for the future well-being of humanity (Balmford and Cowling 2006).

The term “Anthropocene” was coined recently by Crutzen and Stoermer (2000), who regard the influence of humans on Earth’s environment in recent centuries, especially since the Industrial Revolution of the nineteenth century, as so significant as to constitute a new geological epoch for Earth’s lithosphere and atmosphere. Other scientists link the new term to the Neolithic Revolution and the beginning of agriculture, deforestation and permanent human settlement around 12,000 years Before Present (BP). This led to growing human influence on natural ecosystems, starting in the Fertile Crescent, in the former Egypt, Phoenicia, Assyria and Mesopotamia around the Tigris and Euphrates Rivers (Breasted 1916; Burrichter et al. 1993). In the meantime, human societies have grown and the impact of our actions has increased; we are now among the main causes of environmental change on earth. But we do not know where this will lead (Steffen et al. 2007; Ehlers 2008).

Tall, complex, species-rich forests in the world can be found in three major ecozones. First, large areas exist near the equator between 5° N and S in areas

Fig. 6 Tropical rainforest covers most of the Amazon Basin of South America, more than half of the planet's remaining rainforests with highest species diversity. This rainforest was formed during the Eocene thermal maximum, 55 million years ago. As the largest tract of tropical rainforest in the Americas, the Amazonian rainforest has an unparalled structure, with emergents and the highest biodiversity of living plant and animal species in the world (Manaus, Brazil, 2000)

affected by convection in the inter-tropical convergence zone. The absence of pronounced seasons enables the establishment of the richest of all tropical plant communities, the lowland evergreen rainforests in the Amazon and Orinoco-area, in the Congo basin, in South-East Asia, and on many of the Pacific Islands (Figs. 6, 7 and 8).

Towards the subtropical high-pressure zones the tropical rainforests change into semi-evergreen, semi-deciduous and deciduous forests. Second, smaller areas of rainforest occur along the windward eastern continental margins that often receive high rainfall from easterly trade winds. Due to the rainfall seasonality in these regions, semi-evergreen rainforests are predominant, like the Mata Atlantica rainforests in Brazil (Fig. 8), actually the most endangered and nearly completely destroyed rainforest type on earth. With increasing latitude these rainforests merge into subtropical, warm-temperate and temperate rainforests, as in Madagascar and in eastern Australia (Heise-Pavlov et al. 2008). Third, tropical rainforests can also be found within the tropical zone at high altitude. Here lowland rainforests grade into montane rainforests. These rainforests on earth date originally from the Eocene, about 50 million years ago. Their long existence and their millions of years of persisting co-evolution between animals and plants result in their unique global biodiversity (Fig. 9).

The rainforests in general are home to more species than all other biomes added together. Nearly 80 % of the world's biodiversity is found in tropical rainforests (Wilson 1994). Depending on rainforest type, tall, evergreen broad-leaved trees form leafy canopies over the forest floor, 40–50 m tall, and emergent trees rise still further above the canopy. A rich flora of epiphytes, including bromeliads, orchids,

Fig. 7 The Samoan tropical rainforests constitute the largest continuous rainforests in the floristic Kingdom Oceania. This montane cloud forest contains most of Samoa's endemic native species, many of which are threatened or near extinction (Upolu, National Park, Samoa 1998)

Fig. 8 The *Mata Atlantica* tropical and subtropical moist forest extends along the Atlantic coast of Brazil. This forest is more ancient than the Amazon rainforest and is characterized by high species diversity and endemism. This Atlantic Forest is now designated a world Biosphere Reserve and has a large number of highly endangered species. Almost 90 % of the original forest habitats have been lost and replaced by human-modified landscapes. This Atlantic rainforest is considered the most endangered type on Earth (Iguazu National Park, Argentina, 2000)

mosses and lichens in the branches of canopy-trees, is generally unique to tropical rainforests, maintaining a mostly unknown biological diversity. These forests can be considered as centers of plant evolution, but we know that tropical deforestation not only destroys this diversity but also contributes more than 10 % of all anthropogenic carbon dioxide emissions globally (Holt and Debinski 2003; Friedlingstein et al. 2010; Pott and Hüppe 2010; Lynch et al. 2013).

Destruction of tropical rainforests by human activity such as land conversion, clearing, logging, farming and livestock raising, is increasing rapidly at an approximate rate of 1.5 acres/s, for example in the Amazon Rainforest and in the

Fig. 9 Rainforest with the magnificent 350 million-year-old living-fossil tree fern *Angiopteris evecta* from the Carboniferous, *Agathis robusta* (Araucariaceae) and *Archontophoenix cunninghamiana* (Arecaceae) at Wanggolba creek (Frazer Island, Queensland, Australia, 2004)

rainforests of the Indo-Malaysian archipelago. Rainforests now cover less than 6 % of earth's land surface. The destruction of these tropical forests is one of the gravest threats to the global environment in the twenty-first century. Today we face the prospect of severe depletion or even elimination of tropical rainforests, wetlands, estuaries, mangroves, coral reefs, and other biomes with their exceptional biodiversity and complexity. Their decline could entail severe consequences and an environmental crisis in the future. The loss of rainforests alters greatly the hydrologic cycle, local and regional climates, and perhaps more—all physical rather than biotic in nature.

Re-creating depleted rainforests based on our geobotanical knowledge, by planting native trees, is a challenge for us to rehabilitate forests even in the tropics for achieving a sustainable way of life before it is too late on earth (Miyawaki 2004, 2012; Miyawaki and Box 2007).

Global Problems in the Twenty-First Century

The scale of human pressures on ecosystems increased enormously in the last century—and even more so in the last few decades. Since 1980, the global economy has tripled in size, and the population has grown to 7 billion, i.e., a 30 % increase (Fig. 10). Overall consumption of all commodities, including cereals, paper, refrigerators and oil, has risen in tandem, all at a cost to ecosystems, as was documented in the year 2000 report of the World Resources Institute in Washington (WRI 2000). The 1950s marked the beginning of the great acceleration: Globalization, marketing, tourism and huge investments helped fuel enormous growth and people swarmed into the cities, which become even more powerful engines of creativity. In the span of a single lifetime the well-being of millions improved beyond measure—never had so many had so much health, wealth, security and longevity. In a single lifetime we have grown into a phenomenal global force: We move more sediments and rock annually than all natural processes, such as erosion and rivers. We manage three quarters of all land outside the ice sheets. Such high levels of greenhouse gases in the atmosphere have not be seen for over 1 million years, and temperatures continue to increase. We have made a hole in the ozone layer. We are losing Earth's biodiversity and are altering Earth's natural cycles. Increased land-use intensity, urbanization, industrialization and exploitation of natural resources are just some key aspects of this 'problematique' as it was called at the time of the Limits to Growth study more than 40 years ago (Meadows et al. 1974). And these pressures are not likely to abate, at least not in the immediate future. Demographers expect the population to increase to 9 billion in the next 50 years (WRI 2000; Ceballos and Ehrlich 2002). Thus, the aforementioned pressures will increase further and, too often, they and the forces of competition encourage us to over-exploit ecosystems

Fig. 10 World population clock on January, 1st, 2013, in Hannover, Germany

Fig. 11 The oldest nearly undisturbed beech forest of the type Melico-Fagetum in Germany, with trees more than 350 years old. The dominant long-living species is *Fagus sylvatica*. Gaps caused by fallen beech trees are invaded by successional plant communities: a *Betula alba* pioneer stage followed by a mixed forest (Nature Conservation Area 'Heilige Hallen', Mecklenburg-Vorpommern, Germany, 2013)

for short-term gain and hinder development of policies that favour long-term sustainable use.

Habitat destruction as a result of human activity is widely considered the most pervasive cause of the loss of biodiversity. The world's habitats have been so significantly modified by human impact that terms such as "natural ecosystems", "undisturbed", or "virgin forest" are of little practical use (Fig. 11). Biotic impoverishment—the loss of the characteristic diversity of species, genes and biological communities in a region—is an almost inevitable consequence of the way in which the human species is using and often misusing the environment (McNeely et al. 1995).

Human action has lead to another effect of global concern: Changes in atmospheric composition, mainly through the burning of fossil fuels and deforestation, both of which increase the amount of carbon dioxide in the atmosphere, which has led in the geological past and is now leading to a global warming of the Earth's atmosphere and surface, as a result of an enhanced greenhouse effect (Houghton et al. 1995).

At global scale, the distribution of plant and animal species is controlled largely by climate (Woodward 1987), and it is assumed that changes in temperature and precipitation will affect the distribution of the major ecosystems (Watson et al. 1997). Reports on shifting species ranges and adapted behaviour as a consequence of recent climate change are increasing (see examples in Walther et al. 2001).

Warmer temperatures will lead to a more vigorous hydrological cycle, which translates into the prospect of more severe droughts or floods in different parts of the earth. Sea level is currently rising by 2.4 mm/year and is likely to accelerate with the accelerated melting of glaciers and ice caps (Peltier and Tushingham 1989). Recently, a relationship has been ascertained between increasing northeast Atlantic wave height and rising surface air temperatures (Grevemeyer et al. 2000). Several models indicate an increase in precipitation intensity and a greater frequency of extreme events, as reported since 1992 by the reports of the Intergovernmental Panel on Climate Change (IPCC 2007).

Many factors limit our current ability to project and detect future climate change. We **do** know, however, that the character of the vegetation cover depends ultimately on species migration rates and on changes in soil conditions and other environmental factors. It is not at all certain that the migration capability of each species can keep pace with the rate of changing environmental conditions (Watson et al. 1997). In other words, local extinctions can be expected, for instance on high mountain peaks (Grabherr et al. 1994; Walther et al. 2005; Pott 2005; Pott and Hüppe 2007).

Tasks for Geobotanical Research in the Twenty-First Century

What does the future hold for the discipline of Geobotany? The last few decades have seen an explosion of information in every field (Edwards 2000; Seipel et al. 2012): The scientific community compiles increasingly detailed and accurate maps of the spatial distributions and dynamic temporal patterns of many important physical, biotic and human-related variables and processes on scales from local to global. These data, compiled and made more readily accessible by the use of computer-based packages such as Geographic Information Systems (GIS), depict such phenomena as shifting ocean currents, changing patterns in vegetation in response to global warming, seasonal and inter-annual variation in terrestrial and marine productivity, and changes in the human population and the consequences for habitat conservation and fragmentation.

To date, geobotanical research has concentrated to a large extent on the distribution of organisms over the surface of the earth and over the course of the earth's history. But there remains a list of questions that are not readily answered, such as:

- Why are certain species or higher taxonomic groups confined to their present ranges, and what prevents them from colonising other areas?
- What roles do climate, topography and interactions with other organisms play in limiting the distribution of species; how have historical events shaped these distributions?
- What factors are responsible for the high number of species in the tropics and subtropics, as compared to the higher latitudes?
- How have isolated oceanic islands been colonised and why do they have fewer species than do comparable habitats on the continents?

These questions are readily asked but not easily answered (MacArthur and Wilson 1967; Lomolino 2000). We currently lack much of the baseline knowledge we need to determine ecosystem conditions properly at global, regional or, in many instances, even at local scale (Likens 1989).

Never before has ecology carried such crucial importance in tackling the major social and economic problems that the world faces. However, the growing recognition that there is an essential ecological component to many of these problems itself represents a crisis for ecological science. From that background, one of the fundamental questions can be formulated as follows: Can we make ecological predictions at a scale appropriate to the problems that need to be addressed (Palmer 1990; Edwards et al. 1993; Colwell and Coddington 1994; Cardillo 2006)?

The question of scale is an important aspect of ecological research in general, and for geobotanical research in particular. Tilman (1989) sampled papers published in the journal *Ecology* from 1977 to 1987, identifying a total of 749 papers based mainly on field observations and experiments. In general the studies concentrated on short-term observations and experiments, with an obvious decrease in the number of papers involving long-term scientific research (Fig. 12). Forty percent of the studies sampled lasted less than 1 year (generally a single field season), and more than 80 % lasted three or fewer field seasons. Less than 10 % of the studies lasted five or more field seasons. Most of the studies of duration greater than 10 years, and all of the studies of duration longer than 50 years, were based on chronosequences or palaeoecological reconstructions, and not on direct observation. Only exceptionally are a few papers published with long-term observations of

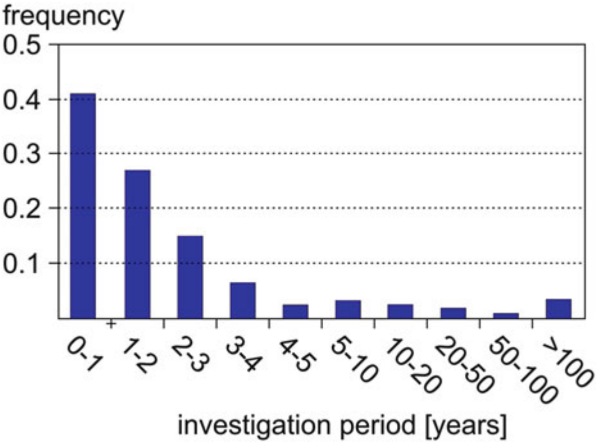

Fig. 12 Duration of research studies published in *Ecology* for a randomly selected subset of issues for 1977–1987. In total, 749 papers were included in the sample, each of which was classified as to the type and duration of the study. Of the 749 papers, 623 were based mainly on field observations and experiments. The frequency of these studies in the different duration classes is shown. The durations shown are based on the inferred duration of the data. Most of the studies of duration more than 10 years, and all of the studies of more than 50 years, were based on chrono-sequences or paleoecological reconstructions, not on direct observation [modified from Tilman (1989)]

more than 10, 20 or even 50 years (e.g., Peter et al. 2009; Juvik et al. 2011; Huwer and Wittig 2012).

Spatial extent also plays an obvious role in the dynamics of plant communities. Not surprisingly, a similar picture resulted, when Kareiva and Anderson (1989) analysed the spatial scales of papers published in the same journal between 1980 and 1986, and dealing with experimentally manipulated resources or populations. Nearly one quarter of the studies used plots no larger than 0.25 m in diameter; one half of the studies used plots no larger than a meter in diameter.

These examples show that most ecological studies in the past century were of short duration or involved very small areas. Maybe, "too many ecologists have yielded to the temptation of finding a problem that can be studied on a conveniently small spatial and temporal scale, rather than striving first to identify the important problems, and then to ask what is the appropriate scale on which to study them" (May 1993).

Hence, the following tasks for ecological research in general, and geobotanical research in particular, may be suggested:

It often requires a long time to detect changes or trends in nature. Very often we are confronted with processes that are changing over time but in which the year-to-year variance is large compared to the magnitude of the trend. Especially in these instances, long-term studies are required in order to separate pattern from "noise" (Franklin 1989). Results from 2 to 3 years of investigation, or even 5–10 years, may be misleading in terms of detecting change or trends (Likens 1989). Geobotanical research deals also with complex, dynamic objects, and the relevance of single relevés to longer time scales is an issue worth reflecting on. Gassmann et al. (2000) consider relevés as no more than single sheets of a pull-off wall calendar, reflecting just one frozen moment of an ever changing biosystem.

The last few decades have seen an explosion of information in every field of ecological research. It is questionable, though, whether ecological knowledge has increased in proportion to the numbers of papers that have been published. In any case, Tilman (1989) found himself surprised when he was told that agronomists, who study annual plants grown in monoculture, require that at least two life cycles of their plants be studied before results are considered publishable, whereas ecologists are willing to publish a 3-month field study of organisms that may live 100 or more years. The short duration of many ecological field studies may have biased our view of the workings of nature. Ecology in general, and geobotany in particular, need a greater emphasis on long-term studies if we are to understand the broad forces that determine nature ultimately. Hence, it is suggested that an appropriate scale for future geobotanical research should depend largely on the life spans of the species of interest and the hypothesis being tested.

We can describe nature as a multi-causal system in which patterns result from

- the direct effects of physical factors,
- intra-specific and inter-specific biotic interactions, and
- indirect and feedback effects of one species or system element on others.

The investigation of complex ecological phenomena involving many interacting factors requires appropriate methodologies. The science of non-linear complex systems is becoming increasingly sophisticated and has introduced new elements, such as circular causality, not only in the fields of physics and chemistry, but also in biology and geobotanical research. Models implementing “Interacting Particle Systems”, including cellular automata, are just one promising approach to be mentioned in this context (Silvertown et al. 1992; Walther et al. 1999; Petersen et al. 2001; Petersen and Pott 2005). Relatively simple non-linear models are able to display complicated dynamics (May 1976; Hastings et al. 1993) such as complex natural spatial patterns (Kenkel and Walker 1996) and the limited predictability of spatio-temporal dynamics of plant communities (Anand and Orlóci 1997; Ouborg et al. 1999).

Outlook

Charles Darwin (1809–1882) solved the mystery of the origin of species (Darwin 1859). His work is based on his extensive observations of natural history during his 5-year journey on the research ship *Beagle* (1831–1836), as well as his subsequent scientific review of his substantial collection in the two decades after the voyage.

Factual natural science, for which Alexander von Humboldt (1769–1859) and Aimé Bonpland (1773–1858) laid the groundwork in South America, and which Charles Darwin continued at broad scale, still constitutes the basis for exploration of the biotic diversity of all habitats on Earth. For the long-term protection of biotic diversity, the dynamics of all biological systems have to be understood. This requires comprehension of both evolution and change of habitats and ecosystems in the past and under today’s conditions. Acquiring such knowledge is the only way to assess the repercussions of anthropogenic intrusions in the environment (Jischa 2008; Lovelock 2009; Watson 2009). The exploration of global biotic diversity is just beginning. The task of cataloging it—and to achieve an understanding of its causal relationships—is a gigantic field of work for geobotany in the endangered present and the uncertain future.

Easter Island, in the midst of the vast Pacific Ocean, and the history of the destruction of its natural environment (Figs. 13 and 14) with all the fatal repercussions on its human population serve as an example for the destiny of our planet in the midst of infinite space (Diamond 2005). The Tapati Rapa Nui Festival on Easter Island is celebrated every summer, at the end of January and into February (Fig. 15). These traditions involve sports, such as sliding down a cliff in a banana tree, or swimming in the ocean, or rowing across the island’s lakes at Ranu Raraku in a reed tortora raft. Dance competitions and the crowning of the queen of the festival are the highlights of the celebrations of this ancient culture of Easter Island.

The list of such examples is not exhausted (Mieth and Bork 2012; Bahn and Flenley 2011). However, it shows that in the broad field of research disciplines, geobotany can assume an important role in future ecological research by using its

Fig. 13 Moais are the monolithic human figures on Easter Island, carved by Rapa Nui people from volcanic rock between the years 1250 and 1500 (Aku Tongariki, Easter Island, 2010)

Fig. 14 Environmental degradation by deforestation destabilized an already precarious ecosystem on Easter Island. Native tree and palm species went extinct, and the island was deforested. Soil erosion because of lack of trees is apparent in some places. Overgrazing by European horses and cattle is obvious too (Anakena Beach, Easter Island, 2010)

Fig. 15 The Tapati Rapa Nui Festival is a vibrant natural ethnic festival celebrating the island's Polynesian culture. This is the most isolated inhabited place on Earth, in the middle of the Pacific Ocean. There is no other land mass for 3000 km (to Chile) or 3700 km to the nearest island neighbor, the Pitcairn Islands. Easter Island is one of the masterpieces of our planet, a magical meeting with the past. It symbolizes its people's mystery and its past, which is known only by a few (Hangaroa, Easter Island, 2010)

powerful methodological tools to carry out investigations at both broad temporal and spatial scales, and so tackle many of the more urgent problems that face us in the twenty-first century.

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