Chapter 5
Vegetation Zonation and Conifer Dominance Along Latitudinal and Altitudinal Gradients in Humid Regions of the Western Pacific

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Abstract In humid regions of the western Pacific, conifers and deciduous broadleaf trees dominate in colder climate while evergreen broadleaf trees dominate in warmer climate. There are two geographically discontinuous forest zones of conifer-dominated forests, i.e., boreal zone and temperate-to-tropical zone. Between them, there is a deciduous broadleaf forest zone with warm summer and cold winter (Kira's warmth index, WI from 45 to 85 °C, and coldness index, CI <-15 °C). Boreal conifer forest is characterized by continental climate with short summer and cold winter (WI <45 °C and CI <-15 °C), whereas temperate-to-tropical conifer-dominated forests in both hemispheres are characterized by oceanic, moderate climate lacking severe winter (WI <144 °C and CI >-15 °C). Boreal conifer forests are distributed at high latitudes or altitudes in Japan ("subarctic or subalpine forest"). Temperate conifer forests occur in a narrow belt on the Pacific Ocean side in Japan and are more extensive and distributed to warmer climate at high altitudes in Taiwan and in temperate zone of New Zealand, where they are called "conifer-broadleaf" forests. These temperate conifer (or mixed) forests grade into tropical conifer forests at high altitudes in Southeast Asia and New Guinea. Thus, these forests may be collectively called "temperate-to-tropical conifer-mixed forests" in contrast to boreal conifer forest. It appears that relatively cool summer (or year-round low temperature on tropical mountains) limits the growth of evergreen broadleaf trees, while mild winter (or the absence of winter on tropical mountains) gives the competitive advantage to conifers over deciduous broadleaf trees, leading to conifer dominance in the temperate-to-tropical conifer-mixed forests.

Keywords Biogeography • Boreal forest • Broadleaf forest • Coldness index • Conifer forest • Forest zone • Mixed forest • Warmth index

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5.1 Introduction

The east and southeast coastal regions of the Asian continent are a unique place on earth in that humid climate continues from equator to high latitudes without being interrupted by dry climate (Kira 1991; Ohsawa 1993, 1995). Similarly, humid regions with annual rainfall >1000 mm are more or less continuously distributed from New Guinea through the east coast of Australia to Tasmania and New Zealand (Wardle 1991; Adam 1992). Moreover, all these regions except northeast Australia have high mountains >2000 m elevation, culminating in the glacier-shouldered summits (up to 4884 m on Puncak Jaya) on New Guinea. Thus, in the western Pacific regions, one can observe how humid vegetation changes across latitudes in both hemispheres and also across altitudes. However, no study has yet been done to summarize the vegetation zonation along latitudinal and altitudinal gradients in the western Pacific including both hemispheres.

Troll (1948) published a diagram depicting vegetation zonation at global scale along both latitudinal and altitudinal gradients to demonstrate "asymmetric vegetation structure" between Northern and Southern Hemispheres. His diagram amalgamates the data from various regions (e.g., tropical zonation primarily from the Andes and northern temperate zonation from Europe) and may not be necessarily applicable to the western Pacific. Ohsawa (1990, 1993, 1995) developed a vegetation template for southern and eastern Asia incorporating both latitudinal and altitudinal gradients, yet he has not extended it to the Southern Hemisphere temperate regions. His template also suffers from combining the data of the Himalayas and coastal Asia at the middle latitudes of 20–30°N, obscuring the pattern in the western Pacific. Dodson et al. (2004) and Hope et al. (2004) presented vegetation maps for the western Pacific including both hemispheres, while they lack the consideration of altitudinal gradient, and the latter was one reconstructed for the last glacial maximum. Here, a new classification system of vegetation zonation along both latitudinal and altitudinal gradients is proposed for the western Pacific regions including both hemispheres.

There are three approaches for the classification of vegetation: ecological, physiognomic, and floristic (Collinson 1988). Ecological and physiognomic approaches are interrelated because vegetation physiognomy reflects underlying ecological factors, and the combination of these approaches is usually employed to define vegetation zones at the global scale (e.g., Walter 1985; Archibold 1995). Yet these two approaches are not entirely compatible. For example, in Archibold's system, physiognomically defined conifer forest biome is distributed in the wide range of climate from boreal to temperate. By contrast, in Walter's system, "zonobiome" of the warm-temperate humid climate (Zonobiome V) includes a range of forest types with different physiognomy (e.g., conifer forest in western North America, mixed conifer-broadleaf forest in Chile and New Zealand, and evergreen broadleaf forest in eastern Asia and southeastern Australia; also see Grubb et al. 2013).

In line with Walter's system, this study primarily adopts an ecological approach, aiming at vegetation classification based on climate. Physiognomic and floristic aspects are also considered, with particular reference to conifer dominance. Conifers are gymnosperms, evolutionarily more ancient than broadleaf trees (angiosperms). With the rise of angiosperms since the Cretaceous, conifers have been losing their dominance in the vegetation on the earth, probably due to the competition with angiosperms. At present, globally, conifers are largely restricted to unproductive habitats at high latitudes and altitudes and on nutrient-poor or dry soils, where growth of angiosperms is reduced. Bond (1989) hypothesized that this reflects less efficient transport system (stereotyped leaves with non-reticulate venation and stems with tracheids) in gymnosperms than in angiosperms. There is a global trend in the humid vegetation that evergreen broadleaf trees dominate in warmer climate, conifers dominate in colder climate, and deciduous broadleaf trees dominate in between. There are many exceptions in individual areas to this global pattern as suggested by Walter's Zonobiome V, and the critical climatic factors for the transition from broadleaf dominance to conifer dominance can be different from place to place. Fortunately, however, climate fairly well explains the pattern of conifer dominance in the western Pacific as will be demonstrated in this study. In particular, this study shows that there are two distinctive zones of conifer-dominated forest under drastically different climates, i.e., boreal versus temperate-to-tropical zones.

5.2 Study Areas and Climate Data

The regions considered in this study are Japan, Taiwan, the Philippines, Borneo, Sumatra, New Guinea, eastern Australia including Tasmania, and New Zealand (Fig. 5.1). All except northeast Australia and Tasmania have high mountains $>$2000 m elevation, facilitating the simultaneous interpretation of latitudinal and altitudinal vegetation zonation. The monthly mean temperature data (calculated as mean of monthly mean maximum and minimum temperatures if not available) of the highest-elevation climatic stations were collected for the following mountains or islands from the websites of the meteorological agencies of respective countries or regions (Fig. 5.2; Japan Meteorological Agency, Taiwanese Central Weather Bureau, and Australian Bureau of Meteorology) except otherwise noted: Taisetsu Mountains (latitude: 44°N; the elevation of the summit followed by the highest climate station: 2290 m, 1700 m; G. Kudo, unpublished data), Mount Hayachine (40°N; 1914 m, 760 m), Mount Fuji (35°N; 3776 m, 3775 m), Aso Mountains (33°N; 1592 m, 1142 m), Kirishima Mountains (32°N; 1700 m, 1325 m; Kagoshima Meteorological Station 1958), Yakushima Island (30°N; 1936 m, 1800 m; Eguchi 2009), Mount Yushan (23°N; 3997 m, 3845 m), Mount Kinabalu (6°N; 4095 m, 3940 m; Kudo and Suzuki 2004), Mount Wilhelm (6°S; 4508 m, 3480 m; McAlpine et al. 1983), Mount Bellenden Ker (17°S; 1582 m, 909 m; the data of the highest climate station from Herberton), Mount Kosciusko (34°S; 2230 m, 1518 m),

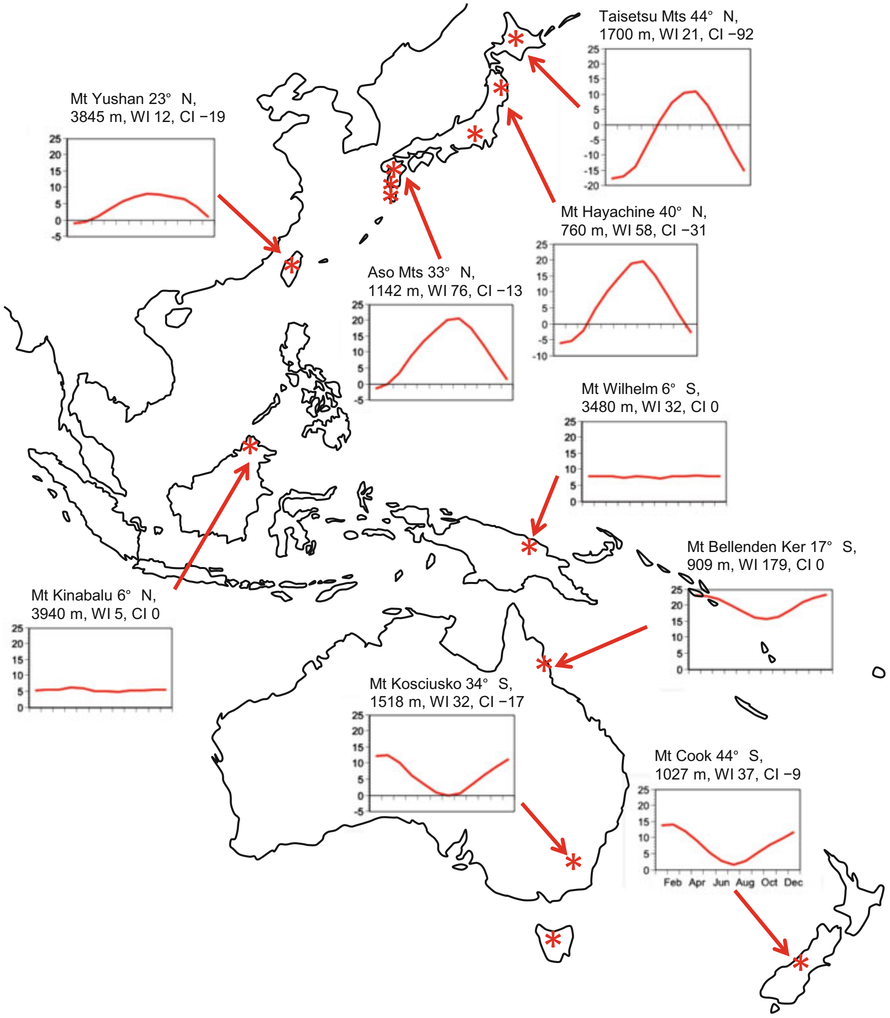

Fig. 5.1 A map of the western Pacific regions showing the locations (*) of mountains where thermal indices were calculated at given altitudes. Seasonal changes in monthly mean temperature are shown for selected climatic stations; the latitude and altitude of the station, the values of warmth index (*WI*), and coldness index (*CI*) are indicated

Tasmania (42°S; 1617 m, 1057 m), and Mount Cook (44°S; 3764 m, 1027 m; Climate-Charts.com 2007). The monthly mean temperature at given elevation was estimated for each mountain or island by assuming a linear lapse rate by using the data of the nearby climate stations at lower elevations. For Japan, only mountains and islands located in the Pacific Ocean side were selected in order to recognize the so-called *Abies firma-Tsuga sieboldii* forest (Yamanaka 1961; Yoshioka 1973; “hemi temperate subzone” of temperate zone, Hämet-Ahti et al. 1974; “temperate

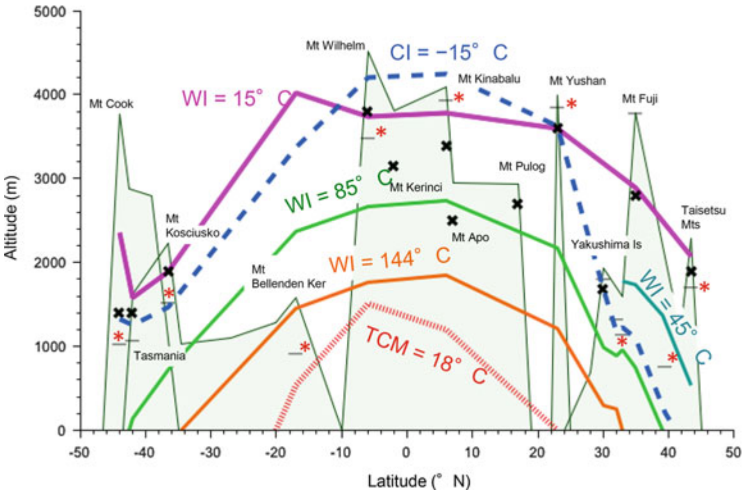

Fig. 5.2 A diagram showing the general topography (*light-colored area with thin outlines*) and the critical values of thermal indices (*thick lines*) along latitudinal and altitudinal gradients in the western Pacific. Thermal indices: *WI* warmth index (*solid lines*), *CI* coldness index (*broken line*), *TCM* monthly mean temperature of the coldest month (*dotted line*). Note that topographic outlines of Japan and Taiwan and those of Australia (including Tasmania) and New Zealand are shown separately. The altitudes of the climatic stations at the highest altitude (−) and treeline (×) on each mountain are also shown. *Asterisks* (*) indicate the climatic station, for which the seasonal changes in monthly mean temperature are shown in Fig. 5.1. The altitude of treeline from Taisetsu Mts, Okitsu (1999); Mt Fuji, Ohsawa (1990); Yakushima Is, Ohsawa (1993); Mt. Yushan, Su (1984); Mt. Pulog (17°N) and Mt. Apo (6°N), Buot and Okitsu (1998); Mt. Kinabalu, Kitayama (1992); Mt. Kerinci, Ohsawa et al. (1985); Mt. Wilhelm, Wade and McVean (1969); Mt. Kosciusko, Williams and Costin (1994); Tasmania, Kirkpatrick (1982); Mt. Cook (northern South Island), Wardle (1991)

conifer forest" *sensu stricto* in this study), which is lacking in the Sea of Japan side, as a distinct forest zone.

5.3 Thermal Indices and Critical Values for the Demarcation of Vegetation Zones

The following thermal indices were calculated from monthly mean temperature t (°C) (Fig. 5.2): warmth index (WI), which is defined as $\Sigma(t–5)$ where the summation is made for months with $t > 5$; coldness index (CI), which is defined as $-\Sigma(5–t)$ where the summation is made for months with $t < 5$ (Kira 1949, 1991); and the monthly mean temperature of the coldest month (TCM). In this study, the following six critical index values were employed, which had been suggested to demarcate vegetation zones in East and Southeast Asia.

1. WI = 15 °C corresponds to forest limit (Kira 1949, 1991; Ohsawa 1990), which is more commonly called "treeline" in recent literature (e.g., Körner 2012).
2. WI = 45 °C corresponds to the lower and southern limit of boreal conifer forest (Kira 1949, 1991).
3. WI = 85 °C corresponds to the lower and southern limit of cool-temperate deciduous broadleaf forest, in particular *Fagus crenata* forest in Japan (Kira 1949, 1991). This value is also effective as a critical value for the transition from tropical montane forest at lower elevations (dominated by evergreen broadleaf trees) to tropical subalpine forests at higher elevations (dominated by conifers) on Mount Kinabalu, Borneo (Kitayama 1992).
4. WI = 144 °C corresponds to the boundary between warm-temperate and subtropical forests. This is taken from the critical value for the transition from *Castanopsis*-*Machilus* forest at lower altitudes to *Quercus* forest at higher altitudes in Taiwan (Su 1984). Kira (1949, 1991) considered WI = 180 °C for the boundary between warm-temperate and subtropical forests; however, this isotherm corresponds to Watase's line (Hämet-Ahti et al. 1974) where biogeography (historical disjunction between Yakushima Island and Ryukyu Islands) caused drastic species turnover and therefore cannot be considered to be universally significant (though WI = 180 °C seems effective for mainland China as well, Kira 1949, 1991). Notably, WI = 144 °C is close to WI = 140 °C, which corresponds to the boundary of the northern and southern subzones of warm-temperate evergreen broadleaf forest in Japan and to the northern limit of evergreen broadleaf forest in China (Kira 1949, 1991).
5. CI = −15 °C corresponds to the upper limit of canopy species of evergreen broadleaf trees (e.g., *Quercus* spp.) in the absence of heavy snowfall, i.e., in the Pacific Ocean side of Japan (Hattori and Nakanishi 1985). This value is adopted instead of CI = −10 °C (Kira 1949, 1991) representing the northern limit of evergreen broadleaf canopy trees along the coastal areas of Japan because the northern limit may be affected by sea spray (Hattori and Nakanishi 1985).
6. TCM = 18 °C corresponds to the boundary between tropical and extratropical climates (Köppen 1923). This value is also effective in distinguishing tropical lowland forest (dominated by dipterocarps) and tropical montane forest (dominated by non-dipterocarp evergreen broadleaf trees) on Mount Kinabalu (Kitayama 1992).

5.4 Vegetation Zonation in the Western Pacific

According to the above critical values of thermal indices, the following vegetation zones are distinguished as summarized in Table 5.1 and Fig. 5.3. WI = 45 °C is considered only for high-latitude region in the Northern Hemisphere in Fig. 5.3 because this isotherm does not appear to be related to vegetation differentiation in other regions. Each vegetation zone is explained in the following sections. Some of the vegetation zones span from tropical to temperate regions in both hemispheres,

Table 5.1 Vegetation zones in northern temperate (including boreal), tropical, and southern temperate regions, as well as their collective names proposed in this study, of the western Pacific in relation to critical values of thermal index

Thermal index (°C)			Northern temperate/ boreal	Tropical	Southern temperate	Collective name
WI	CI	TCM				
<15	–	–	Alpine zone	Alpine zone	Alpine zone	Alpine zone
15–45	< −15	–	Boreal conifer forest	–	Subalpine forest/ alpine zone[a]	–
45–85	< −15	–	Cool-temperate deciduous broadleaf forest	–	–	–
15–85	> −15	–	Temperate conifer forest	Tropical subalpine forest	Cool-temperate rainforest	Temperate-to-tropical conifer-mixed forests
85–144	–	–	Warm-temperate evergreen broadleaf forest	Tropical upper-montane forest	Warm-temperate rainforest	Temperate-to-tropical conifer-mixed forests
>144	–	<18	Subtropical rainforest	Tropical lower-montane forest	Subtropical rainforest	Tropical-to-subtropical evergreen broadleaf forests
–	–	>18	–	Tropical lowland forest	–	Tropical-to-subtropical evergreen broadleaf forests

WI warmth index, *CI* coldness index, *TCM* monthly mean temperature of the coldest month
[a] Subalpine forest in mainland Australia and alpine zone in Tasmania and New Zealand

but they lack the name inclusive of the whole geographic range because such continuity has rarely been recognized by the previous studies. Therefore, names for each region are listed together in the section headings in the order of northern temperate, southern temperate, to tropical regions (e.g., Sect. 5.4.4). If temperate regions of both hemispheres have the common name, the name for temperate regions is followed by the name for the tropics (e.g., Sect. 5.4.6).

5.4.1 Alpine Zone

"Alpine zone" occurs above treelines in both hemispheres where the climate is too cold for the formation and/or maintenance of forest stands (WI <15 °C). The critical value (WI = 15 °C) for treeline was originally derived from the vegetation pattern in Japan and was usually interpreted as indicating that summer is too short to support tree growth. Interestingly, however, the same critical value appears to

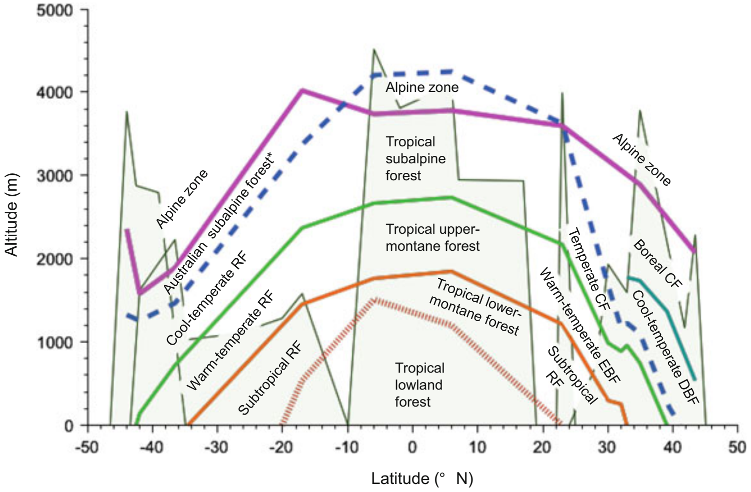

Fig. 5.3 A diagram showing the seven vegetation zones along latitudinal and altitudinal gradients in the western Pacific. Three vegetation zones spanning from tropical montane regions to subtropical and temperate regions in both hemispheres are called by different names in each of these regions. *CF* conifer forest, *DBF* deciduous broadleaf forest, *EBF* evergreen broadleaf forest, *RF* rainforest, *, alpine zone in comparative climate in Tasmania and New Zealand (Fig. 5.2)

explain the treeline on tropical mountains (Kira 1949; Ohsawa 1990) as demonstrated by the data of New Guinea (Fig. 5.2). The lowered treelines on Mount Kerinci and Mount Kinabalu are due to the effects of volcanism and glaciation, respectively (Ohsawa et al. 1985; Kitayama 1992). In the southern temperate regions, the treeline in mainland Australia also corresponds to WI = 15 °C, but those of New Zealand and Tasmania appear to be lower (see Sect. 5.4.2).

The major tree species at treeline are *Abies mariesii*, *A. veitchii,* and *Betula ermanii* in mainland Japan (Kira 1949; Ohsawa 1990; Okitsu 1999), *A. kawakamii* and *Juniperus squamata* in Taiwan (Su 1984), *Dimorphanthera microphylla* and *Rapanea vaccinioides* in New Guinea (Wade and McVean 1969), *Eucalyptus* spp. in Australia and Tasmania (Williams and Costin 1994), and *Nothofagus* spp. in New Zealand (Wardle 1991; Leathwick 2001). The lower treelines in New Zealand and Tasmania may be due to the absence of hardy conifers and deciduous broadleaf trees of the northern origins. In fact, the invasion of introduced *Pinus* spp. has been reported for the alpine zone in New Zealand (Wardle 1985; Froude 2011).

5.4.2 Boreal Conifer Forest and Australian Subalpine Forest

This vegetation zone occurs where summer is short (from 15 to 45 °C in WI) and winter is cold (CI <-15 °C). Globally "boreal conifer forest" is widespread under the continental climate with long, cold winter in the Northern Hemisphere (zonobiome of the cold-temperate boreal climate, Walter 1985). In the western Pacific regions considered in this study, it is restricted at high latitudes and altitudes of Japan, where it is called "subalpine forest" or "subarctic forest" (Kira 1949, 1991; Kira et al. 1976). Although some authors think that there is no or very limited occurrence of true boreal forest in Japan and prefer the name "sub-boreal forest" (Kubota and Hara 1995) or "boreonemoral zone" (*sensu* Walter 1985; Uemura 1994) due to the co-occurrence of cool-temperate deciduous broadleaf trees, climatic conditions corresponding to treeline (WI = 15 °C) do occur in Japan (Fig. 5.2), which may justify the nomenclature adopted here (e.g., Hämet-Ahti et al. 1974; Kojima 1987; Grishin 1995; Okitsu 2000). CI is always <-35 °C in this zone of Japan. Dominant species are *Abies sachalinensis* and *Picea jezoensis* in Hokkaido and *A. mariesii*, *A. veitchii*, *P. jezoensis* (var. *hondoensis*), and *Tsuga diversifolia* in Honshu and Shikoku. This forest zone is absent in Kyushu southward. As will be mentioned below (Sect. 5.4.4), "subalpine forest" dominated by *A. kawakamii* in Taiwan (Su 1984) is not the southern extension of this zone, albeit superficially similar, but should be regarded as "temperate conifer forest" analogous to *A. firma*-*T. sieboldii* forest in the Pacific Ocean side of Japan. This is counter to the traditional viewpoints regarding Taiwanese subalpine forest as boreal conifer forest (e.g., Tsukada 1966; Su 1984; Ohsawa 1990).

The climatically equivalent areas also occur on high mountains in southern temperate areas in Australia, Tasmania, and New Zealand, but the occurrence of forest is restricted to Snowy Mountains, southeast Australia including Mount Kosciusko (Australian "subalpine forest," Williams and Costin 1994). In Snowy Mountains, the dominant tree is evergreen *Eucalyptus pauciflora*, which may be explained by biogeography (winter hardiness evolved in *Eucalyptus*) and/or climate (winter is less furious). The frost resistance of *E. pauciflora* (−20 °C in bud) is among the highest of trees in Australia, Tasmania, and New Zealand, which is similar to that of the hardiest evergreen broadleaf species in Japan (e.g., −18 °C and −22 °C in bud of *Camellia japonica* and *Pieris japonica*, respectively), but is not as high as deciduous broadleaf trees in Japan (e.g., −30 °C and −50 °C in bud of *Fagus crenata* and *Quercus crispula*, respectively; Sakai et al. 1981; Sakai and Larcher 1987). These suggest that milder winter allows the dominance of evergreen broadleaf trees in subalpine forest of Australia. On Mount Kosciusko 15 °C and 45 °C in WI correspond to −31 °C and −9 °C in CI, respectively, whereas on Taisetsu Mountains, these WI values correspond to −107 °C and −50 °C in CI, respectively. Tree-less alpine vegetation occurs in this zone in Tasmania and New Zealand (Sect. 5.4.1), where treelines appear to coincide with CI = −15 °C (Fig. 5.2), indicating that winter coldness limits the tree distribution in these regions. Wardle (1991) suggested that nocturnal minimum temperature determines treeline in New Zealand, which needs to be interpreted in relation to the absence of hardy trees of the northern origins (Sect. 5.4.1).

5.4.3 Cool-Temperate Deciduous Broadleaf Forest

In the western Pacific, “cool-temperate deciduous broadleaf forest” occurs only in the Northern Hemisphere where summer is warm (45–85 °C in WI) and winter is cold (CI <-15 °C). This vegetation zone is widespread in eastern Asia, Europe, and eastern North America (zonobiome of the temperate-nemoral climate, Walter 1985). It appears that the combination of warm summer and cold winter gives the competitive advantage to deciduous broadleaf trees over both conifers and evergreen broadleaf trees. We need to note that this is the case only in productive habitats on fertile soils. In less productive habitats such as on steep slopes and on immature volcanic soils, conifers may attain high dominance (upper part of “temperate conifer forest” *sensu lato*). This zone does not occur in Taiwan where the climate is oceanic with less thermal seasonality.

The climatically equivalent area to this northern cool-temperate deciduous broadleaf forest does not exist in the southern temperate regions of the western Pacific with oceanic climate similar to Taiwan (compare Mt. Yushan with Mt. Bellenden Ker southward in Fig. 5.1). As was mentioned above (Sect. 5.4.2), WI $=45$ °C corresponds to CI $=-9$ °C on Mount Kosciusko that has the least oceanic climate among humid areas in Australia, Tasmania, and New Zealand.

Deciduous broadleaf forest is virtually absent in Taiwan and in Southern Hemisphere temperate regions with two exceptions: *Fagus hayatae* forest in northern Taiwan (Hukusima et al. 2005) and *Nothofagus gunnii* forest in Tasmania (Veblen et al. 1996), both occurring in warmer climate than this zone. Similar outliers of deciduous forest dominated by *Nothofagus* spp. occur in Chile, South America (Veblen et al. 1996).

5.4.4 Temperate Conifer Forest, Cool-Temperate Rainforest, and Tropical Subalpine Forest

This vegetation zone occurs under oceanic, moderate climate without severe winter (15–85 °C in WI and CI >-15 °C). The forest in this zone is called “temperate conifer forest” (lower part of “temperate conifer forest” *sensu lato*) in northern temperate regions and “cool-temperate rainforest” in the southern temperate regions. Although WI at the threshold CI $=-15$ °C is much higher (i.e., summer is warmer) in Japan (WI $=59$ °C on Yakushima) than in Taiwan (WI $=14$ °C) and southern temperate regions (WI $=35$ °C on Mount Kosciusko), the lack of severe winter characterizes this zone. The climatic equivalence between the temperate forests on both hemispheres can be confirmed by frost resistance of the dominant conifers (Table 5.2).

In Japan, this zone roughly corresponds to *Abies firma-Tsuga sieboldii* forest (Yamanaka 1963; Kira et al. 1976). The lack of severe winter (CI >-15 °C) allows the existence of canopy trees of a few evergreen broadleaf species (e.g., *Quercus* spp.) admixed with conifers. Other dominant conifers include *Cryptomeria*

Table 5.2 Freezing resistance (°C, maximum of leaf or bud) of cut shoots (determined by Sakai and his coworkers) and horticultural hardiness rating (1, hardiest; 11, least hardy; Bannister and Neuner 2001) of conifer species by forest zones

Forest zone and species	Freezing resistance	Hardiness rating	Distribution	Reference
Boreal conifer forest				
Abies mariesii	−70	6	Japan	Sakai and Malla (1981)
A. sachalinensis	−70	5	Japan	Sakai (1983)
A. veitchii	−70	3	Japan	Sakai and Malla (1981)
Picea jezoensis	−70	2	Japan	Sakai (1983)
Tsuga diversifolia	−70	5	Japan	Sakai and Malla (1981)
Temperate conifer forest				
Abies firma	−30	6	Japan	Sakai (1983)
A. kawakamii	−30	6	Taiwan	Sakai (1983)
A. spectabilis	−25	7	Himalaya	Sakai and Malla (1981)
Chamaecyparis obtusa[a]	−20	6	Japan and Taiwan	Sakai and Okada (1971)
Cryptomeria japonica[a]	−25[c]	6	Japan	Sakai and Kurahashi (1975)
Juniperus squamata	−25	5	Taiwan and Himalaya	Sakai (1983)
Picea morrisonicola	−20[c]	8	Taiwan	Sakai (1979)
P. torano[a]	−30	6	Japan	Sakai and Kurahashi (1975)
Tsuga dumosa	−20[c]	8	Himalaya	Sakai and Malla (1981)
T. sieboldii	−25	6	Japan	Sakai and Malla (1981)
Cool-temperate rainforest				
Athrotaxis cupressoides	−20[c]	8	Tasmania	Sakai et al. (1981)
Halocarpus bidwillii	−23	7	New Zealand	Sakai et al. (1981)
Phyllocladus alpinus	−22	8	New Zealand	Sakai et al. (1981)
Podocarpus lawrencei	−22	7	Australia	Sakai et al. (1981)
P. nivalis	−22	7	New Zealand	Sakai et al. (1981)
Warm-temperate rainforest and warm-temperate evergreen broadleaf forest				
Agathis australis	−7[c]	9	New Zealand	Sakai et al. (1981)
Dacrycarpus dacrydioides	−7	9	New Zealand	Sakai et al. (1981)

(continued)

Table 5.2 (continued)

Forest zone and species	Freezing resistance	Hardiness rating	Distribution	Reference
Dacrydium cupressinum	−8	9	New Zealand	Sakai et al. (1981)
Podocarpus hallii	−13	8	New Zealand	Sakai and Wardle (1978)
P. macrophyllus	−13	7	Japan	Sakai and Kurahashi (1975)
P. totara	−7[c]	9	New Zealand	Sakai et al. (1981)
Prumnopitys ferruginea	−10	9	New Zealand	Sakai et al. (1981)
Taiwania cryptomerioides	−15[c]	9	Taiwan	Sakai and Kurahashi (1975)
Subtropical rainforest and tropical lower-montane forest				
Araucaria cunninghamii[b]	−5[c]	10	New Guinea and Australia	Sakai et al. (1981)
Tropical upper-montane forest and tropical subalpine forest				
Dacrycarpus compactus	−5+[c]	NA	New Guinea	Sakai et al. (1981)
Papuacedrus papuana	−5	10	New Guinea	Sakai and Larcher (1987)
Phyllocladus hypophyllus	−3	10	New Guinea	Sakai and Larcher (1987)
Podocarpus brassii	−6	NA	New Guinea	Sakai and Larcher (1987)

NA no data available

[a] Also in cool-temperate deciduous broadleaf forest

[b] Also in tropical upper-montane and tropical lowland forests

[c] Planted trees

japonica, *Chamaecyparis obtusa,* and *Picea torano*, which also occur in unproductive habitats in cool-temperate deciduous broadleaf forest (upper part of “temperate conifer forest” *sensu lato*, Sect. 5.4.3). As mentioned above (Sect. 5.4.2), “subalpine forest” (3100–3600 m) dominated by *A. kawakamii*, as well as “upper-montane forest” (2500–3100 m) dominated by *T. chinensis* and *P. morrisonicola* in Taiwan (Su 1984), also fall in this category. This climatic characterization of species is supported by their frost resistance (Table 5.2).

In cool-temperate rainforest of the Southern Hemisphere, the dominance of conifer may not be necessarily high, e.g., at the treeline in New Zealand showing the mono-dominance of *Nothofagus* spp. (Wardle 1991; Leathwick 2001). However, where *Nothofagus* is absent, mixed conifer-broadleaf forests occur in this zone (see Sect. 5.5). Conifers (e.g., genera *Athrotaxis*, *Lagarostrobos,* and *Phyllocladus*) are also dominant in cool-temperate rainforests in Tasmania (Jarman et al. 1987). Conifers are virtually absent in comparable vegetation in mainland Australia, with only one species (*Podocarpus lawrencei*; Gibson et al. 1995), which may be explained by the past climate (Sect. 5.4.5), although *P. lawrencei* can become dominant in subalpine thickets (Adam 1992).

This zone in tropical forest corresponds to "tropical subalpine forest." Tropical mountains lack winter even at high elevations, so that CI is >0 °C up to treeline (where WI = 15 °C). On non-volcanic high mountains, which show the full development of vegetation, conifers (e.g., genera *Dacrycarpus*, *Phyllocladus,* and *Podocarpus* on Mount Kinabalu and New Guinea and *Papuacedrus* on New Guinea) become dominant occupying the forest upper story (Aiba et al. 2013) or sometime becoming emergents (Grubb and Stevens 1985). Thus, one may call this zone on tropical mountains as "tropical conifer forest" (Tagawa 1995). Ohsawa (1991, 1995) and Buot and Okitsu (1998) suggested that high-altitude forests of Asian tropical mountains showed structure and composition equivalent to the understory of the lower-altitude forests. Their suggestions are based on observations of mountains where conifers are rare at high elevations probably due to the effects of volcanism and/or fires and cannot be accepted as a general rule for the tropical mountains in the western Pacific (Aiba 2011).

5.4.5 Warm-Temperate Evergreen Broadleaf Forest, Warm-Temperate Rainforest, and Tropical Upper-Montane Forest

The climate of this vegetation zone is similar to that of the abovementioned zone (Sect. 5.4.4), but is warmer overall (85–144 °C in WI). The forest in this zone is usually called "warm-temperate evergreen broadleaf forest" in the northern temperate regions and "warm-temperate rainforest" in the southern temperate regions. CI is >-15 °C in Japan and almost always >0 °C in Taiwan and southern temperate regions, leading to the dominance of evergreen broadleaf trees. These thermal conditions largely encompass three regions (Japan, New Zealand, and Australia) of "warm-temperate rain forest" in the western Pacific recognized by Grubb et al. (2013). In limited inland areas of Japan with relatively continental climate, however, winter becomes too cold (CI <-15 °C) to allow the growth of canopy trees of evergreen broadleaf species, where an exceptional "warm-temperate deciduous broadleaf forest" is found (Kira 1949, 1991; Kira et al. 1976).

In the actual vegetation in Japan, warm-temperate evergreen broadleaf forest literally contains few conifers. However, this may reflect historical logging of conifers, especially *Cryptomeria japonica* and *Chamaecyparis obtusa*, dating back to around 600 AC (Totman 1989). There are some areas still showing high abundance of temperate conifers such as *Abies firma* and *Tsuga sieboldii* (e.g., Miyajima Island, Kuroda et al. 2003; Boso Peninsula, Ozaki and Ohsawa 1995), and there used to be more such areas in the past before the large-scale logging started (e.g., the lowland of Yakushima Island, Kira and Yoshino 1967). By contrast, the warm-temperate forest (c. 1500–2500 m) in Taiwan generally shows the greater dominance of conifers such as *Chamaecyparis formosensis*, *C. obtusa* (var. *formosana*), *Pseudotsuga wilsoniana*, *Taiwania cryptomerioides,* and *Cunninghamia konishii*, where historical logging had been less intense (Su 1984; Liao et al. 2014). Kira (1991) proposed the term "warm-temperate lucidophyll forest" for this forest zone in Japan based on leaf properties of the dominant evergreen broadleaf trees with shiny, middle-sized leaves, which are distinct from smaller sclerophyllic leaves and larger tropical leaves.

Like Taiwan, warm-temperate rainforest in New Zealand is also essentially mixed conifer-broadleaf forest including giant conifers such as *Agathis australis*, *Dacrycarpus dacrydioides*, *Dacrydium cupressinum*, *Podocarpus totara,* and *Prumnopitys ferruginea* (Wardle 1991; Leathwick 2001; Lusk 2002). This forest type is characterized by varying degrees of conifer dominance and variously called such as "conifer-broadleaf" (Wardle 1983), "conifer/broad-leaved" (Wardle 1991), or "conifer-broadleaved" forest (Leathwick 2001). In warm-temperate rainforest of eastern Australia, there are two conifer species with highly restricted distributions (the Greater Blue Mountains, 34°S). *Wollemia nobilis* occurs as emergents in the groves in steep canyons (Benson and Allen 2007), while *Microstrobos fitzgeraldii* occurs as a shrub on cliffs generally within the spray zone of waterfalls (Gibson et al. 1995). The paucity of the conifer flora and the lack of conifer dominance in the cool- and warm-temperate rainforests of southeast mainland Australia may be explained by the past climate (Sect. 5.4.4), which will be discussed in Sect. 5.7.2.

Tropical forest in this zone corresponds to "tropical upper-montane forest." This is the lower extension of tropical subalpine forest explained above (Sect. 5.4.4), with reduced dominance of conifers. In the influential book of Whitmore (1984), there is an often-cited diagram of vegetation zones in Malay Peninsula showing that Ericaceae and Myrtaceae, as well as conifers, characterize the upper-montane zone. The review of the literature indicated that conifers and Myrtaceae are by far the dominants and quantitative vegetation data supporting the dominance of Ericaceae (though species richness may be high) is lacking (Aiba 2011).

5.4.6 Subtropical Rainforest and Tropical Lower-Montane Forest

This vegetation zone occurs where climate is generally hot (WI >144 °C) but winter (or relatively cooler season in the tropics) can be still recognized (TCM <18 °C). Forest in this zone is called "subtropical rainforest" at the middle latitudes of both hemispheres and "tropical lower-montane forest" on the tropical mountains. In this zone, conifer dominance is greatly reduced: only scattered individuals of *Calocedrus* (Taiwan, Liao et al. 2014), *Podocarpus,* and *Nageia* (Japan and Taiwan, Kohyama and Aiba 1997) are found in northern temperate regions, but conifer dominance can become higher in drier areas in southern temperate regions (*Araucaria* forest in Australia, Winter et al 1987; Adam 1992) and on poor soils on tropical mountains (e.g., on ultramafic rocks, Kitayama et al. 2011). Notably, *Araucaria cunninghamii* is distributed in both New Guinea and eastern Australia, demonstrating the climatic equivalence between these two regions. Though this species has a wide distribution range, the centers of the distribution are in lower-montane forest in New Guinea and in subtropical forest in Australia (de Laubenfels 1988; Enright and Hill 1995).

The abovementioned diagram of tropical vegetation zones in Malay Peninsula (Sect. 5.4.5; Whitmore 1984) indicates that Fagaceae and Lauraceae dominate in tropical lower-montane forest. However, the review of the literature revealed the following (Aiba 2011). In the western Malesia (west of Wallace's line, Whitmore 1984), the dominance of Fagaceae is restricted to mountains with nutrient-rich soils affected by volcanism (e.g., the Philippines, Sumatra, and Java), and Myrtaceae and conifers are more dominant on non-volcanic mountains with nutrient-poor soils (e.g., Borneo and Malay Peninsula). In the eastern Malesia (New Guinea, Sulawesi, and Seram), Fagaceae dominates in the lower part of the lower-montane forest, but Myrtaceae and conifers become dominant in the upper part. There is no quantitative vegetation study showing the dominance of Lauraceae (though species richness of Lauraceae may be high as Ericaceae in tropical upper-montane forest, Sect. 5.4.5). Ashton (2003) also pointed out that oak-laurel lower-montane forest is very restricted in Borneo where soils are generally infertile.

5.4.7 Tropical Lowland Forest

"Tropical lowland forest" occurs where climate is hot throughout the year (TCM >18 °C). The northern limit is in the southern lowland of Taiwan (23°N), the southern limit is at around 20°S in eastern Australia, and the upper limit is at around 1500 m in New Guinea. Kira (1991) considered WI = 240 °C as a thermal limit for tropical zone, but TCM = 18 °C roughly corresponds to WI = 210 °C in Taiwan (Lanyu Island), 220 °C in eastern Australia, and 160 °C on New Guinean mountains (note that TCM = 18 °C coincides with WI = 156 °C in perfectly aseasonal climate). The dominant tree family is Dipterocarpaceae in the Philippines and Sundaland (including Borneo and Sumatra), while Dipterocarpaceae is a minor element in New Guinea located in the east of Wallace's line and is absent in Taiwan and Australia. Conifers are essentially absent. The exceptions are *Agathis* and *Araucaria* in New Guinea, *Agathis* in Australia, and *Agathis* and *Dacrydium* on swampy or sandy ("kerangas") soils in Southeast Asia. *Agathis robusta* occurs in lowlands of both New Guinea and Australia, similar to *Araucaria cunninghamii* that tends to occur in cooler climate (Sect. 5.4.6; de Laubenfels 1988). Though not included in the present study, New Caledonia (22°S) is the most notable exception in this zone in having rich conifer flora (Enright and Hill 1995).

5.5 Vegetation Zones in the Tropics and in the Southern Hemisphere

The critical values of thermal indices adopted in this study had been shown effective in explaining the vegetation zones in East and Southeast Asia, especially in the temperate to subtropical regions of the Northern Hemisphere (Japan and Taiwan). Did these fit to the vegetation zones in the tropics and in the Southern Hemisphere?

For the tropical forests below the treelines, the present study recognized four vegetation zones (lowland, lower montane, upper montane, and subalpine) on high mountains (Fig. 5.3). This qualitatively fits the zonation pattern shown by earlier studies conducted for higher mountains (>3000 m) such as New Guinea and Mount Kinabalu (Grubb and Stevens 1985; Kitayama 1992; Ashton 2003), although the subalpine forest is generally lacking on lower mountains <3000 m (Whitmore 1984).

For temperate forests in New Zealand, the present study recognized two vegetation zones, warm-temperate and cool-temperate zones (Fig. 5.3). These zones qualitatively correspond to warm-temperate and cool-temperate belts, the latter including subalpine belt, defined by Wardle (1991). Wardle's subalpine belt is a narrow belt of almost pure stand of *Nothofagus* spp. marking the treeline. The same *Nothofagus* species are shared by the cool-temperate belt *sensu stricto* (excluding subalpine belt); hence, subalpine belt may be considered to be an upper subzone of the cool-temperate belt *sensu lato*. Leathwick (2001) predicted the potential forest pattern in New Zealand based on extensive datasets and classified forests into five groups: (1) conifer-broadleaf forests in warm, wet climate; (2) mixed forests in cool, wet climate; (3) *Nothofagus*-dominant forests in cool, wet climate, including those at treeline; (4) conifer-dominant forests in warm, dry climate; and (5) *Nothofagus*-dominant forests in cool, dry climate. The climates for groups (2) and (3) are similar, suggesting that *Nothofagus* dominance is related to biogeographic factors such as the range contraction of *Nothofagus* in the last glaciation (Sect. 5.7.2). This classification, though incorporating the wet-dry axis, also supports the warm versus cool dichotomy of New Zealand forest zones recognized in the present study.

For eastern Australia to Tasmania spanning from tropical to temperate regions, the present study recognized four forest zones excluding the small areas of subalpine zone restricted to high elevations in southeast mainland: tropical lowland, subtropical, warm-temperate, and cool-temperate zones (Fig. 5.3). There has been no consensus as to the classification of Australian rainforest, but the physiognomic system proposed by Webb (1978) has been most widely used (Adam 1992; Bowman 2000). Webb's system may be translated to the classification based on climate, in which four climatic zones are recognized (tropical, subtropical, warm temperate, and cool temperate; Webb 1968; Winter et al 1987; Adam 1992). Thus, the classification proposed in the present study qualitatively matches the zones shown by Australian rainforests as well.

5.6 Tropical-Temperate Dichotomy or Continuity Across Latitudes?

In the present study, boreal conifer forest (Sect. 5.4.2) and cool-temperate deciduous broadleaf forest (Sect. 5.4.3) occur only in the Northern Hemisphere, as was depicted by the Troll's diagram of the "asymmetric vegetation structure" of the earth (Troll 1948). On the other hand, the vegetation zones at the lower latitudes and lower altitudes span from tropical mountains to temperate regions in both hemispheres (Sects. 5.4.4, 5.4.5, and 5.4.6). This is again in line with the general idea of Troll (1948), but is in contrast to Ohsawa (1990, 1993, 1995) who distinguished the altitudinal zonations on tropical versus temperate mountains with transitional zonation at 20–30°N in eastern and southern Asia. Although Ohsawa (1990, 1993, 1995) admitted that tropical lower-montane forest belongs to the same zone with subtropical forest in mid-latitude lowland (corresponding to Sect. 5.4.6 in the present study), he did not take into account the relationship between tropical upper-montane forest (including tropical subalpine forest) and temperate forests. The basis of vegetation zone classifications by Troll and Ohsawa is mostly climate. Based on floristics and physiognomy along with climate, Shimizu (2014) pointed out that tropical upper- and lower-montane forests correspond to warm-temperate and subtropical forests, respectively, which is qualitatively consistent with the present study, but he did not give the detailed explanation about the similarity between tropical and temperate forests.

Should we distinguish tropical versus temperate zones, or should we consider the continuous change in forest vegetation from tropical to temperate regions? The answer will depend on the objectives of the vegetation classification. If we aim to demonstrate the effects of the climate seasonality on vegetation, then tropical and temperate zones should be distinguished. If we aim to clarify the controlling factors for the resemblance between tropical and temperate vegetation, then the continuity between tropical and temperate zones should be explored. As will be discussed below, the continuous system adopted here is effective in understanding the geographic pattern of conifer dominance. Tropical climate, though lacking seasonal change, exhibits diurnal fluctuations in temperature, and the nighttime temperature can become low just like winter in temperate regions (e.g., Kudo and Suzuki 2004). Southern Hemisphere temperate and tropical high-altitude environments are similar in that freeze-thaw event can occur at any time of the year (Feild et al. 2002). Therefore, there seems to be no absolute reason to assume that tropical and temperate zones are fundamentally different.

5.7 Biogeography and Ecology of Conifer Dominance

5.7.1 Geographic Pattern of Conifer Dominance

In the western Pacific regions, there are two forest zones showing conifer dominance (conifer forests or mixed conifer-broadleaf forests), i.e., boreal forest (Sect. 5.4.2) versus temperate-to-tropical forests (Sects. 5.4.4 and 5.4.5), separated by cool-temperate deciduous broadleaf forest zone (Sect. 5.4.3) with warm summer and cold winter (45–85 °C in WI and CI <-15 °C; an example of climate shown for Mount Hayachine in Fig. 5.1). Boreal conifer forest is characterized by continental climate with short summer and long, cold winter (15–45 °C in WI and CI <-15 °C), occurring only at high latitudes and high altitudes (above the cool-temperate deciduous broadleaf forest) in Japan ("subalpine or subarctic forests"). By contrast, temperate-to-tropical forests showing conifer dominance in both hemispheres are characterized by oceanic, moderate climate without severe winter (15–144 °C in WI and CI >-15 °C). These climatic differences between boreal versus temperate-to-tropical forests can be seen if one compare climate of Taisetsu Mountains with those of Aso Mountains southward in Fig. 5.1.

In Japan, at the lower altitudes or latitudes than the cool-temperate deciduous broadleaf forests, the temperate conifer forest (Sect. 5.4.4) is distributed in a narrow geographic belt on the Pacific Ocean side with climatic condition from 45 to 85 °C in WI (so-called *Abies firma-Tsuga sieboldii* forest). However, the restriction of conifer dominance to this narrow belt is probably due to the historical logging (Sect. 5.4.5). If we look at vegetations in Taiwan and New Zealand, the coexistence of conifer and broadleaf trees is the rule in warm-temperate forests in warmer climate (85–144 °C in WI). Thus, temperate forests showing high conifer dominance (conifer forests or mixed conifer-broadleaf forests) are more extensive in temperate regions outside Japan. These temperate conifer or mixed forests grade into tropical conifer forests (tropical subalpine and upper-montane forests) at high elevations in Southeast Asia and New Guinea. Therefore, we may collectively call these forests (Sects. 5.4.4 plus Sect. 5.4.5) as "temperate-to-tropical conifer-mixed forests" in contrast to boreal conifer forest confined to high latitudes and altitudes in the Northern Hemisphere (Fig. 5.4 and Table 5.1). "Conifer-mixed forest" (Devito et al. 1999) rather than "conifer forest" is appropriate for the temperate-to-tropical zone since even so-called temperate conifer forests and tropical conifer forests always accompany broadleaf trees with varying degrees of mixture, especially in the understory.

Similarly, tropical and subtropical forests dominated by evergreen broadleaf trees (Sects. 5.4.6 plus Sect. 5.4.7) can be collectively called "tropical-to-subtropical evergreen broadleaf forests." Subtropical and tropical lower-montane forests (Sect. 5.4.6) can be regarded as impoverished variations of rich, gigantic tropical lowland forest (Sect. 5.4.7) under the suboptimal thermal conditions. On the other hand, Tagawa (1995) merged warm-temperate, subtropical, and tropical montane forests (excluding those dominated by conifers) in Asia and New Guinea

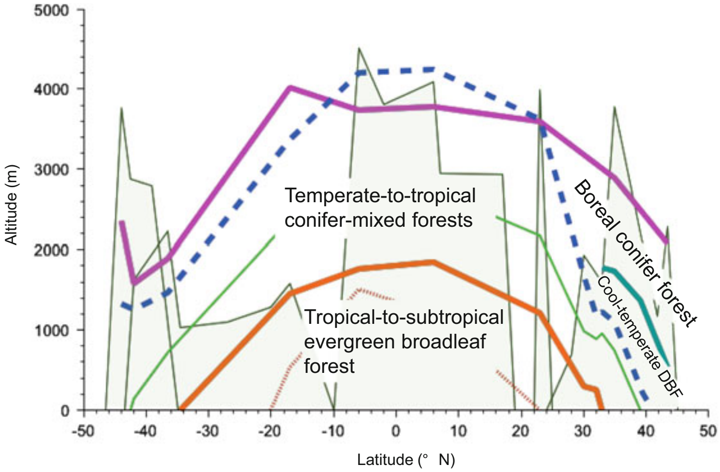

Fig. 5.4 Four forest zones broadly defined by conifer dominance and climate. See Fig. 5.3 for the abbreviation

(Sects. 5.4.5 plus Sect. 5.4.6) into “lucidophyll oak-laurel forest” formation from the physiognomic and floristic viewpoints; however, as was explained earlier (Sect. 5.4.6), the term “oak-laurel forest” is inappropriate as the general name even for tropical lower-montane forest.

What climatic factors make temperate-to-tropical conifer-mixed forests a distinctive vegetation zone from tropical-to-subtropical evergreen broadleaf forests and from cool-temperate deciduous broadleaf forest? It appears that relatively cool summer (or year-round low temperature on tropical mountains) limits the growth of evergreen broadleaf trees while mild winter (or the absence of winter on tropical mountains) gives the competitive advantage to conifers over deciduous broadleaf trees, leading to conifer dominance in the temperate-to-tropical conifer-mixed forests. The latter situation should make photosynthesis possible in winter (or all year round in tropical mountains), as is the case for conifer forests in the western North America (Waring and Franklin 1979; Han and Mukai 1999; Weng et al. 2005). The unproductive habitats on poor soils also help conifers outcompete broadleaf (both evergreen and deciduous) trees and locally modify the vegetation zonation. Aiba et al. (2013) suggested that lower growth of broadleaf trees in cold and/or nutrient-poor environments results in sparser forest canopy, allowing shade-intolerant conifers to dominate the forests.

The boreal conifer forest in Japan is dominated by *Abies mariesii*, *A. sachalinensis*, *A. veitchii*, *Picea jezoensis,* and *Tsuga diversifolia*. Temperate conifer forest is dominated by *A. firma*, *T. sieboldii*, *Cryptomeria japonica,* and *P. torano* in Japan and by *A. kawakamii*, *T. chinensis, and P. morrisonicola* in Taiwan. Therefore, boreal and temperate conifer forests share congeneric species. Assigning these genera to particular climate is therefore not persuasive. *Picea* and *Tsuga* were often considered as purely boreal and cool-temperate elements, respectively, while *Abies* as representing both boreal and cool-temperate zones in the pollen analysis (e g. Takahara et al. 2000; Gotanda et al. 2002). On the other hand, Sakai (1983) demonstrated that these genera showed similar ranges of frost resistance, all with wide interspecific variations (Table 5.2). Therefore, a precaution is needed in interpreting the vegetation reconstructions based on pollen analysis. In particular, it is stressed here that the dominance of *Abies* and *Picea* is not restricted to boreal forest. In this study it was shown that "subalpine forest" dominated by *A. kawakamii* as well as "upper-montane forest" dominated by *T. chinensis* and *P. morrisonicola* in Taiwan are considered as temperate conifer forest analogous to *A. firma-T. sieboldii* forest in Japan, not as boreal conifer forest. Though not included in the present study, subalpine forests in the Himalayas dominated by *Abies spectabilis* (and other high-elevation forests including *Abies*, *Picea,* and *Tsuga*) should also be considered as temperate conifer forest, judging from their similar frost resistance to *A. firma*, *A. kawakamii*, *P. morrisonicola,* and *T. sieboldii* (Table 5.2; Sakai and Malla 1981).

5.7.2 Biogeography and Ecology

There is a marked floristic discontinuity in the southern tip of Taiwan (Takhtajan 1986) or between Taiwan and the Philippines (Hsieh 2003; Raes and van Welzen 2009). There, holarctic and paleotropical elements predominate northward and southward, respectively. Dominant conifers in temperate zones of Japan and Taiwan (Pinaceae and some Cupressaceae; hereafter "northern conifers") are probably of northern or Laurasian origins, while those in temperate-to-tropical zones of Southeast Asia, New Guinea, Australia, and New Zealand (Araucariaceae, Podocarpaceae, and other Cupressaceae; hereafter "southern conifers") had been the significant components in southern or Gondowana flora (Hill and Brodribb 1999; LaPage 2003; Mao et al. 2012). Temperate northern conifers such as *Abies firma* and *A. kawakamii* lack extreme cold hardiness, unlike boreal northern conifers (Table 5.2). Contrarily, some southern conifers (e.g., *Halocarpus bidwillii*, *Phyllocladus alpinus*, *Podocarpus lawrencei,* and *P. nivalis*) have evolved to acquire moderate hardiness comparable to temperate northern conifers, although southern conifers are generally less frost resistant than northern conifers (Sakai and Larcher 1987; Bannister and Neuner 2001). Thus, temperate-to-tropical conifers in both hemispheres include exceptions to the global pattern that northern conifers are associated with continental climate in which winter is furious while southern conifers are with maritime climate in which winter is mild or absent (Brodribb and Hill 2004; Bannister 2007).

How almost non-overlapping distributions between northern and southern conifers in the temperate-to-tropical conifer-mixed forest zone arouse and are maintained is an interesting question. Among southern conifers, the genus *Dacrydium* was present in Japan in the past (c. 15 million years ago, Morley 2000), so that its current absence in northern temperate regions (Taiwan and

Japan) at first look seems to be explained by the lack of cold tolerance. However, *D. cupressinum* is distributed to as far south as 47°S in New Zealand, and its leaves can tolerate −8 °C freezing, which is comparable to some evergreen broadleaf trees (e.g., *Elaeocarpus sylvestris* and *Litsea japonica*) in the southwestern part of mainland Japan (Sakai and Larcher 1987; Wardle 1991). This suggests that biogeography (such that *Dacrydium* has not crossed the geographic barriers under the current climate) likely explain the present geographic distribution of *Dacrydium*. Among northern conifers, *Pinus* and *Taxus* have crossed the sea (though probably they moved mostly on land via exposed Sundaland) from Asian continent to insular Southeast Asia (Sumatra and the Philippines for *Pinus* and *Taxus* and Sulawesi for *Taxus*, de Laubenfels 1988), again suggesting that biogeography (geographic barrier) rather than ecology (climatic niche) explains their present ranges of distribution that are biased toward the Northern Hemisphere. However, it is possible that some taxa adapted to seasonal climate cannot sustain their populations in tropical climate (such that flower bud formation requires winter chill).

The possible role of the past climate in determining the current vegetation pattern was suggested for *Nothofagus* dominance in cool-temperate zone in New Zealand (Sect. 5.5). The similar situation may apply to the poor diversity and the lack of dominance of conifers in the cool- and warm-temperate rainforests of southeast mainland Australia (Sects. 5.4.4 and 5.4.5), which had only three species of conifers (*Podocarpus lawrencei*, *Microstrobos fitzgeraldii,* and *Wollemia nobilis*; the latter two species have extremely localized distributions; Gibson et al. 1995; Benson and Allen 2007). The fossil records indicated that the cooler and drier climate in the past have caused the extinction of many rainforest conifer taxa in southeastern Australia (Hill and Brodribb 1999; Kershaw and Wagstaff 2001). This contrasts with relatively rich conifer flora of dry forests and open woodlands in Australia (*Callistris* and *Actinostrobos*; Bowman and Harris 1995). In sum, distributions of tropical-to-temperate conifers should have been constrained by both historical and ecological factors.

The majority of temperate-to-tropical conifers in both hemispheres are shade-intolerant species, which persist in forest overstory due to long lifespan, and they depend on occasional natural disturbances for regeneration (Enright and Hill 1995; Aiba et al. 2013). Some temperate-to-tropical mixed forests with either northern or southern conifers in the western Pacific (Japan, Taiwan, New Guinea, and New Zealand) show “additive basal area” phenomenon, which indicates vertical niche partitioning between shorter, shade-tolerant broadleaf trees and emergent, shade-intolerant conifers (Enright 1982; Ogden 1985; Enright and Hill 1995; Lusk 2002; Aiba et al. 2007; Liao et al. 2014). Thus, temperate-to-tropical conifers of both hemispheres are ecologically similar in many ways irrespective of taxonomy, meaning that these conifers can be considered as a functionally coherent group. These considerations justify the climatically defined vegetation zones proposed here, some of which span from tropical to temperate regions in both hemispheres.

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