Mammal Habitats in Europe: Geology, Vegetation, and Climate

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Abstract

This chapter starts with the physiogeographical structure of Europe, its borders, areas, and locations. Some parts of Macaronesia (Madeira, Canary Islands, Azorean islands) are added. The geology, orography, and soils are described in the summary. A detailed physiogeographical organization describes ten areas of Northern Europe, Western and Central Europe, Southern Europe, Eastern Europe, and Macaronesia. They each are subdivided in different physiogeographical regions and provinces. Geographical location, landmass distribution, and topography determine the climatic patterns of Europe. Five main thermal zones can be distinguished from north to south: arctic, boreal, temperate, submeridional, and meridional. The climatic classification of Europe is the basis for the phytogeographical division of Europe. It includes floristic zones and regional subdivisions. At the end the Late-Glacial and Holocene vegetation history of Europe is summarized.

Keywords

Geology · Climate · Biogeography · Vegetation history · Landscape development

Introduction

Landscapes, habitats, and organisms in Europe developed as a result of geological and climatic changes. Geological processes and ecological situations up to the last ice age have formed European landscapes. A decrease of species during the ice age changed into an increase of species due to rewarming of the climate and anthropogenous activity forming a cultivated landscape.

All these forming processes differ over Europe by influence of increasing continental climate, degree of latitude, and elevation and form a couple of different climatic and geological situations. These differences can be monitored by vegetation which can be arranged by transects from North to South or East to West. During vegetation history, a lot of different areal types were formed. The floristic composition might be important for the differentiation of vegetation types but also influence of humans and animals. Seeing vegetation types as biocoenosis, we are talking about habitats. Therefore, the geologic, climatic, and cultural development of Europe is important for building mammal areas with their habitats.

Following the political situation, we add parts of Macaronesia (Canary Islands, the Azores, and Madeira archipelago) to Europe.

Physiographical Structuring of Europe

The Borders, Area, and Location of Europe

Europe is part of the Eurasian supercontinent. At the end of the Tertiary Period, its current form developed. Its geographical location and paleogeographic development have been most influencing parameters in forming Europe's highly pronounced physical differentiation and thus have affected profoundly biogeographical relationships.

On three sides, Europe's geographical borders are clearly defined: in the west by the Atlantic Ocean; in the north by the Norwegian Sea, the Barents Sea, and the Arctic Ocean; and in the south by the Mediterranean Sea and the Black Sea. In the east, the eastern slope of the Urals has commonly been set as the boundary to Asia due to paleogeographic, structural, and climatic aspects. It continues to the south of the Ural River and reaches the western shore of the Caspian Sea. The Great Caucasus is generally included in Europe today (Kondracki and Schlüter 2003).

Europe covers approximately 10 million km^2, excluding the Macaronesian region. About 0.74 million km^2 are located on islands genetically associated with the European mainland. The largest are Great Britain (224,000 km^2), Ireland (84,000 km^2), Sicily (26,000 km^2), Sardinia (24,000 km^2), and the genetically independent volcanic island of Iceland (103,000 km^2). The major peninsulas are the Scandinavian (824,000 km^2), Iberian (587,000 km^2), Apennine (149,000 km^2), and Balkan peninsulas (about 500,000 km^2). Islands and peninsulas cover well over one third of the total area of Europe. The diverse coastline has an overall length of 37,200 km (Kondracki and Schlüter 2003).

For our handbook, we include Macaronesia, a collection of four archipelagos in the North Atlantic Ocean off the coast of the continents of Europe and Africa. Apart from the Azores which are considered mainly as part of Europe, the islands of Macaronesia are geographically closer to Africa. Madeira and the Canary Islands are part of our distribution study, but not Cape Verde. The Azorean islands cover an area of 2,333 km^2, Madeira Islands 801 km^2, and Canary Islands 7,493 km^2 (Afonso 1988; Sziemer 2000).

From south to north, the mainland extends over 3,900 km, latitude between 36° and 71° N, including the islands over 5,300 km and about 48° of latitude. From west to east, it spreads about 5,000 km, that is, 78° of longitude. The northernmost point of Europe lies at 82° N on the Arctic islands of Svalbard and Franz Joseph Land and on the mainland at North Cape (71° 16’ N). The furthest point in the southwest is Cape Marroqui in Spain, which reaches as far as 35° 58’ N. The Mediterranean island of Crete lies about 1° further to the south. The westernmost point is at 9° 27’ W at Cabo da Roca in Portugal, although the island of Ireland projects 1° further to the west (Iceland is not considered here since it is in fact an isolated island in the North Atlantic). The easternmost point of Europe is the mouth of the Bajdarata River that flows into the Kara Sea at 68° 14′ E.

The Azorean islands are a group of three archipelagos composed of nine inhabited islands in the Atlantic Ocean between 36° 55′ and 39° 43′ northern latitude and between 24° 46′ and 31° 16′ western longitude. The shortest distance to the European (Portuguese) coast is about 1,300 km. The eastern archipelago consists of the islands of Santa Maria, Sao Miguel, and the uninhabited Formigas Reef. The central archipelago consists of the islands of Terceira, Sao Jorge, Graciosa, Pico, and Faial. The two smaller islands, Ilha das Flores and Corvo, make up the western archipelago. The distance between the eastern- and westernmost islands, Santa Maria and Ilha das Flores, respectively, is about 600 km (Schäfer 2002; Dias et al. 2005).

Madeira is a Portuguese island and is the largest of the Madeira archipelago. The location is 32° 39’N and 16° 54’W. It covers an area of 741 km^2, 57 km in length (from Ponte de São Lourenço to Ponta do Pargo), while approximately 22 km at its widest point (from Ponte da Cruz to Ponte São Jorge), with a coastline of 150 km (Wirthmann 1970).

The Canary Islands are located in the Atlantic Ocean, about 100 to 500 km west of Morocco. The main islands are (from largest to smallest) Tenerife, Fuerteventura, Gran Canaria, Lanzarote, La Palma, La Gomera, and El Hierro. Included are also a number of smaller islands and islets: La Graciosa, Alegranza, Isla los Lobos, Montaña Clara, Roque del Oeste, and Roque del Este. Coordinates for the location are 27° 38′ to 29° 25’ N and 13° 25′ to 18° 10’ W. El Hierro, the westernmost island, covers 268.71 km^2, making it the smallest of the major islands. Fuerteventura, with a surface of 1,660 km^2, the most ancient of the islands, is the one that is eroded the most. Gran Canaria’s surface area is 1,560 km^2. In the center of the island lie Roque Nublo (1,813 m) and Pico de las Nieves (“Peak of Snow” 1,949 m). La Gomera has an area of 369.76 km^2. Geologically, it is one of the oldest islands of the archipelago. Lanzarote is the easternmost island and also one of the most ancient of the archipelago, and it has shown evidence of recent volcanic activity. It has a surface of 8,455.94 km^2. The Chinijo Archipelago includes the islands La Graciosa, Alegranza, Montaña Clara, Roque del Este, and Roque del

Oeste. It has a surface of 40.8 km^2. With 29 km^2, La Graciosa is the smallest inhabited island of the Canaries and the major island of the Chinijo Archipelago (Acosta et al. 2005).

La Palma, covering an area of 708.32 km^2, shows no recent signs of volcanic activity, even though the volcano Teneguía last entered into eruption in 1971. In addition, it is the second-highest island of the Canaries, with the Roque de los Muchachos (2,423 m) as highest point. Tenerife is, with its area of 2,034 km^2 the most extensive island of the Canary Islands. The Teide, with 3,718 m is the highest peak of Spain.

Geology, Orography, and Soils

Paleogeographic development, especially tectonic processes in the Tertiary and repeated glaciation in the Quaternary, formed Europe's present-day surface. This diverse relief is the crucial factor for its physiographic structure (following Kondracki and Schlüter 2003).

The oldest part of the European mainland is the Precambrian basement, which is exposed as the Baltic Shield (Fennoscandia) in the north and the Ukrainian Shield in the southeast. Between these areas in the east European lowlands, these ancient rocks are overlain with Paleozoic and Mesozoic strata. This Palaeo-Europe was separated by a fault zone from Meso- and Neo-Europe. Meso-Europe arose – similar to the Urals – at the end of the Paleozoic during the Hercynian folding. During the Mesozoic these structures were levelled and covered by a series of marine and continental sediments.

Neo-Europe began to develop in the Mesozoic and attained its final shape in the Tertiary, when the folded structures of the high mountain regions (Sierra Nevada, Pyrenees, Alps, Apennines, Dinaric, Pindos and Balkan Mountains, Carpathian Mountains, and also the Caucasus) were uplifted. During this vertical movement, the horizontally folded rock formations were uplifted, while the Mediterranean and intramontane basins were lowered (Kondracki and Schlüter 2003).

wThe last major phase of relief formation was the repeated Quaternary glaciation – apart from erosion persisting to the present day. The main areas of the glaciation were Fennoscandia, the British Isles, and the Alps (Fig. 1). From the north, massive glaciers moved far into the Eastern, Central, and Western European plains and reached the Harz and Sudeten mountains and even the Western Carpathian Mountains. During the last glacial period, an inland ice sheet covered the Baltic Sea and the mainland to Jütland, the lower courses of the Elbe and the Oder valley, the middle Weichsel and Memel valleys, as well as the Duena valley (Andersen and Borns 1994).

In the cold periglacial climate, permafrost soils were widespread even outside of the glaciated regions. Especially in winter windblown dust material was deposited, often as thick loess, on the peripheral tundra and cold steppes surfaces. At the end of the last glaciation, glaciofluvial and fluvial sands were blown by wind to form dunes in areas that were still forest-free. Forests established in these areas only at the beginning of the Holocene.

In Fennoscandia and the other centers of glaciation, ancient rock formations were exposed by the retreating ice, while in the adjoining peripheral areas around the Baltic Sea, glacial till was deposited as moraines and glaciofluvial and glaciolimnic sediments (sands, gravels, clays). These deposits can be up to several hundred meters thick and rise up to 300 m above sea level.

Due to the postglacial warming, glaciers melted which caused the general rise of the mean sea level, the flooding of low mainland areas, the formation of the Baltic and North Seas, and the separation of the British Isles from the European mainland. This inland advance of coastline, or "transgression," was simultaneous to the isostatic elevation of areas earlier covered by massive glaciers (particularly in Fennoscandia), a process that continues today. The upward thrust of these areas is causing a recession particularly of the northern coast of the Baltic Sea, while on its southwestern shores as well as on the southern coasts of the North Sea, by contrast, the coastline is advancing inland in the course of further transgression (Kondracki and Schlüter 2003).

77The orography of Europe is quite diverse. Lowlands predominate the broad eastern half of

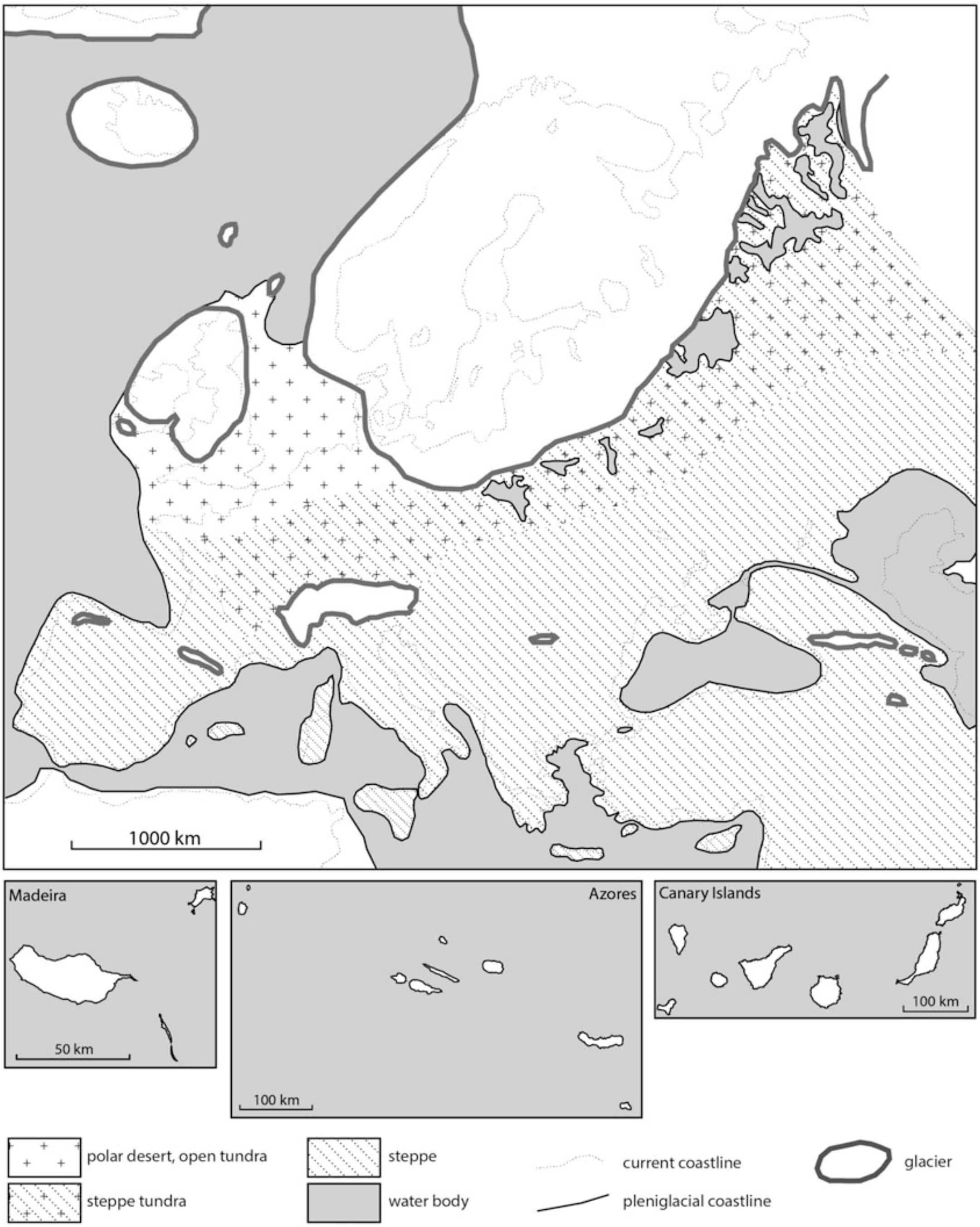

Fig. 1 Vegetation of Europe during the last glaciation around 20,000 BP (maximum expansion of ice during the last ice age). Map recreated and modified, area boundaries following Andersen and Borns (1994) and Lang (1994)

the continent which results in the mean elevation of Europe being only about 340 m above sea level (compared to 960 m in Asia) (Fig. 2). In contrast prominent mountain ranges dominate the southern half of Europe. These include the Alps (Mont Blanc 4,807 m), the Pyrenees (Pico de Aneto 3,404 m), the Apennines (Corno Grande 2,914 m), the Balkan Mountains (Botev

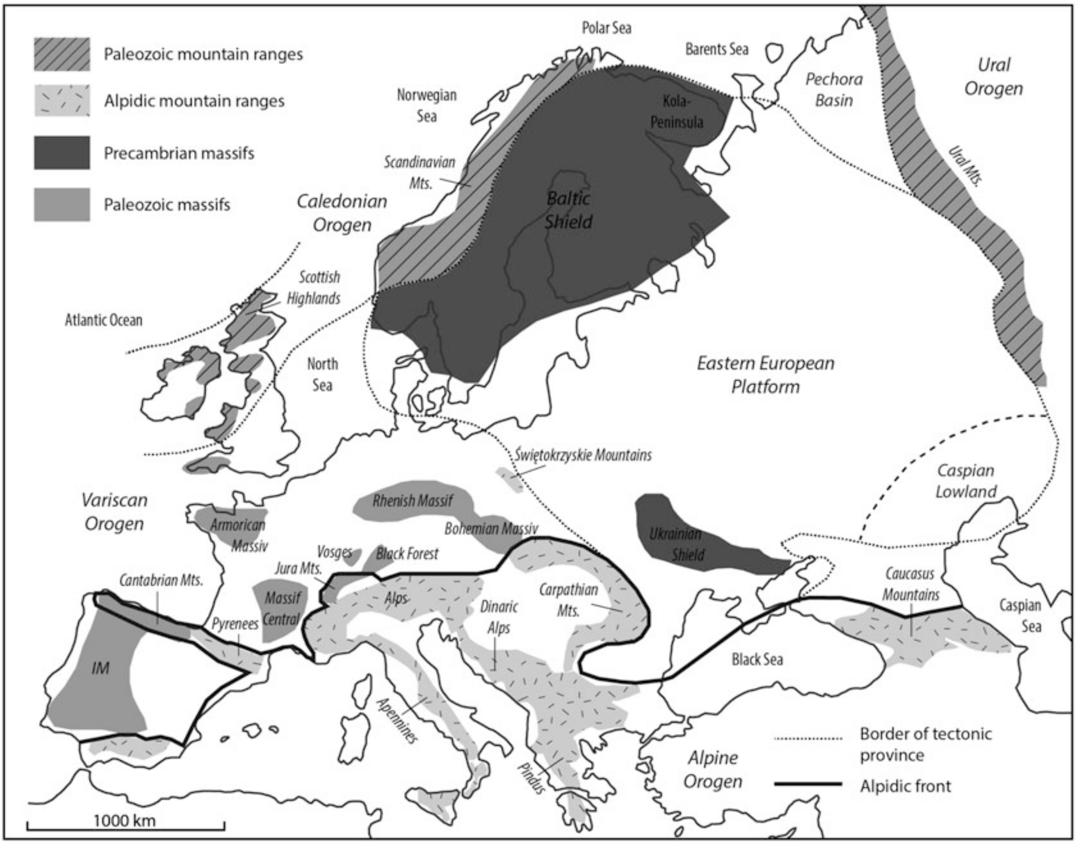

Fig. 2 High and low mountain ranges: Geological significance of important topographical features of Europe. Map recreated and modified, area boundaries following Park (2015)

2,376 m), the Carpathian Arch (High Tatras 2,655 m), and the Great Caucasus with seven peaks higher than 5,000 m (Elbrus 5,642 m). Hilly uplands extend to the west and north of the Alps (in the west, the French Massif Central (1886 m) with the Cevennes (1,699 m) and the Jura (1,718 m); in the northwest, the Vosges (1,424 m) and the Black Forest (1,493 m); and in the northeast, the Bavarian and Bohemian Forests (1,457 m) followed by the Hercynian mountain ranges, of which the Harz (1,142 m) extends furthest into the north German lowlands), while the ridge of the Erzgebirge (1,244 m) continues on to the east to the adjacent Sudeten mountains (1,603 m). The south Central European Uplands have counterparts in the Scandinavian highlands of Norway (2,470 m) as well as the Urals (1,894 m), of which the latter represent the northeastern boundary of the European mainland (Kondracki and Schlüter 2003).

In Macaronesia, several volcanic peaks exist. The highest peaks in the Azorean islands are Montanha do Pico (Pico Island, 2,351 m), Pico da Vara (São Miguel, 1,103 m), and Pico da Esperança (São Jorge, 1,053 m). The Azores are of volcanic origin without any parts of continental crust. They are located close to the Mid-Atlantic Ridge, a slow-moving sea floor-spreading zone, reaching from Jan Mayen and Iceland in the north to Tristan da Cunha in the south (Carracedo et al. 1998).

In the Azores region, the Eurasian, the African, and the American plates are drifting away from each other, causing constant tectonic disturbances. Magma reaches the upper parts of the crust and escapes, forming volcanoes. Today, 12 active volcanoes, 5 of them submarine, can be found in the Azores. Examinations of rocks and fossils revealed important differences in age between the islands of the area. Santa Maria, the easternmost island, developed probably in the Miocene about 5 to 14 million years ago. The northeastern parts of São Miguel are said to be 4 million years old, whereas the western parts seem to have existed for less than 2 million years. The lavas of Faial, São Jorge, and Graciosa were produced less than 750,000 years ago. With its 40,000 years, Pico, the highest mountain of Portugal, is the youngest island of the group. In general, the Azores are much younger than most of the other Atlantic Islands: the Madeira group is said to be 60 to 70 million years old, and the age of the Canary Islands ranges between 3 and 25 million years (Schäfer 2002).

Madeira is at the top of a massive shield volcano that rises about 6 km from the floor of the Atlantic Ocean, on the Tore underwater mountain range. The volcano formed atop an eastwest riff in the oceanic crust along the African plate, beginning during the Miocene epoch over 5 million years ago, continuing into the Pleistocene until about 700,000 years ago (Geldmacher et al. 2000). The most recent volcanic eruptions were on the west-central part of the island only 6,500 years ago, creating more cinder cones and lava flows (Carracedo et al. 1998).

Madeira has a mountain ridge that extends along the center of the island, reaching 1,862 m at its highest point (Pico Ruivo), while much lower (below 200 m) along its eastern extent. The primitive volcanic foci responsible for the central mountainous area consisted of the peaks Ruivo (1,862 m), Torres (1.851 m), Arieiro (1,818 m), Cidrão (1,802 m), Cedro (1,759 m), Casado (1,725 m), and Ferreiro (1,582 m). At the end of this eruptive phase, an island circled by reefs was formed; its marine vestiges are evident in a calcareous layer in the area of Lameiros, in São Vicente.

Also the seven major islands, one minor island, and several small islets of the Canary Islands were originally volcanic islands. The Teide volcano on Tenerife is the highest mountain in Spain and the third tallest volcano on Earth on a volcanic ocean island. All the islands except La Gomera have been active in the last million years; four of them (Lanzarote, Tenerife, La Palma, and El Hierro) have historical records of eruptions since European discovery.

The islands rise from Jurassic oceanic crust associated with the opening of the Atlantic. Underwater magnetism commenced during the Cretaceous and reached the ocean surface during the Miocene. The islands are considered as a distinct physiographic section of the Atlas Mountains Province, which in turn is part of the larger African Alpine System division (Del Arco Aquilar and Delgado 2018).

Zonal soil types have been defined based on different geologic substrates, numerous orographic landforms, and earlier geomorphological processes, as well as climatic factors and the development of the vegetation cover. The arctic zone shows arctic frost debris and tundra (gley) soils (Gelic Regosols, Gelic Histosols) and the boreal zone podzol soils (Podzols, Podzoluvisols), gley-podzols, and peat soils (Histosols). In the temperate zone main soils are brown earths (Cambisols) and para-brown earths (Luvisols) and also podzol soils on base-poor substrates. In the eastern forest steppe and steppe zones, gray forest soils (Luvisols) and chernozems are dominant. In the warm humid areas in the south of the Colchis, mainly yellow and red earths (Acrisols) occur. Typical soils of the Mediterranean sclerophyllous forests and scrub are cinnamon-colored, reddish-brown, and red soils (Calcic Cambisols, Chromic Luvisols). As climate and vegetation, soil types vary according to altitude (Kondracki and Schlüter 2003).

Macaronesian soils mainly developed from airborne volcanic deposits, especially basic ashes. They are rich in amorphous weathering products and volcanic glass and therefore finely coarse, with low bulk density, but nevertheless, they are usually quite slicky. The ion exchange capacity is rather high, which make these soils very fertile. The soils in Azorean islands are classified as Andosols (Schäfer 2002).

Climate is crucial for the zonal differentiation of vegetation types and soil formation. At the

Fig. 3 Physiographical structure of Europe. (After Kondracki and Schlüter (2003), modified. Reproduced with permission from Bundesamt für Naturschutz/Federal Agency for Nature Conservation/2018)

same time, soil types, especially concerning moisture regime, nutrient status, and texture, have a great influence on the formation of regional vegetation types and mosaics and are helpful in the recognition of biotopes at landscape level.

Physiographical Structuring

Unless indicated otherwise, this chapter follows Kondracki and Schlüter (2003).

Natural landscapes are formed by numerous natural factors, altered by varying human influence. The orography and lithology of rocks are the most stable factors of landscapes. The most unstable factor is vegetation, which is also highly affected by human land use. As a result, the potential natural vegetation represents its natural composition, structure, and spatial distribution. The potential natural vegetation is the most prominent landscape-ecological feature and corresponds to the description of biotopes representing the integration of all natural landscape components.

For physiographical regionalization, the horizontal differentiation of climate, bedrock, and soil properties and the vertical sequence from lowland to hill country (colline), upland (montane), and high mountain (alpine and nival) regions are most important and have a great influence on the spatial differentiation of the natural vegetation. For our small-scale consideration of Europe, we only require the highest hierarchical spatial units, subdivided according to their overall physiographical character into super-region, region, and province (see Fig. 3).

Adriatisches Meer	Adriatic Sea
Ägäisches Meer	Aegean Sea
Alpen	Alps
Andalusien	Andalusia
Apennin-Halbinsel	Apennine Peninsula
Atlantik	Atlantic Ocean
Atlantisches Frankreich	Atlantic France
Balearen	Balearics
Balkangebirge	Balkan Mountains
Balkanhalbinsel	Balkan Peninsula
Bäreninsel	Bear Island
Barentssee	Barents Sea
Böhmisches Massiv	Bohemian Massif
Bottnischer Meerbusen	Gulf of Bothnia
Cevennen	Cévennes
Chalkidike	Chalkidiki
Der Kanal	(English) Channel
Deutsche Bucht	German Bight
Dinarisches Gebirge	Dinaric Alps
Dnjepr-Platte	Dnieper Upland
Dnjeprniederung	Dnieper Lowland
Donezplatte	Donbass
Don-Hügelland	Hills of River Don
Dvina-Mezen-Niederung	Dvina-Mezen-Valley
Färöer Inseln	Faeroe Islands

(continued)

Fennoskandien	Fennoscandia
Finnischer Meerbusen	Gulf of Finland
Finnisch-Karelische Masse	Finnish-Karelian Massif
Finnisch-Karelische Seenplatte	Finnish-Karelian Lakeland
Finnmark	Finnmark
Franz Josef Land	Franz Joseph Land
Golf von Biskaya	Bay of Biscay
Grönland	Greenland
Großbritannien	Great Britain
Großer Kaukasus	Greater Caucasus
Halbinsel Kola	Kola Peninsula
Herzynisches Mitteleuropa	Hercynian Europe
Iberische Halbinsel	Iberian Peninsula
Irland	Ireland
Island	Iceland
Jura-Gebirge	Jura Mountains
Kantabrisches Gebirge	Cantabrian Mountains
Kara See	Kara Sea
Kaspische Senke	Caspian Depression
Kaspisches Meer	Caspian Sea
Kastil. Scheidegebirge	Central System (Sistema Central)
Kattegat	Kattegat
Kleiner Kaukasus	Lesser Caucasus
Korsika	Corsica
Kreta	Crete
Lappland	Lapland
Ligurisches Meer	Ligurian Sea
Mitteleuropäisches Tiefland	Central European Lowlands
Mittelrussische Platte	Central Russian Upland
Mittelrussisches Tiefland	Central Russian Lowlands
Mittlerer Ural	Central Ural
Moskauer Becken	Moscow Basin
Nördlicher Ural	Northern Ural
Nördliches Alpenvorland	Northern Alpine Foothills
Nordrussischer Landrücken	Northern Ridge, Northern Uvaly
Nordrussisches Tiefland	North Russian Plain
Nordsee	North Sea
Nowaja Semlja	Novaya Zemlya
Oka-Don-Niederung	Oka-Don Lowlands
Olymp	Mount Olympus
Ostbaltisches und Belarussisches Tiefland	East Baltic and Belarusian Plain

(continued)

Ostkarpaten	Eastern Carpathians
Östliches Mittelmeergebiet	Eastern Mediterranean
Ostsee	Baltic Sea
Paj-Choj	Pay-Khoy Ridge
Pannonisches Becken	Pannonian Basin
Pecora-Niederung	Pecora Valley
Peloponnes	Peloponnese
Pindos	Pindos
Po-Ebene	Po Valley
Polesje	Polesie
Polnische Platten	Poland Uplands
Pyrenäen	Pyrenees
Sardinien	Sardinia
Schwarzes Meer	Black Sea
Schwarzmeer-Niederung	Black Sea Lowland
Sizilien	Sicily
Skandinavische Halbinsel	Scandinavian Peninsula
Skandinavisches Gebirge	Scandinavian Mountains
Skandinavisches Tiefland	Scandinavian Lowland
Spitzbergen	Svalbard
Südkarpaten	Southern Carpathians
Südlicher Ural	Southern Ural
Südrussisches Tiefland	South Russian Lowlands
Thrakien	Thrace
Timanrücken	Timan Ridge
Transkamagebiet	Trans-Kama region
Transwolga-Hügelland	Transvolga
Tyrrhenisches Meer	Tyrrhenian Sea
Untere Donauebene	Lower Danubian Plain
Uralvorland	Ural foothills
Vorkaukasus-Ebenen	North Caucasus region
Waldaihöhe	Valdai Hills
Weißes Meer	White Sea
Westkarpaten	Western Carpathians
Westliches Mittelmeergebiet	Western Mediterranean
Westrussischer Landrücken	Belarusian Ridge
Wolgaplatte	Volga Upland
Wolynisch-Podolische Platte	Podolian Upland
Zentrales Frankreich	Central France
Zentrales Mittelmeergebiet	Central Mediterranean
Zentralmassiv	Massif Central
Zypern	Cyprus

According to a convention of the International Federation for Documentation (FID 1971), Europe is physiographically divided into nine super-regions. A useful overview can be obtained by first subdividing the continent into four parts following the cardinal directions. This results in four subcontinents to which the nine super-regions can be related. Macaronesia will be added as the 10th super-region.

Northern Europe

1. Fennoscandia, Iceland, Arctic islands

Western and Central Europe

2. British Isles and France
3. Northern Central Europe
4. Alps
5. Carpathian Mountains

Southern Europe

6. Mediterranean Southern Europe

Eastern Europe

7. Caucasus and Crimea
8. East European Lowland
9. Ural Mountains

Macaronesia

The Super-Regions of Europe (Following Kondracki and Schlüter 2003)

Northern Europe (approximately 1,500,000 km^2) is separated from the mainland of the continent by several waters: the North Sea, Skagerrak, Kattegat, the Baltic Sea with the Gulf of Finland, Lake Ladoga and Lake Onega, the White Sea, and the Barents Sea. It can be divided into two large parts of different geological origin, the Precambrian shield of Fennoscandia and the early Paleozoic (Caledonian) folding of the Scandinavian Mountains. Another part of Northern Europe are the Arctic islands Novaya Zemlya, Franz Josef Land, Svalbard, Bear Island, Jan Mayen, and Iceland, although the latter is of oceanic-volcanic and not continental origin.

Quaternary glaciation marked Northern Europe's surface significantly with glacial erosion leaving basins filled by lakes or mires and deeply cut fjords in the landscape on the western side of the Scandinavian Peninsula. Mountain ranges in the southern part stand out with altitudes exceeding 2,000 m above sea level (Galdhøpiggen 2,469 m) and extensive glaciers (Jostedalsbreen, approximately 1,000 km^2).

The climate in Northern Europe is influenced by the warm Atlantic Gulf Stream with maritime air causing moist, less severe winters, cool summers, and precipitation distributed over the whole year. In the western and southern part of the peninsula, this oceanic influence is restricted by the Scandinavian Mountains which stretch across almost 2,000 km from the southwest to the northeast. Thus the northeastern parts have a more continental climate with very cold winters, as in Finland and Karelia (mean January temperatures of −8 °C to −16 °C).

Four phytogeographical zones can be distinguished in Northern Europe, from north to south: arctic polar deserts and tundras, boreal birch and coniferous forests (taiga), hemiboreal mixed broadleaved-coniferous forests, and nemoral broadleaved forests in the south and southwest (Kondracki and Schlüter 2003).

Northern Europe is subdivided as follows:

1 *Fennoscandia, Iceland, Arctic islands*
11 Iceland
12 Jan Mayen Island
13 Faeroe Islands
14 Scandinavian Peninsula with its offshore islands
15 The Finnish-Karelian Shield
16 The Kola Peninsula
17 Svalbard and Bear Island
18 Franz Joseph Land
19 Novaya Zemlya

Western and Central Europe (approximately 2,250,000 km^2) covers the western part of the Eurasian mainland with the British Isles and shows a complicated geological composition which has been broken up by manifold faults, uplifts, and sinkings, in particular during the periods of mountain formation which include the Caledonian, Hercynian, and Alpine foldings. In the course of these processes, during a sinking between Northern and Western Europe, the North and Baltic seas area and the Central European lowlands developed. Today the lowlands are covered by Tertiary and Quaternary sediments.

Several uplands formed as a result of the foldings. On the British Isles, these are the Scottish Highlands (1,343 m) and the uplands in Cornwall and Wales (1,085 m) that extend as far as the south and southeast of Ireland. On the European mainland, mountainous areas extend from France across Germany to Poland: one arch beginning in Brittany, France, extending to the Massif Central (Puy de Sancy 1,886 m), and a second area extending from there to the northeast: the Ardennes (694 m), the Rhenish Slate Mountains (841 m), the Vosges (1,424 m), the Black Forest (1,493 m), and the Harz (1,142 m). The Bohemian Massif with its prominent ridges, namely, the Bavarian and the Bohemian Forests (1,457 m), the Thuringian Forest (982 m), the Erzgebirge (1,244 m), and Sudeten mountains with the Giant Mountains (1,603 m), is a special mountainous area in the eastern part.

The mountain foldings were often accompanied by the formation of intermontane basins which often also represent special climatic and phytogeographical conditions as in continentally influenced dry areas. Examples for such areas are the Thuringian Triassic basin (annual precipitation <500 mm) with the adjacent Magdeburger Börde to the east (chernozems) or the Prague Basin.

The Alps and the Carpathian mountains form the third orographic element of Central Europe. These are the high mountain ranges including their respective basins both within and around the mountains. The Western and Central Alps are higher and more "compact" with several peaks over 4,000 m (Mont Blanc 4,807 m) than the Eastern Alps, which feature no peaks higher than 4,000 m (Großglockner 3,797 m). Pleistocene glaciations shaped the alpine relief significantly and also led to the formation of large morainal ridges and lakes (Lake Constance, Lake Geneva, Lake Garda, Lake Maggiore, etc.). The second high mountain range in the northeast is the Carpathian Mountains, which exceed 2,500 m only in their western and southeastern parts (High Tatras 2,655 m, Fagarash Mountains 2,543 m). The Pannonian Basin is more than half surrounded by the Carpathian Arch. In the southeast, the rivers Sava and Lower Danube define the border of Central Europe, where they divide the Pannonian and Carpathian regions from the Balkan Peninsula.

Pleistocene sediments are the main components of Central European lowlands consisting of glaciogenic terminal and ground moraines as well as glaciofluviatile and fluviatile sediments, with altitudes which rarely exceed 200 m and only reach 300 m in exceptional cases. In the east Central Europe's border is defined climatically and biogeographically, in the northwest from Eastern Poland through Western Ukraine to the southeast in Eastern Romania.

Central Europe lies between 43° and 58°N and belongs to the relatively warm temperate zone with deciduous broadleaved forests. There is a notable climatic differentiation although climatic zonation is rather indistinct. The strongly differentiated orography and the influence of the seas in the north and south have a strong impact on climatic characteristics. There are vegetation zones affected by increasing dryness of climate up to in part the presence of forest steppe as in the Pannonian Basin, the Romanian Danube lowlands and the eastern foothills of the Carpathian Mountains. Another dominant climatic zone is moderately warm and moist suboceanic with decreasing precipitation and larger ranges in seasonal temperature with increasing continentality toward the east. These are the areas north of the Alps and Carpathian mountains. The mountain ranges are dominated by altitudinal belts with both climatic conditions and vegetation types changing according to altitude. There is a considerable rise in precipitation and drop in temperature on a yearly average as altitude increases.

The Western and Central European superregion is subdivided into the following physiographical regions and provinces:

2 *British Isles and France*
21 Ireland
22 Great Britain and neighboring islands
23 a Atlantic France
23 b Central and Southern France
3 *Northern Central Europe*
31 Central European lowlands
32 Hercynian Central Europe (low mountains and cuesta landscape)
33 The Bohemian Massif and its surrounding mountain ranges
34 The Polish uplands
4 *Alpine Countries*
41 Jura mountains
42 Northern foothills of the Alps
43 Alps
44 North Italian lowlands
5 *Carpathian Countries*
51 Western Carpathian Mountains and outer foothills
52 Eastern Carpathian Mountains and outer foothills
53 Southern Carpathian Mountains and outer foothills
54 Transylvanian basins and mountains
55 Pannonian Basin
56 Lower Danube plain

Southern Europe (approximately 1,250,000 km^2) is not a contiguous mainland area; it is composed of the three large Mediterranean peninsulas with their neighboring islands. The formation of the peninsulas is closely connected to the orogenesis of the relatively recently formed Alpine mountain chains. The rather compact Iberian Peninsula is delimited in the north by the Pyrenees (Pico de Aneto 3,404 m) and the Cantabrian Mountains and in the southeast by the Baetic Cordillera with the Sierra Nevada (Mulhacen 3,478 m) which continues on to the Balearic Islands. The islands of Corsica and Sardinia are remnants of the sunken Tyrrhenian Massif. The Apennine mountain chain (Corno Grande 2,914 m) extends along the Apennine Peninsula and forms the peninsula lengthwise, continuing on to Sicily. The Balkan Peninsula is formed in the center by the older Thracian-Macedonian Massif (Musala in the Rila Mountains 2,925 m, Olympus 2,918 m, the

Pindos with Smolikas 2,637 m, Nkiona 2,510 m) which is surrounded by the Dinaric Mountains (Prokletije 2,693 m) and the Balkan Mountains (Botev 2,376 m). Its southern part has been tectonically broken up into peninsulas such as the Peloponnese and Chalcidice as well as the Aegean Islands (Kondracki and Schlüter 2003).

A peculiarity of Southern Europe is its seismic instability with the active volcanoes Mount Etna (3,340 m) on Sicily, the Aeolian island Stromboli with Mount Stromboli (926 m), and Mount Vesuvius (1,277 m), all located on the Apennine Peninsula. These are the only volcanoes still active on, resp., near the European mainland.

The characteristics of Southern Europe climate, belonging to the Mediterranean climate type, are warm and dry summers as well as moist and almost frost-free winters. Primarily this applies to lowlands and coastal areas of all three peninsulas and the Mediterranean Sea with its islands. Because of the dominating mountain ranges on the peninsulas, in inland areas, continentality tends to increase, particularly on the Iberian and Balkan Peninsulas.

Due to the predominant climate and the closely related soil types, vegetation, and drainage regime, the Mediterranean area differs quite strongly on the whole from Western and Central Europe. Mediterranean Southern Europe is subdivided into the following regions:

6 *Mediterranean Southern Europe*
61 Iberian Peninsula with Balearic Islands
62 Central Mediterranean area
63 Apennine Peninsula
64 Balkan Peninsula and neighboring islands
65 The Balkan Mountains

Eastern Europe (approximately 5,000,000 km^2) with its vast, topographically monotonous landscape differs distinctly from the rest of Europe. This large plain is characterized by the level position of sedimentary rocks on the Precambrian basement which is exposed in Fennoscandia (the Baltic Shield) and in the Ukrainian Shield. Extending eastwards to the Urals are basins covered by Paleozoic and Mesozoic strata. The Devonian Timan Ridge in the northeast, the Kursk Heights with crystalline bedrock at the upper Don, and the Hercynian folding zone in the Dnieper-Donets area represent particularities in the geological structuring of Eastern Europe. The east European lowlands end at the Ural Mountains range chain, while the southern boundary is formed by the northern Black Sea coast, the Crimean Mountains and the Great Caucasus.

The Crimean Mountains (Roman-Kosch 1,545 m) are asymmetrically formed with a steep slope to the south toward the Black Sea. As a result, the coastline is protected from cold air in winter, and a “Riviera” has developed with an almost Mediterranean climate. Further to the east, the immense chain of the Great Caucasus stretches to the Caspian Sea, with several extinct volcanoes higher than 5,000 m (Elbrus 5,633 m). In the east, the Ural Mountains extend in a north-south direction for approximately 2,500 km. The northern part has the highest summits (Narodnaja 1,894 m); the middle part is slightly lower before rising again up to 1,640 m in the southern part.

A number of ridges and plateaux are found in the south of the east European lowlands. These include the Volyn-Podilsk Upland (Kamula 474 m), the Dnieper, Donets, Central Russian, and the Volgian uplands, as well as the Yergeni Hills in the south. Lowland plains are the dominant landscape feature which extend between the ridges and plateaus and further south. These include the Trans-Dnieper, the Oka, Don, as well as the Black Sea and the Caspian lowland in the south and also extensive lowlands, e.g., the Polesje and low uplands such as the West Russian Ridge, the Valdai Hills, the Central Russian Uplands, and the North Russian Ridge further north.

As it is in the Central European lowlands, the topography of the northern part of Eastern Europe is of glacial origin. Glaciers advanced the furthest during the so-called Dnieper Glaciation in the Middle Pleistocene and covered the landscape as far as the Polesje and the Dnieper lowland to Dnipropetrovsk and the Oka-Don lowland to Kalach-na-Donu. The undulating lake landscape in a zone connecting Vilnius, Vitsyebsk, and the Valdai Hills (343 m) and extending to the northeast to Archangelsk on the White Sea was created during the last so-called Valdai glacial period. Periglacial loess deposits are found in the uplands of the southern part of Eastern Europe, while the north Caspian lowland is covered by saline sand and clay sediments dating from the Pleistocene transgressions over the Caspian Sea.

The rather flat, vast land surface of Eastern Europe stretches out across approximately 25° of latitude. This area is also characterized by pronounced geographic zonation. Continentality increases toward the east and causes arid regions in the south and cold regions in the north. The southwest to northeast trend of zonal boundaries results in a narrowing of the mixed broadleaved forest zone toward the east and its complete disappearance east of the Urals.

For the physiographic subdivision of Eastern Europe, climatic, edaphic, phytogeographical, and geomorphological criteria must be taken into account. The classification lists these subdivisions as follows (Kondracki and Schlüter 2003):

7 *Caucasus and Crimea*
71 Crimean Peninsula
72 Pre-Caucasus plains
73 Great Caucasus
74 Colchidian (Rioni) lowlands (belonging to Asia Minor)
75 Kura lowland (belonging to Asia Minor)
76 Lesser Caucasus (belonging to Asia Minor)

8 *East European Lowland*
81–82 North Russian lowland
83 Central Russian lowland
84 East Baltic and Belarusian lowland
85–86 South Russian lowland

9 *Ural Region*
91 Paj-Choj Ridge and Vaygach
92 Polar Urals
93 Northern Urals
94 Central Urals
95 Southern Urals

To add Macaronesia as "part of Europe," the following subdivisions are proposed:

10 *Macaronesia*
101 Azores
102 Madeira Archipelago
103 Canary Islands

Climatic Classification of Europe (Following Walter et al. 1975)

Climatic conditions in Europe are defined by geographical location, landmass distribution, and topography. Five main thermal zones can be distinguished from north to south: arctic, boreal, temperate, submeridional, and meridional. These relate closely to the southward progression of zonal vegetation from arctic tundra through boreal coniferous forests (taiga) to temperate mesophytic and thermophilous broadleaved deciduous woods as well as the steppes and deserts of Eastern Europe and finally to Mediterranean evergreen sclerophyllous forests and scrub.

Geographical latitude and regional differentiation of the surface relief have an effect on the climate mainly in the form of the solar radiation balance, but the climate is also influenced by atmospheric circulation. Northern Europe is warmer than would be expected regarding its latitude. That is because of the westerly circulation and the Gulf Stream; nevertheless very cold arctic air masses can at times reach the area. In the temperate zone, this westerly circulation moderates the temperature leading to relatively mild winters and comparably cool summers. Sometimes, however, dry continental or cold arctic air masses advance to Northern Europe and lead to a great instability in weather patterns and make the course of weather vary considerably over the year. The atmospheric circulation is also influenced continuously by energy input from the sun that varies according to multiphase rhythms (11-year, 35-year and longer cycles between cold-moist and warm-dry periods). In the Mediterranean region, in summer typically warm and dry weather are predominant due to the anticyclone acting as a high-pressure area, while in winter depressions entering from the west bring substantial precipitation. Sometimes this circulation pattern can also reverse (Kondracki and Bohn 2003).

Oceanic air masses warmed by the Gulf Stream mainly affect Western and Northern Europe (despite its gradual weakening), and a warm subtropical North Atlantic Ocean current influences temperatures all the way up to the Kola Peninsula. This is a fundamental aspect of the European climate. Even in the far north, the Gulf Stream moderates the long arctic winters, so that the port of Murmansk north of the Arctic Circle can remain ice-free during the severest of winters.

In Eastern Europe in winter, the Asiatic anticyclone produces a flow of cold, dry air masses causing an increase in the typical characteristics of continental climate from Western to Eastern Europe. This climatic particularity includes an increase in the annual range of average monthly temperatures and a shift toward a summer precipitation maximum.

In the oceanic climates on the western edge of Europe, by contrast, the amount of precipitation that falls per month is almost the same in every month of the year, and the annual amplitude between mean monthly temperatures is small. This implies that winters tend to be mild and frost-free, and summers are relatively cool.

Precipitation is highest in the western part of the temperate climate zone, decreasing from west to east with increasing continentality. Accordingly, mean annual precipitation varies from West to East, Valentia (SW Ireland) with 1,416 mm (with a winter maximum), London with 612 mm, Warsaw 550 mm, and Voronezh (Russia) with 521 mm (the last two places have a summer maximum). In the arctic north, it is even less, in Murmansk (Russia), for example, with 477 mm. In the Mediterranean climate region precipitation differs greatly. In Palma on Mallorca, it is low (498 mm) as it is in Athens (407 mm), while in areas affected by the westerly circulation, it is much higher, with a marked winter maximum, for instance, Genoa receives 1,258 mm, while Rijeka receives 1,593 mm.

Annual precipitation also increases with increasing altitude. In some mountain ranges, it can exceed 4,000 mm (e.g., the Dinaric and Scandinavian mountains, Wales), while in the Alps it is more than 2,000 mm. Mean annual temperature, by contrast, decreases continuously with increasing altitude.

In the eastern part of Europe, the north-south climatic zonation shows most notably, as it represents a contiguous mainland block that is mostly flat and not broken up by mountain ranges or large bodies of water. Temperature and moisture balance considered, the following vegetation-related main zones can be distinguished (Kondracki and Bohn 2003):

Arctic tundra zone
Boreal birch and coniferous forest zone (taiga)
Temperate coniferous-deciduous forest and deciduous forest zone
Submeridional-continental, periodically dry steppe zone
Submeridional arid, continuously dry desert zone

Between these five main zones, the following transitional sub-zones or subregions can be distinguished: subarctic forest tundra, hemiboreal deciduous broadleaved-coniferous forests, subcontinental forest steppes, and semiarid desert steppes. The western part of Europe shows climatic zones that are not as pronounced because of the compensating oceanic influence and the horizontal and vertical structure of the landscape.

The horizontal and vertical differentiation of the climatic factors and the vegetation types that depend on them are crucial in the physiographical classification of the continent.

Ecological Classification of the Climates of Europe

The mapping units and formations of the vegetation map of Europe are related to various climatic types based on the World Atlas of Climate Diagrams (Walter and Lieth 1967). The climatic data (annual precipitation, annual and monthly mean temperatures) for the mapping units were primarily taken from the climate diagrams published in that work and in part also from other publications.

A simplified world map, "ecological climate classification of the continents," was published in 1975 by Walter, Harnickell, and Müller-Dombois (Climate diagram maps of the individual continents and the ecological climatic regions of the earth). The climate zones for Europe are displayed in Fig. 4.

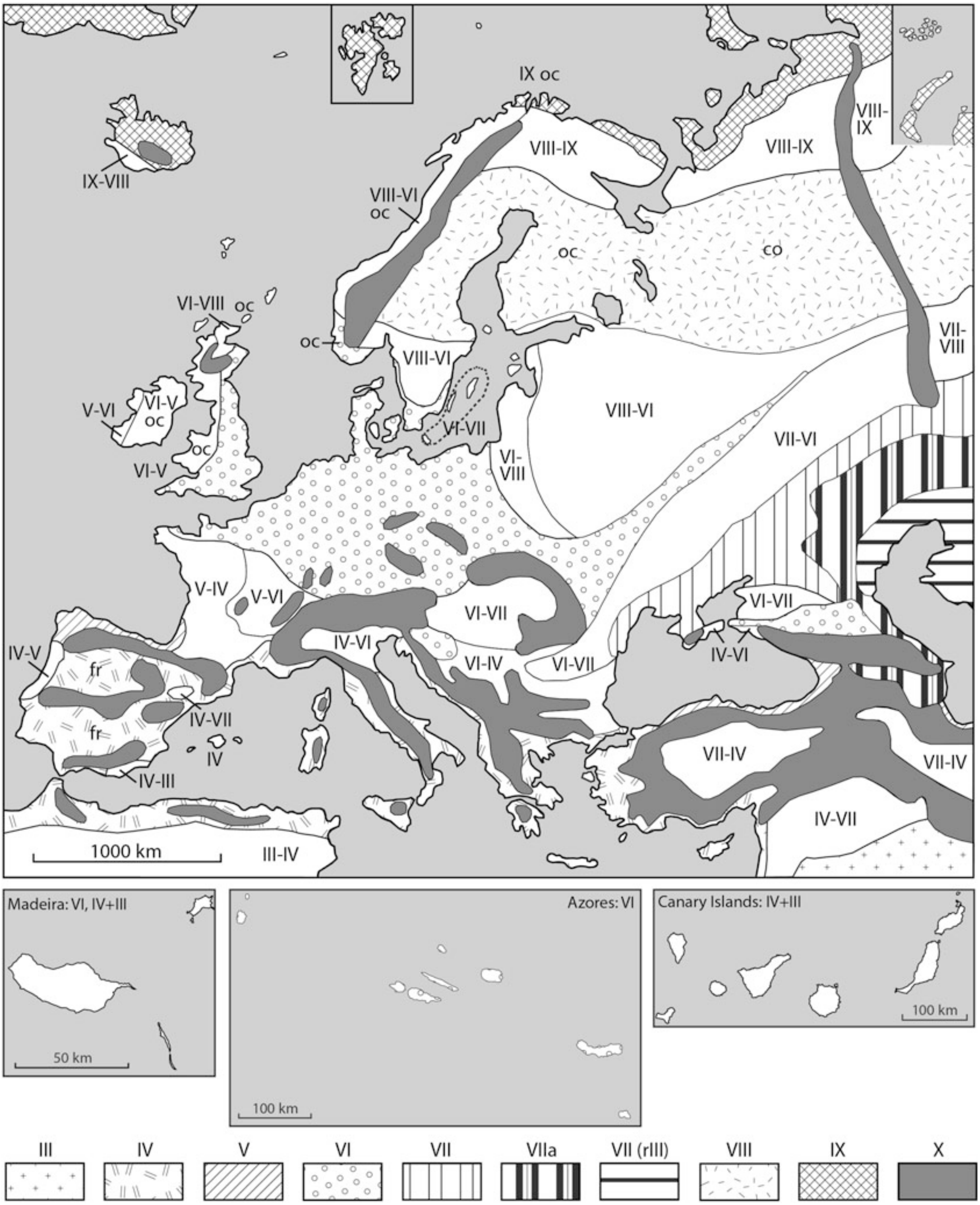

Fig. 4 Climatic classification of Europe. III: Subtropical arid zone of the deserts; IV: Typical Mediterranean climate; V: Warm temperate climate; VI: Typical temperate climate; VII: Semiarid steppe climate; VIIa: Arid semi-desert climate; VII(rIII): Desert climate with cold winter; VIII: Cold-temperate or boreal climate zone; IX: Arctic climatic zone; X: Mountain climates. VI–VII refers to a transition between VI and VIIV (IV) corresponds to a warm temperate climate (V) but with prevalent winter rains (as with IV). VIII–IX: Subarctic zone (the delimitation of zones IX and VIII is based on the duration of the vegetationperiod with daily averages above 10 °C. Its duration at the northern boundary of zone VIII is about 30 days, while at the southern limit it is about 120 days). VIII–VI: Hemiboreal zone VI–VII: Moderately arid temperate, subcontinental forest-steppe zoneVI–IV: Temperate sub-Mediterranean zone V–VI: Submediterranean zone IV–III: Thermomediterranean arid zone. Additional symbols: oc = oceanic; co = continental; fr = frequent frost. (Modified from Walter et al. 1975)

Explanation of the Climate Map (According to Walter et al. 1975)

The map shows the ranges of the climate types I–IX, i.e., the regional climates of large areas with similar topography (mainly lowland, hill country, and lower mountains). The mountain climates have been presented as a single unit (X) without subdivision into altitudinal belts or assignment to the major climatic zones. Transitional zones between the individual climate types are indicated by combinations of the relevant Roman numerals. Climatic gradients (temperature and precipitation) also exist within the ranges of the individual climate types from west to east and from north to south. Variations from the norm are marked with additional characters from the alphabet (a, oc, co, fr, r).

The Macaronesian climate seems to be a mosaic of oceanic temperate climate (VI), warm temperate climate (V), typical Mediterranean (IV), and subtropical arid (III). Del Arco Aguilar and Delgado (2018) differentiate bioclimatic belts in the Canary Islands: intra-Mediterranean, thermo-Mediterranean, meso-Mediterranean, supra-Mediterranean, and oro-Mediterranean. Important is the presence or absence of trade wind clouds; therefore in all belts, ombrotypes from hyperarid, arid, semiarid, dry, subhumid, to humid can exist.

The Azorean climate is temperate oceanic with a mean annual temperature of 17.5 °C and mean annual precipitation between 1,000 and 1,600 mm at sea level. The climate is mainly regulated by a branch of the Gulf Stream and by a high-pressure zone called the "Azores anticyclone." The influence of the anticyclone is at its highest in summer. The average snow line is located at 1,200 m, but may in some exceptions reach as low as 600 m. Rainfall peaks during the time from October to January and is at its lowest in July. Throughout the Azores, rainfall decreases from W to E (Harris et al. 1962). Cloudiness is more common than in any other Macaronesian region, and fog on the islands is also a rather common phenomenon. The influence of NE trade winds is most important in the easternmost island, whereas winds from N, NW, and SW prevail in the central and western groups (Schäfer 2002; Cropper and Hanna 2013).

The climate on Madeira Islands ranges from temperate oceanic in the North to subtropical arid in the South. During summer, the NE trade winds influence the climate on the Canary Islands. Average temperatures are between 15.5 °C (minimum) and 21.9 °C (maximum); the average precipitation is 642 mm.

On the Canary Islands, according to the position of the islands with respect to the northeast trade winds, the climate can be mild and wet or very dry. As a consequence, the individual islands in the Canary archipelagos tend to have distinct microclimates. Those islands lying to the west of the archipelago, such as El Hierro, La Palma, and La Gomera, have a climate which is influenced by the moist of the Gulf Stream. Basically the climate is Mediterranean but can be more humid or dry depending on the position of the islands. Generally, the Canaries have hot, dry summers and warm, humid winters, but locally there are often considerable deviations from this basic pattern (Del Arco Aquilar and Delgado 2018).

The northeast trade winds bring in moisture from the sea, which, when forced to rise by the mountain barriers of the western islands, is cooled and forms a zone of precipitation at about 800 to 1,500 m. This causes a more or less persistent cloud layer at this level on the north side of all western islands and has a great influence on the natural vegetation. The southern sectors of these islands are in a rain shadow and receive much less precipitation. They are generally without a tense-forest zone at mid-altitude level and are much more xerophytic in nature. The climate is more humid and the vegetation more luxuriant. The further west one goes in the archipelago due to the increasingly oceanic position of the western islands and the greater strength of the trade winds (Wirthmann 1970; Cropper and Hanna 2013).

The extreme dryness of the eastern islands and the south of Gran Canaria is partially due to the hot dry Saharian winds, the Levante, which sometimes reach the eastern Canaries blowing for up a week at a time with a strong desiccating effect on the vegetation. The eastern islands are too low to intercept the trade wind moisture except for their highest points (Del Arco Aquilar and Delgado 2018).

Phytogeographical Division of Europe

The division of the Earth into floristic kingdoms, regions, and provinces intends to classify areas with a floristic inventory as homogeneous as possible. The division of Europe presented here was also established for this purpose (Meusel and Jäger 1992). It has already turned out to be useful for characterizing plant species ranges on many occasions.

Unlike vegetation maps, a floristic division is based on the limits of plant distribution ranges and floristic gradients in particular of higher plants. Cryptogams are not considered as their ranges are not yet known well enough. The floristic gradient describes the density of different range limits observed in a single direction within a given distance. The position and distinctiveness of a phytogeographical boundary are defined on the basis of the floristic gradient.

It can be expected that floristic division corresponds largely to the boundaries of principal vegetation types on a continental scale. However, on a global scale, isolation due to the changing distribution of sea and land may cause major floristic differences between areas that show similar types of vegetation due to the effects of convergent evolution (Jäger 2003).

It is not yet possible to establish an objective floristic division that takes into account the ranges of all species due to a lack of data, even for a well-studied area like Europe.

The floristic divisions developed by Meusel and Jäger (1992) are mainly based on regularly occurring distribution limits. In addition to comparing hundreds of distribution maps, all classification proposals of earlier authors were considered (including those proposed in floras).

Methodological problems turn up with all phytogeographical divisions. Phytogeographers find floristic limits and floristic influences from various directions in their narrow working area. It is therefore not surprising that almost everyone speaks of "an interesting transition area." However, depending on the floristic contrast, the floristic boundaries vary in importance and also differ in clarity depending on the floristic gradient. Clear floristic boundaries are quite obvious with steep gradients in physicogeographical factors (Jäger 2003).

Looking at differences in floristic contrast, a hierarchy of floristic areas soon becomes evident. When demarcating the phytochores (floristic areas) of higher rank (floristic kingdoms, floristic regions), the systematic rank of the characteristic taxa is especially emphasized. Thus, for defining floristic kingdoms, several endemic families should be present and for floristic regions, several endemic genera, while floristic provinces must be characterized at least by the presence of a few endemic species.

Floristic division refers to lowland and colline belts as well as to a uniform type of sequence of mountain altitudinal belts in the area considered. However, this is not possible in expansive highland areas, for example, in Central Asia. The Alps, Carpathians, and Caucasus were ranked as subregions in their own right (extending over two zones) as they have many of their own species. The subdivision of the Alps varies depending on the different altitude belts. The montane belt is more homogeneous in composition than the lower ones (Hübl and Niklfeld 1973).

Since plant distribution is influenced by climatic changes, all floristic area limits are dynamic. With winter temperature and precipitation rising at more northern latitudes, a major increase in oceanicity is notable in this region. With an increase in average January temperatures by around 3 °C and summer temperatures by about 1 °C, for instance, the British Isles would be excluded completely from the potential range of *Tilia cordata*, while a rise in the July average by about 3 °C and the January average by about 1 °C would enlarge the potential range of this tree into Ireland. Former changes in climate as the medieval warmings (500–600 and 1,000–1,200 A.D.) and the "Little Ice Age" (1,550–1,700; 1,820–1,860 A.D.), supposedly accompanied by comparable temperature changes, may have led to similar effects (Crawford 2000). The amount of precipitation as well as the changing seasonality of rainfall controls plant distribution. The associated variable leaching and wetting of the soils and also the impact on the permafrost range crucially influence the range limits and the distribution of the natural vegetation (Jäger 2003).

Floristic Zones and Regional Subdivision (Fig. 5)

The arctic zone is made up of polar deserts and arctic tundras of Europe. The southern limit of this zone corresponds in Fennoscandia and Russia with the arctic tree line. This zone is specified by circumpolar species such as *Poa arctica*, *Luzula confusa*, *Cerastium regelii*, and *Draba corymbosa*.

The boreal zone commonly includes the taiga (i.e., northern coniferous forest) areas but in highly oceanic areas, e.g., in Iceland, on the Faeroe Islands, and in Western Norway, also birch forest areas and forest-free areas in which boreal herbaceous perennials and dwarf shrubs occur. Typical species for this zone are *Calypso bulbosa*, *Listera cordata*, *Rubus arcticus*, *Empetrum hermaphroditum*, *Linnaea borealis*, *Ledum palustre*, and *Cornus suecica*.

In the temperate zone, the formation of deciduous broadleaved forest extends from the Atlantic to the Urals, although in the north, taiga elements are interwoven, and in the south, islands of steppe vegetation occur. East of the Urals, small-leaved steppic forests with birch, aspen, and pine are set in the temperate zone, a view supported by the ranges of steppe forest plants which are distributed mainly temperately also in Central and Eastern Europe (*Dracocephalum ruyschiana*, *Crepis praemorsa*, *Hypochaeris maculata*, *Tragopogon pratensis* s. l.). The southern limit of the temperate zone is marked in entire Eurasia by, e.g., *Calamagrostis arundinacea*, *Carex vaginata*, *C. limosa*, *C. lasiocarpa*, and *Calla palustris*.

The oceanicity gradient is very steep in southern zones. In Europe, large parts of the suboceanic areas of the submeridional zone are inhabited by Mediterranean sclerophyllous vegetation. In parts of the central sub-Mediterranean province group (the Apennine and Balkan peninsulas) and in the eastern sub-Mediterranean province group (northern Anatolia and the Crimea to the Caucasus), species-rich deciduous woods predominate because of cold winter and moist summer conditions. In continental, drier areas of the zone, they are gradually replaced by forest steppe complexes and in the central and eastern Pontic zone by steppes. The southern boundary of the submeridional zone is marked in these different regions by the ranges of *Artemisia absinthium*, *Eleocharis acicularis*, or *Carex riparia*, for example.

The southern boundary of the meridional zone corresponds with the boundary of the Holarctic floristic kingdom. The range limits of many taxa of higher rank (Betulaceae, Fagaceae, Salicaceae, Platanaceae, Ranunculaceae, Paeoniaceae, Brassicaceae, Rosaceae, Aceraceae, Primulaceae) determine this boundary. Among the species ranges, there are only a few that can overcome the large span of oceanicity/humidity along this limit. But these species connect the very different vegetation areas at the southern edge of the Holarctic. These consist mainly of elements of azonal vegetation, i.e., aquatic and semiaquatic plants and rock plants that are less influenced by precipitation fluctuation, especially if they are salt-tolerant, as well as plants with synanthropic ranges (*Plantago major*, the genus *Carduus*, *Descurainia sophia*). In west Eurasia, *Bromus tectorum, Poa bulbosa*, and the genera *Colchicum* and *Helianthemum* mark the southern boundary of the meridional zone. The characteristic elements of this zone usually disappear to the north only in the submeridional zone (*Cistus, Daphne oleoides* group, *Arbutus*, etc.). The Macaronesian archipelagoes will be added to this zone.

Floristic Regions of Europe (Meusel and Jäger 1992)

Europe participates in five floristic regions. The Circumarctic and the Circumboreal floristic regions are circumpolar because of recent possibilities of plant dispersal to North America. The boundaries of these floristic regions correspond to the floristic zone boundaries with the same name.

The entire Middle European region with the Atlantic, sub-Atlantic, Central European, and Sarmatic floristic provinces belongs to temperate Europe. Together with the western, central, and eastern sub-Mediterranean provinces, it represents the European broadleaved deciduous forest area. In the Middle European region, a mix of relatively species-poor deciduous forest flora with numerous elements of Mediterranean origin is typical. The excellent growth and naturalization of many non-native laurophyllous woody plants

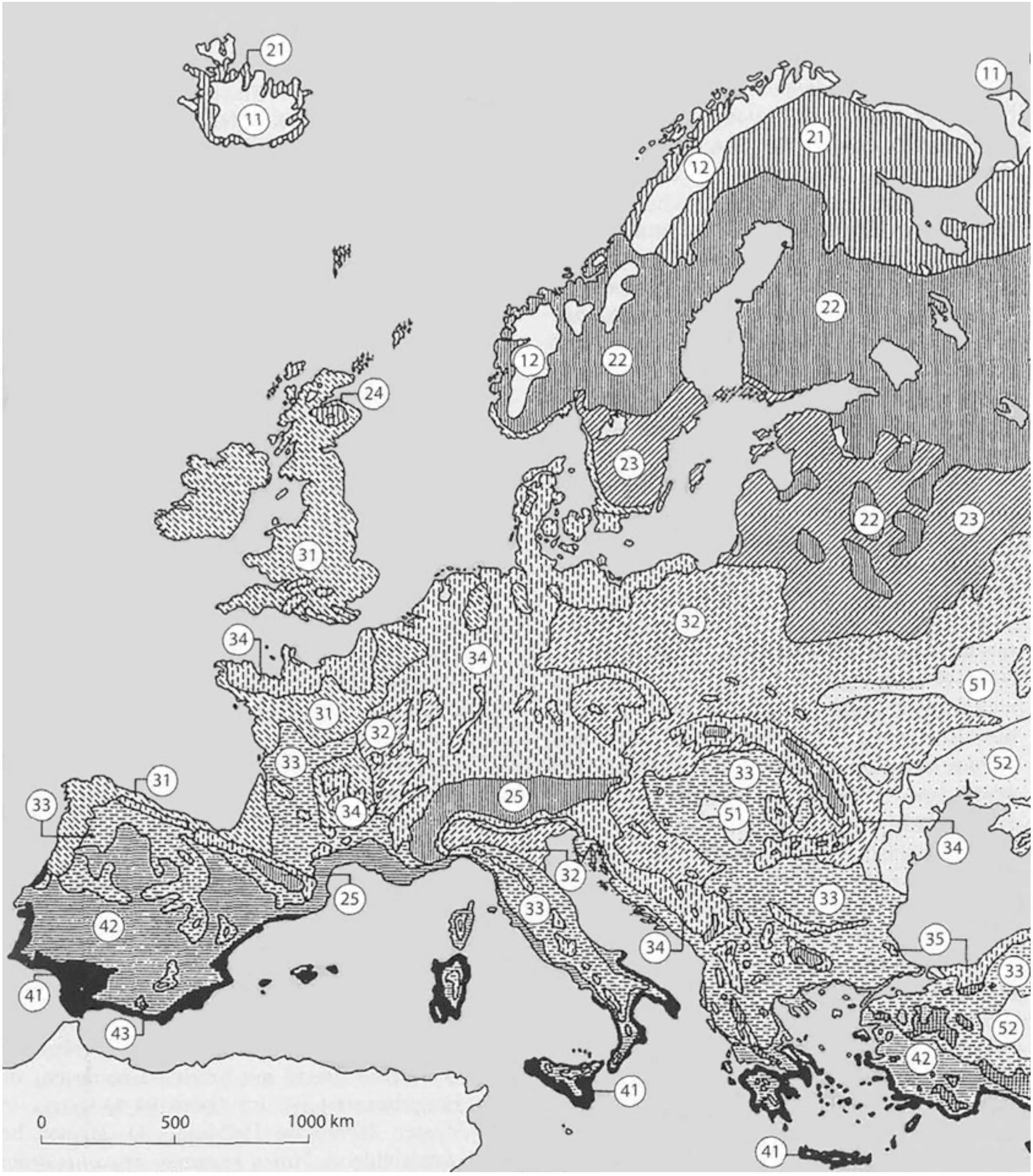

Fig. 5 Actual natural vegetation in a simplified overview. After Pfadenhauer and Klötzli (1994). 1. Polar and subpolar zone (11 = arctic tundra, 12 = alpine tundra). 2. Cold-temperate (boreal) zone (21 = deciduous boreal forests of *Betula pubescens* var. *pumila*; 22 = evergreen boreal conifer forests; 23 = hemiboreal mixed forests of broadleaved wood, spruces, and pines; 24 = boreoatlantic dwarfshrub heathland; 25 = montane and subalpine conifer forests and shrubs). 3. Humid cool temperate (nemoral) zone (31 = Western and Northwestern European oceanic mixed oak forests; 32 = central and Eastern European, subcontinental mixed oak forests; 33 = sub-Mediterranean mixed oak forests; 34 = western, central, and Southern European copper beech and copper beech-fir forests; 35 = Euxinian oriental beech forests). 4. Winter damp, warm moderate (subtropical) zone (41 = thermo-Mediterranean sclerophyll forests and scrubs; 42 = meso-Mediterranean holly oak and kermes oak forests). 5. Arid cool temperate (nemoral) zone (51 = Eastern European forest and meadow steppes; 52 = Eastern European high and short grass steppes). (Reproduced with permission from Springer Nature/2018)

(e.g., *Rhododendron ponticum*) in the Atlantic province is an indication that laurophyllous woody plants and oceanic conifers might dominate in this area, had these taxa not died out due to the late Tertiary-Quaternary cooling and aridization (Jäger 2003).

The south Siberian-Pontic-Pannonian region is part of the southeast of Europe. There are many relatively young steppe plant taxa that are characteristic for the western side of Eurasia and whose origin can be found in the coastal areas of the ancient Mediterranean Sea (Tethys) (species of *Stipa*, *Festuca*, *Koeleria*, *Agropyron* s. str., *Astragalus*, *Onosma*, *Salvia*, *Artemisia*, etc.) (Hurka et al. 2019).

In the extreme southeast of Europe, a small part belongs to the Oriental-Turanian region which is mainly situated outside of Europe in the meridional zone (central Anatolian, Armenian, Syrian, Araksian, Hyrcanian, Iranian, and South Turanian provinces) and the sub-meridional Aralo-Caspian province. Common taxa are geophytic taxa (*Muscari*, *Tulipa*), thorn-cushion taxa (*Acantholimon*), thistle relatives (*Centaurea*, *Cousinia*), and hapaxanthic xerophytes (*Verbascum*).

The Macaronesian-Mediterranean region extends beyond Europe into the northwest African mountain ranges and along the southern coast of the Mediterranean Sea to Egypt, further into the western outskirts of Asia Minor and the Near East (Israel, Lebanon, West Syria, the Mediterranean margins of Turkey). It is marked by elements of evergreen sclerophyllous forests (*Quercus ilex*, *Q. coccifera*, *Q. suber*, *Olea europaea*, *Ceratonia siliqua)* and remains of laurel forest vegetation (*Laurus nobilis*, *Prunus laurocerasus*, *P. lusitanica*, *Laurus azorica*, etc.) (Fernández-Palacios et al. 2011). Many of these elements extend to the sub-Mediterranean subregion (e.g., *Pistacia*, *Punica*, *Arbutus*, *Cistus*, *Rhamnus alaternus*, *Buxus*, *Laurus*, *Prunus laurocerasus*, *Rhododendron ponticum*). This region covers the richest refuge areas for broadleaved deciduous forests in their central and eastern provinces (particularly in mountainous regions such as the Caucasus, northern Anatolia, Balkans, Illyria, and the southeastern Alps). Thermophilous forests of *Quercus pubescens*, *Q. pyrenaica*, *Q. faginea*, *Q. cerris*, *Q. frainetto*, *Q. polycarpa*, *Carpinus orientalis* as well as *Ostrya carpinifolia*, *Fraxinus ornus*, and *Pinus nigra* predominate over large areas. Evergreen vegetation, most genera are of Mediterranean origin, occur in mild winter coastal areas of this subregion. The Atlantic islands (Canaries, Madeira, and the Azores), never been connected to the mainland, were colonized mainly by species from the Mediterranean region. Therefore, they are associated with the Mediterranean region as the Macaronesian subregion characterized by many plants of laurel forests (Press and Short 2016).

The endemic flora of the islands reflects their considerable age (Axelrod 1975). Fossils of leaves and fruits found in many places in the Mediterranean region and South Russia (Barcelona, Rhone Valley, S. Italy, Godanski Pass, etc.) are of plants identical to species now found only in the Canary Islands and Madeira. These fossils of plants such as the Dragon tree, the Canarian laurels, and many of the Canarian ferns date from the Miocene and Pliocene periods of the Tertiary Epoch and are up to 20 million years old (Cronk 1992). During this period the Mediterranean region formed part of the basin of an ancient ocean, the Tethys Sea, which separated Europe from Africa. On the margins of this subtropical sea, the vegetation must have been very similar in compositions and appearance to the laurel forest communities of the present-day Canary Islands (Bramwell and Bramwell 1974; Del Arco Aguilar et al. 2010). The vegetation dynamics on the European and African continents since the islands emerged provide the key to their main sources of flora (Del Arco Aquilar and Delgado 2018).

The Late-Glacial and Holocene Vegetation History of Europe (Lang et al. 2003)

Introduction

Since the end of the Tertiary, the development of the present-day vegetation cover of Europe has been decisively influenced by pronounced climatic changes. From the beginning of the Quaternary, several glacial periods alternating with warmer interglacials occurred, apparently as a consequence of periodic changes in the Earth's orbit. The repeated climatic changes led to a successive shift in the distributions of plant species and in particular to a gradual loss of woody species within Europe (Lang et al. 2003).

In the development of the present vegetation, the Late-Glacial (15,000 to 10,000 BP) and the Post Glacial or Holocene (10,000 BP to present) eras have been decisive periods. All age data characterized with BP relate to conventional radiocarbon years before present, i.e., to uncalibrated carbon-14 data. So these date specifications are 500–1,000 years too young in the middle and early Holocene compared to calendar years, which are given in years BC (Before Christ) or AD (Anno Domini). From the end of the Last Glacial Epoch/Period, when most of Europe was unforested (Fig. 1), woodland gradually developed to become the dominant natural formation of today. As in the preceding interglacials, vegetation development was determined by natural climatic changes, particularly temperature, and the development of soils. Subsequently this led to a relatively rapid migration of plants.

The development of the present real vegetation ("aktuelle Vegetation") during the Holocene, however, was to a great extent influenced also by a second factor, which was absent during the interglacials, which is the constant increasing influence of humans from the beginning of the Neolithic period. Over the period from 10,000 to 5,000 BP, non-nomadic agricultural communities spread from the Near East to Southeast Europe and then to the northwest, north, and northeast. This led to considerable changes and displacement of vegetation especially of woodland and resulted in a change from a "natural" landscape to a "cultural" landscape. That implies changes in mesoclimates, transformations of forest soils into agricultural ones, changes in the water regimes, and the appearance of erosion. Regional effects were secondary plant migration, changes in vegetation zonations (both horizontal and altitudinal), the development of new agricultural and synanthropic ecosystems, steppes and deserts (aridization and desertification), as well as increased paludification and expansion of peatlands, especially in the uplands and in the north (Lang 1994).

Because the Late-Glacial and Holocene vegetation history of Europe is so diverse, the continent ought not to be dealt with as a whole. Instead vegetation development should be considered in several individual and smaller regions. The zonation of the present natural vegetation can be used as a basis for this purpose (Fig. 5). This includes a sequence of zones extending from north to south, i.e., from arctic tundras to boreal coniferous forests, temperate (nemoral) deciduous forests, Mediterranean sclerophyllous forests, and Pontic-Caspian steppes and semideserts. In addition, three major forest regions can be distinguished from west to east corresponding to their decreasing oceanicity and increasing continentality; the Colchis and Caucasus region is also included in the east of Europe. Naturally, most of these areas are not heterogeneous in themselves due to differences in, e.g., relief (valleys and mountain ranges) and substratum (limestone and silicates), with their own individual influence on the development of vegetation. As far as possible, this fact shall be considered in the following description. However, we are not able to discuss the changes in azonal vegetation, because of the limited scope of this text. Regarding the order of the regions described, we shall start in the south and southeast, effectively following the Late-Glacial and Holocene spreading of forests from the south/southeast to the north/northwest, as well as the more or less similarly directed advance of permanent agricultural settlement throughout Europe (Lang et al. 2003).

The present distribution of plant communities and their zoning, as shown in the vegetation map of Europe, should be considered the result of a long and extremely variable development. Inducing and controlling factors during the course of the Holocene were not just the continuous changes in environmental conditions but also the increasing scale of human intervention. Probably there is not a single part of Europe that has been untouched by human activities. Even the highest mountain peaks or arctic tundra have been affected, whether it be directly or indirectly as a result of air pollution or other emissions (Lang et al. 2003).

Of course, present vegetation patterns do not represent an end of the developments described, and they will indeed continue to develop in the future, irrespective of whether such changes will be shaped by natural or artificial forces. Following Lang et al. (2003), the vegetation history will be described for every region.

Mediterranean Zone

The Late-Glacial and Holocene vegetation history of the Mediterranean area can be differentiated from the northern parts of Europe in main features. Notably, by the presence of evergreen forests already since the Tertiary, by the survival of many deciduous forests in glacial refugia during the Pleistocene ice ages, and by the intense and long-lasting agricultural influence on vegetation during the Holocene, three areas can be distinguished, namely, the western, central, and eastern region.

Western Mediterranean Region

This region covers the major part of the Iberian Peninsula and the southern coast of France, which represent areas with variable relief, climate, and flora. Relatively little information is available regarding the vegetation history (Sainz Ollero and van Staalduinen 2012).

Artemisia steppes with scattered occurrences of *Pinus* were common during the early Late-Glacial. In the more recent Late-Glacial and at the start of the Holocene, deciduous *Quercus* forests spread out, with *Betula* at higher altitudes. *Corylus* was always of less importance. During the Pleistocene ice ages, both deciduous and evergreen *Quercus* species were presumably able to survive in glacial refugia in this region. Evergreen *Quercus* and other evergreen trees were already present near the coast in the south and southwest during the Late-Glacial and in other areas from about 8,000 BP. Presumably human influence like grazing, fire, and consequent soil erosion encouraged the expansion of evergreen tree and shrub species inland to the north. *Abies pinsapo*, an endemic species, most likely existed in the south Spanish mountain range in a glacial refugium. In the first half of the Holocene, *Fagus* and *Abies alba* spread out to the south of France and the Pyrenees from the east.

The oldest Neolithic cultures, which date back to about 7,500 BP, have been confirmed in Southern Spain and the south of France. However, in other parts of the region, the influence of grazing on vegetation has also been observed from this time on. In the montane plateaus of Portugal and Spain, pollen analyses have revealed that intense cultivation of cereals and *Olea* was already practiced from about 3,000 BP which produced major landscape and vegetation changes, e.g., *Erica arborea* expanded as a result of increasing grazing (Lang 1994; Kosmas et al. 2002).

The land degradation in the Mediterranean, for example, in Spain results from various factors including climatic variations and human activities (Thornes 2002). These definitions of "desertification" include the degradation of soil, vegetation, as well as ecological processes that operate within the system (Millána et al. 2005; D'Odorico et al. 2013).

Central Mediterranean Region

Corsica, Sardinia, and Sicily, the greater part of the Apennine peninsula, and the narrow eastern margin of the Adriatic coast belong to this region. As other parts of the Mediterranean, it is characterized by a very varied relief (with peaks of 3,270 m in Sicily and 2,710 m in Corsica) and a correspondingly varied climate and vegetation. Local mountain glaciation during the ice ages had scarcely any direct influence on the vegetation development.

During the early Late-Glacial, the region was characterized by extensive open treeless vegetation. The *Artemisia* dominated steppes were presumably scattered with small stands of deciduous trees and also *Abies,* particularly in the southernmost parts of the Apennine peninsula. The region is considered to be an important glacial refugium. In the younger Late-Glacial, a scrub vegetation (open woodland) developed, with different deciduous broadleaved trees (*Ulmus*, *Tilia*, *Fagus*, *Carpinus*, *Corylus*) but mainly deciduous *Quercus* species, as well as various *Pinus* species and sporadic *Abies*.

In the early Holocene, mixed deciduous *Quercus* forests covered the lower altitudes, while *Fagus-Abies* forests were predominant in the mountains. In the second half of the Holocene, evergreen vegetation gradually began to replace the deciduous oak forests, an effect of more and more activities of the Neolithic populations, grazing by domesticated animals as well as fire and increased soil erosion. In Southern Italy, archaeologists have dated the beginning of the Neolithic Age to about 7,000 BP (6,300 BC) and the start of cereal cultivation at about 6,500 BP. However, the extensive deforestation and intensive arable farming occurred later at about 3,000 BP. Islands such as Corsica have, in some respects, run through slightly differing vegetation histories: *Pinus nigra* subsp. *laricio* was locally present since about 12,000 BP; *Erica arborea* has prevailed since the first half of the Holocene. Particularly in the central Mediterranean, great changes in vegetation occurred during the period of the Roman Empire when numerous secondary plant communities originated (Lang et al. 2003).

Eastern Mediterranean Region

The Eastern Mediterranean region is made up of the southern part of the Balkan Peninsula and the Aegean Islands region. Diverse climatic and floristic conditions occur due to the large variations in altitude in this area (Mount Olympus 2,911 m). The local mountain glaciation during the Pleistocene ice ages had hardly any influence on the development of the vegetation.

In the early Late-Glacial period at middle altitudes, steppes with *Artemisia* and *Ephedra* among other species dominated with probably sporadic small trees and/or shrubs. The region was a glacial refugia for many European forest trees, presumably, e.g., for *Abies*, *Acer*, *Carpinus betulus*, *Ostrya*, *Fagus*, *Fraxinus*, *Ulmus*, *Tilia*, *Corylus*, *Olea*, and *Quercus* (both deciduous and evergreen species). After that, the deciduous forests expanded (deciduous *Quercus* species, *Ulmus, Tilia, Ostrya*), while coniferous forests with *Pinus* spread locally. Forests with *Fagus* and *Abies* occurred sporadically at higher altitudes. In the first half of the Holocene, mixed deciduous forests covered the region up to high altitudes. After about 6,500 BP, these were accompanied by *Ostrya/Carpinus orientalis*.

Settlement began very early in the lower parts of the region with mixed deciduous oak forests. From about 10,000 to 9,000 BP, first agricultural grazing cultures, keeping goats and sheep, are known. Between 9,000 and 8,000 BP, archaeologists dated the first cereal cultivation. According to palynological data, from about c. 3,000 BP, which corresponds approximately to the Hellenistic era, intense agriculture began. This includes fruit farming (cereals, *Olea*, *Vitis*, *Juglans*, *Castanea*) connected with widespread timber-felling. A secondary expansion of evergreen trees (*Quercus ilex*, *Pistacia*, etc.) was initiated by clearing, grazing, and fire with subsequent soil erosion. In limestone areas severe soil erosion led to karst formations. Apparently natural xeric plant communities formed as a result of secondary migrations of numerous plants, and shifts in vertical vegetation belts occurred. Only a few mountain areas kept their natural character (Lang et al. 2003).

Temperate Zone

The temperate zone includes the majority of Western, Central, and Eastern Europe as well as mountain ranges with deciduous forests in this area. In the Late-Glacial and early Holocene, the vegetation development of these areas is characterized by a succession from forest-free vegetation to *Betula-Pinus* stands, and a subsequent expansion of mixed broadleaf woodland followed, sometimes with a contribution from various conifers. During the entire Pleistocene Epoch, in spite of climatic alternations, soils and their vegetation cover remained, although subject to many changes in the non-glaciated periglacial areas. By contrast, in the glaciated areas, the development of soils and vegetation began repeatedly with initial phases on bare, vegetation-free ground. In the temperate zone, human settlement started at the latest at around 7,500 BP from the southeast and went on until the Middle Ages. Related human activities resulted in an extensive deforestation and changes in vegetation, as described below in further detail. Thus, eight regions can be distinguished including separate mountain ranges, characterized by specific vegetation sequences (Lang et al. 2003).

Balkan Region

The region covers a considerable part of Southeast Europe, the mountain ranges of the Balkan Peninsula (the Dinaric Alps, Rhodopes, etc), and the Danubian lowlands. During the last glacial period, local glaciers occurred. As the Eastern Mediterranean Zone (Mc), the region particularly served as an important glacial refugia for many Central European trees, e.g., for *Abies alba*, *Acer*, *Carpinus betulus*, *Fagus*, *Fraxinus excelsior*, *Ostrya*, *Tilia*, and *Ulmus*, and some deciduous *Quercus* species. Despite this importance, just a few studies have been made on the vegetation history of this area.

In the Late-Glacial period, montane areas were covered with open steppe vegetation, with sporadic occurrences of *P. sylvestris*, *P. nigra*, *P. heldreichii*, etc. Refugial stands of Central European deciduous trees during the glacial as mentioned above were most probably present at low altitudes. In the Holocene, above all, a strong expansion of mixed *Quercus* forests with *Carpinus*, *Ostrya*, *Ulmus*, and *Tilia* took place. In the middle Holocene these forests reached much higher altitudes than they do today. The mass expansion of *Abies* occurred between 4,000 and 6,000 BP, while that of *Fagus* started later, after about 4,000 BP.

Similar to the Eastern Mediterranean region, agriculture started very early in this region. According to archaeological findings, Neolithic settlements date back to about 7,500 BP. After 3,500 BP, considerable mountainous areas were deforested by the ancient Greeks for sheep breeding. This led to soil erosion, karst formation, and the secondary expansion of many plants (Lang et al. 2003).

Central European Region

This region consists of lowlands in the north and at the southern edge of the Alps as well as numerous low mountain ranges, including the Harz (1,142 m maximum), the Sudetic Mountains (1,602 m), the Erzgebirge (1,244 m), the Bavarian-Bohemian Forest (1,456 m), the Black Forest (1,493 m), the Vosges (1,426 m), the Massif Central (1,886 m), and the North Apennines (2,165 m). The Pyrenees (Tf), the Alps (Tg), and the Carpathian Mountains (Th) are described individually later. During the last glacial period, the northern parts of the Central European Region were covered by spurs extending from the northern ice sheet. The Alpine glaciers extended far over the foothills, but the higher low mountain ranges showed only local glaciation. During the early Late-Glacial period, all these glaciers started melting. However, most of the region remained ice-free during the whole Pleistocene. Those periglacial areas that remained ice-free during the penultimate ice age (Riss glaciation) permitted the continuous development of soils and vegetation for a considerable period of time.

At low altitudes the progress of reforestation of open steppe-tundra landscapes had already started in the Late-Glacial: in the south at around 12,500 BP during the Bølling and in the north, a little later, during the Allerød period. *Betula* dominated the vegetation in the northwest and west and *Pinus sylvestris* in the southwest, southeast, and east. In the first half of the Holocene, vegetation development, especially in the Boreal, was marked by the mass expansion of *Corylus* particularly in the west and then later in the Atlantic by the spreading of *Quercus*, *Ulmus*, *Tilia* and other deciduous trees. In the second half of the Holocene, *Fagus* spread continuously from the southeast to the north and northwest. In the southeast and east, it invaded *Picea* stands, and in the west, it replaced some *Quercus* mixed forests. In the south, *Fagus* was accompanied and sometimes even replaced by *Abies alba*. In the Holocene, *Picea* abies migrated gradually from east to west into the low mountain ranges north of the Alps. But it was never as frequent as in the high Carpathians or the interior of the Alps.

The first isolated forest clearings in loess areas of early settled landscapes mark the start of the Neolithic period, which dates back to 7,000 BP in the lowlands, the southeast, and the center and in the north to around 5,000 BP. From the Bronze Age and the Iron Age to the Middle Ages, human interference grew more and more. Low mountain ranges are the most recently settled areas, and the beginnings of agriculture often date back only to the Middle Ages. Extensive human impact as clearing, grazing, and crop farming often caused secondary plant migrations, modified the natural boundaries of vertical vegetation belts, and led to the formation of xerothermic communities on flat land (Bazha et al. 2012). In lowlands agricultural activities locally resulted in soil waterlogging, at higher elevations and at higher altitudes in the expansion of open damp vegetation. The formation of meadows, pastures, and other substitute communities of cultural landscapes can be traced back to these processes (Lang et al. 2003).

Atlantic Region

This region includes most of the British Isles as well as coastal strips of the European mainland from southwest Norway to the north of Portugal. The area is made up of mountains as well as lowlands with accordingly different present vegetation and different vegetation history.

During the last glacial period, the highlands of Scotland and Northern England, Wales, and Ireland were mostly covered under a continuous ice sheet. By the end of the Late-Glacial, this had melted to relatively small remnants. In the Late-Glacial, the ice-free areas were settled by open pioneer vegetation with features of dwarf shrub tundra with *Salix herbacea*, *Betula nana*, *Juniperus*, etc. During the Allerød oscillation, birches trees may have been present occasionally. In the Preboreal *Betula* and *Pinus sylvestris* became the dominant tree species. *Corylus* expanded from 9,000 BP. During the Atlantic scattered mixed deciduous *Quercus* forests developed with *Quercus* and *Ulmus*. *Alnus* also spread rapidly during this period. Simultaneously a gradual decrease in forestation began with increasing paludification and the formation of blanket bogs at the same time. The beginning of intensive human interference with the vegetation may have occurred between the first Neolithic settlement around 5,000 BP and the Bronze Age. From around 3,500 BP, agricultural activities grew more intense. Especially, cattle and sheep grazing promoted the formation of blanket bogs and led to the development of heaths and grasslands.

In the lowlands of England, Ireland, and the Atlantic coastal strips, the sequence of vegetation development was very similar in the Late-Glacial and early Holocene. During the Boreal and Atlantic periods, *Quercus* mixed forests are dominated, and *Alnus* expanded rapidly in this area. A specific incident in the vegetation history of this region is the so-called Elm decline at around 5,000 BP. *Fagus* arrived in the region between 3,000 and 1,000 BP, but could not establish itself as an important component of the vegetation. In Ireland, Northern England, and Scotland, *Fagus* is naturally quite absent.

As mentioned above, anthropogenic transformations of the vegetation began during the Neolithic period at around 5,000 BP in this part of Europe. The agricultural activities of the early settlers consisted basically of arable farming and grazing. Typical early settlements were scattered local clearings within a forest landscape, the so-called Landnam. More extensive deforestation followed from the Bronze Age onwards and reached its maximum during Roman times and the Middle Ages (Lang et al. 2003).

Eastern European Region

The west of Ukraine, southern Belarus, and parts of central Russia belong to this region. The characteristic landscape is flat or slightly hilly lowland. Most of this area remained ice-free during the last glacial period. Huntley and Birks (1983) assumed that *Acer*, *Ulmus*, *Tilia*, and maybe also *Corylus* found glacial refugia in this region.

In the older Late-Glacial, typical vegetation in this region was steppes. During the Allerød they were replaced by *Pinus-Betula* forests. In the early Holocene deciduous trees, *Quercus*, *Acer*, *Tilia*, *Ulmus*, and *Carpinus* spread into the pine-dominated forests. Mixed deciduous *Quercus* forests with *Corylus* spread out particularly in the west in the middle Holocene. At the same time, expansion of *Alnus* started, and *Picea* spread from the northeast. *Fagus* and *Abies* never reached this area.

In this region, according to archaeological data, the Neolithic period started at around 6,000 BP, though Ukrainian and Russian pollen diagrams have provided almost no evidence for any early agricultural cultures. The oldest available signs of agriculture from pollen analyses, the record of cereals and *Centaurea cyanus*, date from the period between 2,500 and 2,000 BP. *Fagopyrum* pollen grains have been verified from around 900 BP in Kulikovo Pole, south of Moscow (Khotinskij, unpublished results). Belarus and northwest Ukraine were settled by hunters and fishermen; this kind of land use did not particularly change the natural landscape. The continuity of farming cultures was repeatedly interrupted because of repeated attacks by belligerent nomadic peoples from Asia, so that settlement discontinuities were characteristic. This applies to the Pontic Zone (P) too (Lang et al. 2003).

Hemiboreal Region

This region includes Southern Scandinavia, the Baltic States, and the extreme southwest of Finland, as well as northern Belarus with wedges extending eastwards into central Russia and is located at the southern margin of the boreal zone. Large parts of this region were under a continuous ice sheet during the last glacial period, but the whole region had already become ice-free by the end of the Late-Glacial.

At the beginning of the Holocene, *Pinus sylvestris* and *Betula* sect. *Albae* were the predominant trees. From glacial refugia located in the east, *Picea* abies gradually spread to the west reaching the Baltic by around 5,000 BP and Southern Sweden by around 2,000 BP. In the early Holocene, several deciduous broadleaved trees, such as *Corylus*, *Quercus*, *Tilia*, and *Ulmus*, immigrated from the south. Particularly during the Atlantic Period, forests consisted of these deciduous trees and conifers. *Carpinus* reached the region only after 5,000 BP.

This region has been settled more or less continuously since the Bronze Age (at the latest). Local hunters and fishermen lived in the region with little influence on the vegetation. For the south of Sweden, pollen diagrams show first traces of clearing and farming between 4,000 and 3,500 BP. In the Baltic States, pollen diagrams record first agricultural activities considerably later from around 1,000 BP. Though archaeological findings date cereal farming back to a period between 3,800 and 3,000 BP, the absence of pollen records indicates that it probably was not widespread at this time. Major agricultural expansion leading to severe deforestation and changes in landscape only started in the Middle Ages (Lang et al. 2003).

The Carpathian Region

The major part of the Carpathian Region remained ice-free during the Pleistocene. Only local glaciers covered the highest mountains (High Tatras 2,663 m and South Carpathian Mountains 2,544 m) during the last glacial period. By the early Late-Glacial period, they had already melted. The highly variable topography leads to diverse climate, soil, and vegetation conditions, respectively. At low altitudes, in the intermontane basins of the west, Carpathian Mountains glacial refugia of conifers *Larix*, *Pinus cembra*, and *Picea* forests were situated. In the Late-Glacial, *Pinus* was the main woody plant in the entire region. Special conditions existed in the intermontane basins of the Western Carpathian Mountains. There is evidence of open forests with *Pinus* *cembra*, *P. sylvestris*, and possibly also *P. mugo*, *Larix decidua*, *Picea abies*, and *Juniperus* in this area. After about 4,000 BP, the earlier *Pinus-Picea* stands were replaced by mixed beech forests with *Abies* and *Picea* at mid-altitudes. *Picea* kept its dominance only in the altimontane belt, especially in the High Tatras and their foothills. Deciduous *Quercus* forests mixed with *Ulmus*, *Tilia*, and *Corylus*, developed at low altitudes already during the Preboreal and Boreal in the southern and eastern Carpathian Mountains, but in the Western Carpathian Mountains, this shift occurred later in the Atlantic Period. *Carpinus* spread to the northwest from the southeast of the Carpathians during the early and middle Holocene.

The lowlands of the Carpathian Mountains and their foothills were inhabited by Neolithic settlers already around 7,000 BP. Agricultural exploitation increased from the Bronze Age onward. The most intensive deforestation and clearance occurred particularly in the Middle Ages and during the Wallachian colonization in the sixteenth and seventeenth centuries. The Wallachian livestock farming, with summer grazing in the mountains, has greatly influenced the contemporary landscape and vegetation and led to an anthropogenic lowering of the natural alpine tree line in many places.

Alpine Region

The Alps were covered by an enormous ice sheet during the last as well as preceding glacial periods. Only the southwest and the extreme east of the mountain range was not covered by glaciers, and some few nunataks (ice-free mountain peaks within glaciated regions) existed at the northern and southern margins of the Alps. During the Late-Glacial, the glacier masses receded in the inner alpine area; today, only a few glaciers remain. Considerable variability in both altitude and geology determines a great ecological variety in this region.

In the northeast, eastern, and southeast margins of the Alps, in local climatically favorable sites, *Picea abies* may have survived through the last ice age. In the younger Late-Glacial, *Pinus sylvestris*, *P. cembra*, *Larix*, and *Juniperus* dominated at lower altitudes, while at higher altitudes, open pioneer vegetation, alpine tundra, and grasslands were found. In the subsequent Holocene, vegetation developed differently in the marginal and in the Central Alps. In the Central Alps, *Picea abies* spread out from the east and southeast, mostly between 11,000 and 5,000 BP, without reaching the French southwestern Alps. During the Atlantic period, the tree line, with open *Pinus cembra-Larix-Juniperus* forests, may have been a maximum of 200 m higher than it is today. At the tree line, *Alnus alnobetula* was also an essential element of vegetation from about 5,000 BP in many places. In the marginal Alps and their foothills, *Corylus* occurred in great quantities at the lower elevations in the Boreal and Atlantic periods. Then mixed deciduous *Quercus* forests developed, into which *Carpinus* migrated from the southeast from about 6000 BP. Later mixed forests with *Fagus*, *Abies*, and sometimes *Picea* developed between 7,000 and 5,000 BP.

Neolithic people colonized lower parts of the Alps and their foothills from about 7,000 BP. Animal farming and intense grazing in the mountains can be traced back to Roman times. At the same time, the earlier local deforestation reached greater dimensions in the wide alpine valleys and basins. Present-day landscape was formed in the Middle Ages. The anthropogenic deforestation and grazing encouraged a secondary expansion of the alpine flora and led to a general lowering of the tree line (Lang et al. 2003).

Pyrenean Region

This high mountain range in the southwest of Europe has peaks of over 3,400 m. As in the Alps and the Carpathian Mountains, large differences in altitude produce remarkable climatic and vegetational variations which also show in the vegetation history. During the early Late-Glacial period, glaciation of the last ice age already melted away rapidly.

Already in the early Late-Glacial, the initially dominating steppe landscape turned into *Pinus-Betula* forests at lower (300–1,100 m) and middle altitudes (1,100–1,800 m). At the beginning of the Holocene, mixed deciduous *Quercus* forests with *Corylus* and *Ulmus*, and later with *Tilia*, started to develop. Between 8,000 and 5,000 BP, *Abies* expanded from east to west, followed by *Fagus* between 4,500 and 4,000 BP. *Fagus-Abies* mixed forests originated at middle altitudes. *Picea*, a characteristic component in the vegetation of the Carpathian Mountains and the Alps, did not reach the Pyrenees. Throughout the entire Holocene *Pinus* predominated at higher altitudes (about 1,800–2,000 m). It can be supposed that significant variations occurred in the Alpine tree line. Mixed deciduous *Quercus* forests may have advanced to higher altitudes in the middle Holocene than they do today.

In the Pyrenean Region, pasturing has been recorded from about 4,000 BP, even though no major deforestation occurred before the Middle Ages. At lower altitudes and in the foothills, the oldest signs of arable farming could be dated back to about 5,000 BP, at middle altitudes; however, arable farming did not start before the Middle Ages (Lang et al. 2003).

The Colchis and Caucasus Zone

This region can be divided into four subregions, the Great Caucasus, the Lesser Caucasus, the plateau lying between them in the east with the river valley of the Kura, and the Colchis in the west. However, they are not marked on the map in Fig. 5, yet the four subregions are described in the following text. During the coldest periods of the Pleistocene, the high mountain ranges were glaciated. Today, however, only small glaciers are left over at the highest altitudes in the Great Caucasus. Characteristic of the Colchis and Caucasus are considerable differences in altitude (Elbrus 5,633 m), diverse geological conditions, and the location at the juncture of several Eurasian phytogeographical zones. These features have all had a major influence on the vegetation-historical development and effects on the current status, respectively. During the Quaternary, migration, expansion, and replacement of plant species to and from other areas of Europe were limited because of various barriers and the lack of any suitable migration routes. Migration and exchange were only possible via the Crimea or northern Anatolia, for example. Because of this isolation, the present flora and vegetation are highly specific, and the Caucasus represents an important refugial area and center of speciation. Within Europe it has the highest number of endemic plant taxa.

During the entire Holocene, the ice-free parts of the Great Caucasus were a woodland mountain range. After the decline of mountainous glaciation, subalpine and alpine tundra communities developed in these areas primarily. At middle altitudes the tundra was already replaced by *Pinus kochiana* and *Betula-Salix* forests in the early Holocene. Then during the middle Holocene, extensive *Fagus sylvatica subsp. orientalis, Abies nordmanniana*, and *Picea orientalis* forests developed, which still exist today.

During the Holocene, unlike the Great Caucasus, the Lesser Caucasus seemed to be covered with herb-rich, xerophytic steppe, and forest steppe, that is largely forest-free. Only small areas were wooded, and these developed similar to those of the Great Caucasus.

In the periglacial areas between the two main mountain ranges, including the Kura river valley, forests and forest steppe have been recorded with scattered relict stands of deciduous broadleaved forests, for the last glacial period. From the early Holocene, the forests expanded and then achieved dominance during the middle Holocene. The forests were made up of *Juglans*, *Quercus*, *Castanea*, *Ulmus*, *Carpinus*, *Acer*, *Fagus*, *Pterocarya* and with some *Picea* to be found. At the same time, extensive floodplain forests developed in the valleys.

In the Colchis, the eastern Caucasian lowlands, and in Armenia, very early arable farming has been confirmed. This type of land use probably spread from Mesopotamia. The large mountain ranges were populated by hunters and shepherds. The Caucasian countries were invaded or traversed by neighboring peoples on many occasions and became especially important as a metallurgical center. The present severely deforested, agriculturally and horticulturally influenced landscape developed, in large part, during the early feudal periods of Transcaucasian history, between the third and ninth centuries AD (Lang et al. 2003).

The Pontic-Caspian Zone

The Pontic Zone of Europe is a flat lowland which forms the western spur of the extensive Eurasian belt of wooded steppe, steppe, and semidesert. Vast aeolian Quaternary sediments (loess with chernozem soils and sands) and alluvial sediments are characteristic. The area remained ice-free during the Quaternary Period.

Only a few pollen analysis have been published from this zone so far, so a subdivision into regions is not possible yet. Today the region represents a floristically modified remnant of the cold steppe and *Artemisia* semidesert areas that was once widespread throughout Europe during the glacial period. The vegetation development in this zone was characterized by the dominance of steppe communities with *Artemisia*, Poaceae, and Chenopodiaceae during the entire Holocene. The non-tree pollen (NTP) values always lie between 70 and 90% of the total pollen count. From 6,000 BP pollen of deciduous trees as *Quercus* and *Tilia* has been verified sporadically, as has pollen from *Pinus* and *Betula*. But rates of these last-named species are so low that the presence of these trees could be considered as questionable. The concept of glacial refugia of deciduous broadleaved trees in river valleys of the Southern Ukraine and Russia has not been confirmed so far. In Eastern Romania and Eastern Bulgaria, the extreme southwest part of the zone, a temporary penetration of forest steppe into the steppe region, was observed in the middle Holocene. The species found were deciduous *Quercus*, *Ulmus*, *Tilia*, *Carpinus*, and *Corylus* (Hurka et al. 2019).

In pre-agricultural times, the population of the ancient settled areas in Southern Ukraine and Russia were hunters and fishermen. They lived near the rivers and did not affect or change the steppe grassland. First signs of arable farming date back to about 7,000 BP on the Bulgarian Black Sea coast and to about 4,000 BP in the upper Don region. Initially the conversion of steppe into arable land was moderate. The main reason for this was repeated invasions of Asiatic nomadic tribes which interrupted and impeded any agricultural activity (Smelansky and Tishkov 2012). Large-scale agricultural exploitation of the steppe only began in the Middle Ages and was almost entirely destroyed during the final decades of the former Soviet Union (Lang et al. 2003).

The Boreal Zone

The circumpolar Boreal region extends all the way across the north of the Northern Hemisphere through the Eurasian and the American continent. This zone represents the European part of it. The typical vegetation consists mainly of coniferous forests. During the Pleistocene ice ages, the greater part of the European region was covered by the extensive, contiguous Scandinavian ice sheet. This ice sheet melted away and left only small relicts in the Scandinavian Mountains and Iceland during the interglacial periods. The extensive and long-term ice cover has strongly influenced surface forms, soils, and vegetation and certainly also the vegetation development during the Late-Glacial and Holocene. Apart from the High-Oceanic Region in the west, *Betula* and *Pinus sylvestris* were the dominant trees during the entire Holocene. Another important tree species in boreal coniferous forests (taiga) was *Picea abies*, although its expansion from east to west took place a little later. Compared to the temperate zone, the human intervention and influence on vegetation is significantly lower, and arable farming in this region is of minor importance.

The Boreorussian Region

The region covers the larger part of Northern Russia east of Lake Ladoga and south of the Kola Peninsula. During the last glacial, the western part was covered by inland ice and became ice-free during the Late-Glacial. The eastern part remained completely ice-free.

During the Late-Glacial and Holocene, the dominant tree species were *Betula* and *Pinus sylvestris* and slowly spreading from the east *Picea abies*. Presumably in the ice-free areas of the western foothills of the Urals, *Picea* had a major glacial refugia, from which this conifer spread over almost the entire Fennoscandia Region during the Holocene. Deciduous broadleaved trees as *Corylus*, *Tilia*, and *Ulmus* and sometimes also *Quercus* could, if at all, be found only during the Atlantic Period and sporadically in southern parts of this region. The polar tree limit shifted clearly northwards in the marginal parts of present forest tundra in the middle Holocene and moved to the south again after 5,000 BP with *Betula* sect. *Nanae* (dwarf birches) and *Alnus* sect. *Alnobetula* becoming more important.

Until modern times, human influence on vegetation is hardly noticeable and affected probably only restricted areas. Signs of local clearings have been traceable by pollen analyses only since the Middle Ages at the earliest, but there are no signs of any arable farming. Major activities of the local population were hunting, fishing, and grazing at least since the Bronze Age onwards (Lang et al. 2003).

Fennoscandia Region

This area covers the main part of Fennoscandia including the Scandinavian Mountains, apart from the south and a narrow coastal strip in the west and the north. During the last glacial period, the complete area was covered by inland ice. The enormous ice masses withdrew only during the early Holocene, between 9,000 and 8,000 BP, leaving local mountain glaciers that corresponded approximately to their present pattern of occurrence. In Northern Europe the melting of the ice sheet led to several modifications in the coastline, which also had an influence on the development of the vegetation.

After the retreating of the ice cover, *Pinus sylvestris* and *Betula* migrated rapidly to the ice-freed areas forming the taiga-type coniferous forest. As in the Boreorussian Region, *Betula* was common during the colder periods of the Late-Glacial and the Holocene, while *Pinus* was dominant in the warmer periods. *Picea* spread from its glacial refugia to the west and southwest. The species reached Eastern Karelia around 7,500 BP, while central Norway was first reached around 1,000 BP. Deciduous broadleaved trees (*Corylus*, *Ulmus*) advanced only temporarily into the southernmost parts of the region during the Atlantic Period; *Alnus* arrived between 8,000 and 7,000 BP. In the Scandinavian Mountains, at higher altitudes, the initial mountain tundra was replaced by *Betula pubescens* (s. l.) forests. As in the polar region, the alpine tree line was also subject to changes, at the end of the Boreal and during the Atlantic periods, it may have been situated about 150–200 m higher and many kilometers further north than today.

According to archaeological findings, human settlement and agriculture occurred in southern areas since about 3,500 BP, i.e., since the Bronze Age. The forest character of the landscape remained and was only locally interrupted by clearing, grazing, and hay making. Sporadic signs of arable farming have been found from the Middle Ages onwards (Lang et al. 2003).

Boreoatlantic Region

This region is made up of Northern Scotland including the Outer Hebrides, the Norwegian coast, the islands in the North Atlantic, and Iceland. During the last glacial period, the entire region was covered with ice but became ice-free from the beginning of the Holocene. Only on Iceland, extensive glaciers still remain today.

The Holocene vegetation development of the region was strongly affected by *Betula*. In the greater part of Scotland and the North Atlantic islands, open scrub tundra with *Betula nana*, *Juniperus*, and *Calluna* predominated; forest apparently did not develop during the Holocene. Trees such as *Pinus sylvestris*, *Quercus*, and *Corylus* spread only locally into the region from the Boreal Period onwards. On the Norwegian coast *Betula pubescens* (s. l.) dominated in the vegetation development from about 12,000 BP.

Pinus sylvestris may only have appeared occasionally, if at all. On Iceland the ice-free areas were colonized by open tundra and scrub tundra. Especially in the south of the island and only during the Atlantic period, taiga-like birch stands expanded. However, in consequence of woodcutting, fire, and grazing, these stands disappeared more and more from the Subboreal period onwards, especially after the Vikings colonized Iceland around about 1,100 BP.

The population practiced sheep farming in most parts of the region (the Norwegian coast, Shetland Islands, and the Faeroe Islands). The grazing sheep promoted the development of grasslands and heaths. Compared to other parts of Europe, anthropogenic impact on the vegetation remained quite limited (Lang et al. 2003).

Arctic Zone

This zone describes the northernmost part of Fennoscandia and Russia and the Arctic islands in the Arctic Ocean. During the last glacial period, the western part was covered by ice which had already melted away by 13,000 BP.

During the Late-Glacial, different vegetation types spread across the ice-freed soils, freeze-thaw polygonal tundra, and then lichen-moss tundra and eventually dwarf shrub and open birch tundra. In the mainland areas, during the Boreal Period, birch forest tundra was present. In the subsequent Atlantic period between 7,000 and 5,000 BP, the tundra was replaced by taiga with *Picea abies* predominating. During this period *Pinus sylvestris* occurred as well as *Pinus sibirica* in the east, and most of today's subarctic bogs development started. After 4,000 BP the taiga withdrew southward, and scrub and birch forest tundra spread again. By the end of the Subboreal period, approximately 2,500 BP, the present vegetation patterns developed (Lang et al. 2003).

Until the very recent past continuous settlements did not exist in this region. Human influence on vegetation has only occurred over the last decades as a result of geological prospecting and mining activity, etc., mainly in the form of mechanical damage.

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