

**REVIEW AND SYNTHESIS**

# Climatic definitions of the world's terrestrial biomes

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## Abstract

**Question:** Is it feasible to establish a classification of large biotic units of the world related to climatic types? **Study area:** The world. **Methods:** A total of 616 localities have been selected, their climatic parameters calculated and subjected to a PCA. The climatic characterization of biomes and subbiomes has been completed after data analysis. **Results:** A hierarchical classification is proposed for the biotic units within four main domains: Cryocratic, Mesocratic, Xerocratic and Thermocratic, divided into 7 ecozones, 9 biomes and 20 subbiomes linked to climatically defined territories. Most of the units are intercontinental. The mountains represent an abbreviated version of the latitudinal zonation and the altitudinal belts are related to the corresponding units of the lowlands. For the bioclimatic units, a parallel classification is proposed to fit with that of the biotic units: 4 Macrobioclimates and 10 bioclimates. Furthermore, 7 ombrotypes and 7 thermotypes are recognized to frame the climatic variation within each climatic territory due to terrain ruggedness, particularly in relation to large or medium sized mountains. **Conclusions:** The southern hemisphere is substantially more oceanic than the northern hemisphere. This is due to the distribution of the land masses and the modifying effect they have on the flow of air and marine currents. As a result, there is one biome and one subbiome exclusively found in the northern hemisphere (6. Biome of the steppe, and 5.b Continental scrub and woodlands subbiome) and two others which are almost confined to it (2. Biome of the boreal forest, and 3. Biome of the temperate deciduous forests). The 7. Biome of the deserts and 5. Biome of the temperate arid/semi-arid evergreen forests and shrublands occur on the western side of the continents and expand in their interior favoured by rain shadow and continentality effects.

**Taxonomic reference:** The Plant List (2013).**Abbreviations:** ITCZ = Inter Tropical Convergence Zone; NH = Northern Hemisphere; PCA = Principal Component Analysis; SH = Southern Hemisphere.

## Keywords

biome, biotic unit, climate of the world, domain, ecozone, large scale vegetation units, potential natural vegetation, subbiome, terrestrial ecosystem

## Introduction

Describing the world's vegetation on a global scale in a way that reflects the factors determining its distribution is as old as geobotany itself (von Humboldt 1806). To achieve this goal successfully, two things are needed: a

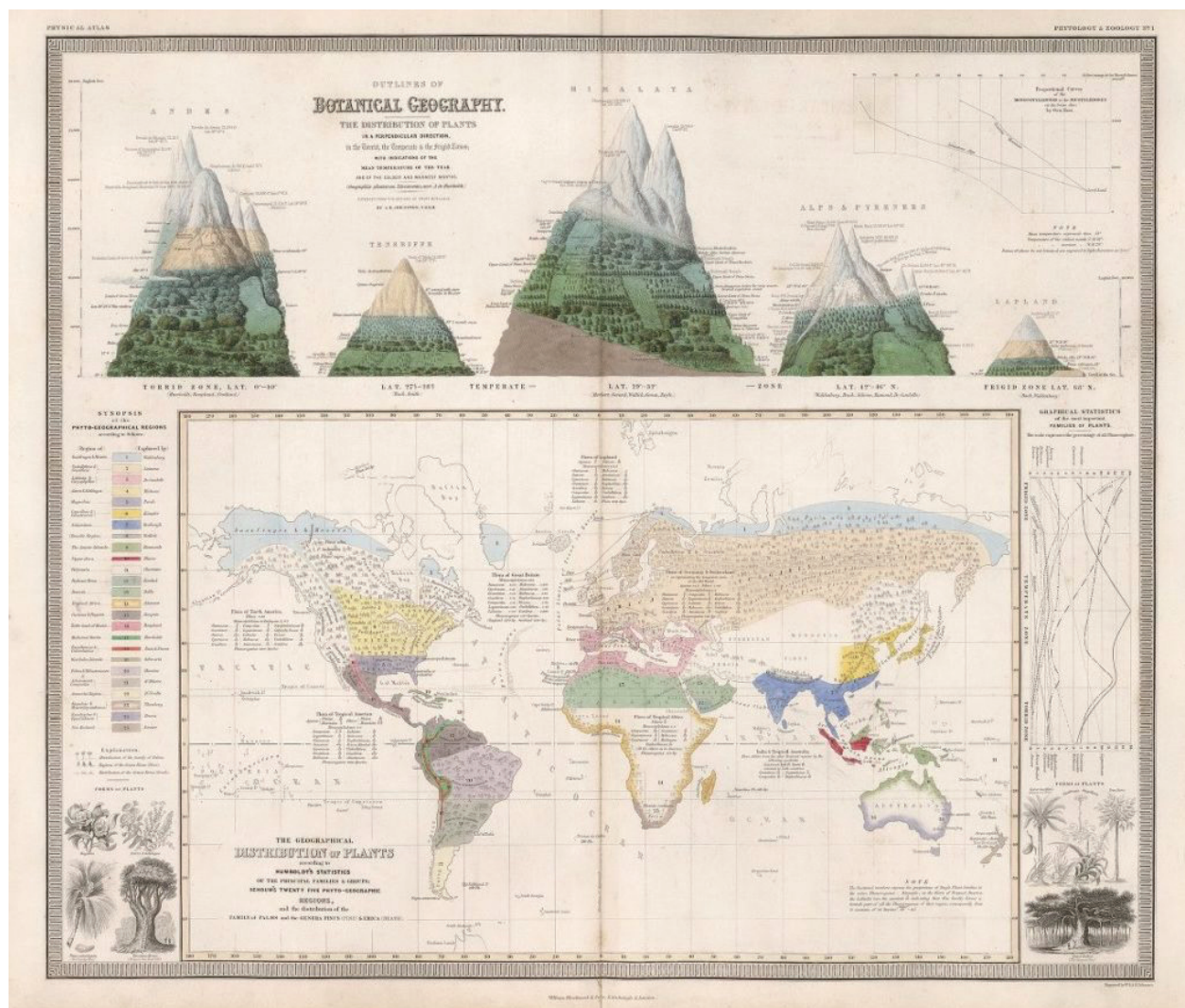
scheme of broad-scale descriptive units that are dependent on the factors that shape ecosystems at such scale, and an extensive knowledge of them. The main factor shaping ecosystems distribution at this scale is climate (Box and Fujiwara 2005). This global point of view led to the establishment of the concept of biome and there have

been important contributions in the 19<sup>th</sup> century, which have continued to the present, as documented by Hunter et al. (2021). Along with that history, there have been several attempts to model the relationships between climate and vegetation at a broad planetary scale. Among the first approaches, there was Humboldt and Bonpland in 1805 (Figure 1) and Brockmann-Jerosch and Rübel (1912) with their “Ideal Continent”, which was followed by Troll (1948), Losa et al. (1974) and Box and Fujiwara (2005) (Figure 2). Other important schemes are those of Whittaker (1970), Schroeder (1998) and Pfadenhauer and Klötzli (2014). The term biome has been defined in different ways and as of yet there is no clear agreement about its meaning. It is not our intention to review the approaches that have been previously made, some of them very comprehensive, or to summarize the world's vegetation in its various aspects (Faber-Langendoen et al. 2016; Keith et al. 2020), but rather to establish a classification of the biomes that is effectively consistent with a global climate classification using tools that are currently available.

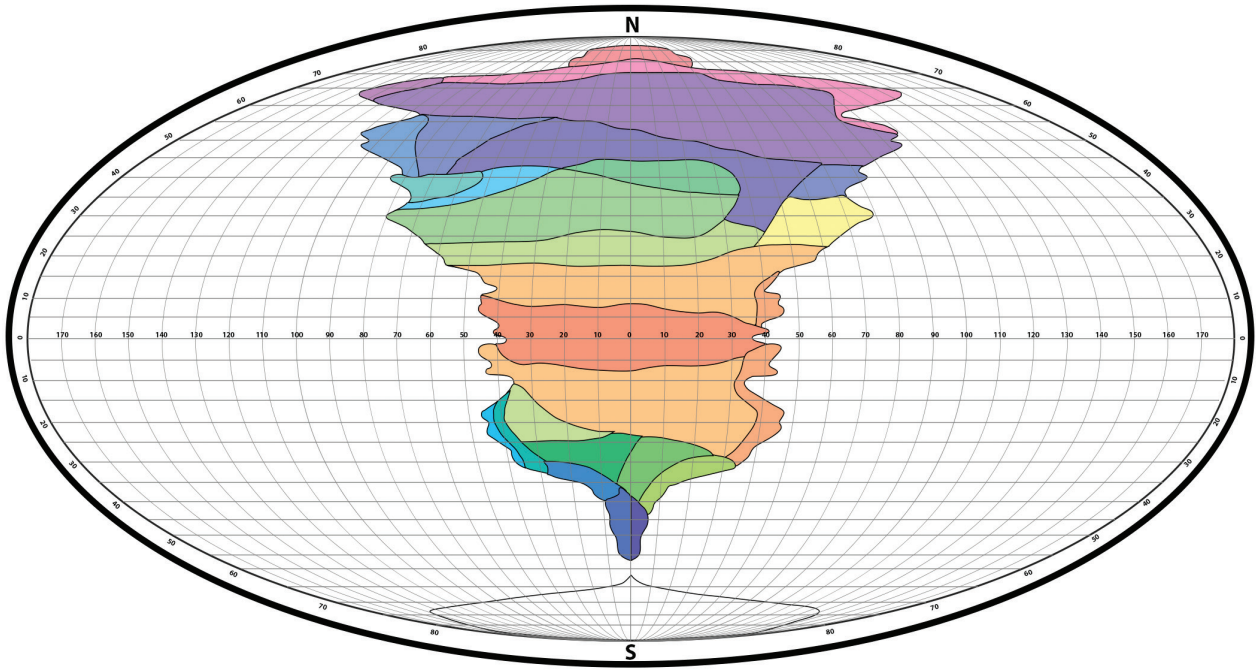
## Biomes and bioclimates

A broad-scale typology of biomes has to fulfil the two following conditions:

1. An easily recognizable set of features characteristic of each biome, yet overcoming regional floristic patterns so that the biome can extend across several continents and distant territories bearing different floras.
2. A consistent correlation with broad climatic units to be recognizable across the world. Broad climate types are intercontinental. If biomes have to be so, then they should also be related to the climatic types. Other conditions such as substrate, disturbance regimes and human influence lead to a more local typology of biomes and align them to a description of vegetation communities on a regional scale. In our opinion, a biome is basically a zonal unit which can diversify into more regional ones by means of relevant edaphic, hydrologic and disturbance conditions.



**Figure 1.** A scheme of the main vegetation formations of the world with several of its mountains compared by Humboldt and Bonpland 1805. The display of the mountains tries to establish a certain homology between their vegetation belts.



**Figure 2.** The “mean continent” by Troll 1948 modified.

### How do we define a biome?

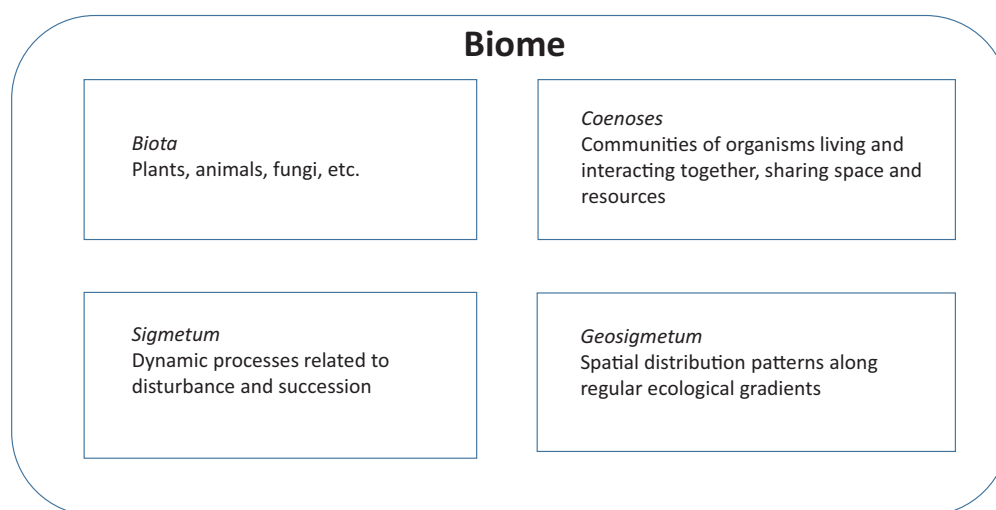
This section explains the conceptual framework of what could be understood by the scientific community under the term Biome. As it is an old concept (Clements 1917) we should be careful in defining and using it. Languages evolve in a natural way, and scientific language is also drawn into that process. Thus, concepts can evolve but have to be subject to certain core conditions so that we understand the same things by using the same words, or at least we can interpret correctly what was meant by the previous authors when they used such terms. A single term has to avoid changing its original semantic area, i.e., naming the group of elements encompassed by it. If the group of encompassed elements changes, a new term has to be established. A typical example is the term “species”, which is used for centuries to always refer to groups of individuals which can interbreed. The idea of what a species is was quite different in the past from that we have currently, it has been intensely enriched with the recent advances in genetics and physiology, but it encompasses basically the same objective elements as when it was applied by botanists in the past. The concept has grown vertically in depth but it has not substantially changed horizontally, that is, adding innew elements and losing others. The latter means a change in meaning (semantic area displacement) and confusion appears. Science needs the highest terminological accuracy so that each concept has to be univocal and universally understood. Thus, new concepts need new names and old concepts have to conserve the original meaning and be applied to the same elements.

To reach an agreeing and unifying concept, so that polysemy and progressive “babelization” upon such term could be avoided, and connecting with the tradition of

origin and use of it, two drifts should be prevented in the case of biomes: the regional drift and the dynamism drift:

**Regional drift:** Many attempts to describe the biomes of the world fall to the temptation of considering vegetation units that are particular to specific regions. As examples, we can mention “Evergreen Nemoral *Nothofagus* Forest” (Pfadenhauer and Klötzli 2014), which referred to a particular tree genus only existing in the southern hemisphere (hereafter SH), or the “Pampa” in Schroeder (1998), which refers to a strongly anthropized grassland existing in some subtropical latitudes of South America. Such drift is enhanced by the specific types that are present in certain regions and not in others being the combination of physiognomy and climatic conditions particular to them. This is almost inevitable in some cases, but it should be avoided as much as possible if it is intended to create a universal typology not dependent on specific regional species compositions. A single biome can have different dominant groups in the different regions it occurs. For instance, conifers can be more abundant in some areas than in others, as is the case of the “Biome of the temperate pluvial evergreen forest, shrublands and grasslands”, which in some areas such as North America bears a higher number and dominance of conifers due to the particular evolutionary history of that region. However, evergreen and oceanic character is shared with the rest of the territories where this biome exists.

**Dynamical drift:** This results from the acceptance of units that are the result of dynamic processes, often human induced, that occur under certain disturbance or management regimes, such as the “scrub and shrub biomes” of Keith et al. (2020). They usually represent intermediate states in the succession that are stabilized by a certain type of land use. An extreme example of this is the “Intensive land-use biome” that has been coined by Keith et al.



**Figure 3.** Content of a Biome. All the biological elements in all the levels of organization, from the species to the landscape level.

(2020). These units are inherently unstable and disappear as soon as the disturbance regime is released or changed.

As Mucina (2019) and Keith et al. (2020) indicate, a biome is a large-scale synthetic concept including a series of elements which can be summarized in four categories (Figure 3):

- *Biota*: all the biological diversity that can be found within its limits (plants, animals, fungi, etc.).
- *Coenoses*: all the forms of assemblages of these living beings (populations, communities).
- *Sigmatum* (Loidi 2021): all the processes taking place in the two aforementioned components (ecosystem functioning, disturbances and dynamics, evolution, etc.).
- *Geosigmatum* (Loidi 2021): the spatial distribution patterns occurring within the territory of the biome, which are determined by local topography such as the crest-slope-valley zonation, and the azonal ecosystems occurring within it.

We suggest to define global-scale units exclusively by climate while other relevant ecological factors such as soil fertility, hydrologic regime, natural disturbance regime, etc., can be used to define regional or successional units.

As an integrative concept to be applied at a large scale, the biome should be defined by natural features: natural biota (flora, fauna, etc.), natural ecosystems and natural landscapes. In such a way, the biome can be used as a reference for an ideal natural situation. This implies the removal of anthropic disturbances such as farming, stock-breeding, housing, etc. In other words, as most current disturbances are human induced, we need to remove them from ecosystems and establish a “theoretical” natural state.

Moreover, the inclusion of human influence in the conceptual framework of biome has the following problems:

1. Modernity. Human influence is a relatively new phenomenon on earth. It began having notable impacts on terrestrial ecosystems approximately 11 Ky ago

when the Neolithic age began with agriculture and cattle raising in the Fertile Crescent. Before that period, the impact of human species was scarcely higher than that of a medium sized mammal. After that, these activities expanded throughout the world at very different paces and intensities, transforming the territories in numerous ways, and reached a truly global scale only in the last few centuries. Nonetheless, human influence in terrestrial ecosystems has been enormous, and manifests in a huge complexity of ways depending on geographical conditions and on cultural variability.

2. Selective character. The way and intensity in which humans have influenced terrestrial ecosystems has also been heavily influenced by the natural conditions inherent to them. This has to do with profitability or capability of extracting goods for human use in the ecosystem in question. Humans distribute pressure, and thus modifications, concentrating it upon the most fertile environments leaving the infertile landscapes much less disturbed (YODFELS [Young, Often Disturbed, Fertile Landscapes] as opposed OCBILS [Old, Climatically Buffered, Infertile Landscapes] of Hopper 2009). For example, compare the contrast of human exploitation of deserts and arid lands with that of the evergreen tropical forest, or the tundra with the temperate deciduous forest area.
3. Changing character. Modern technology favours a homogenization of land uses in a much greater way than was done centuries ago, so that today it is possible to grow oranges in the Arctic and corn in the desert. It is only necessary to install powerful greenhouses in the first case and irrigate intensively in the second, although the necessary energy inputs increase enormously. Thus, human influence, in addition to being diverse because it has already been conditioned by the diversity of natural ecosystems, is changing with technology and population growth.

Therefore, we propose that human influence should not be considered as a defining element for biomes, as they provide a natural reference. The creation of Anthromes (Ellis 2020) is likely to be counterproductive and has the effect of obscuring natural conditions. The current state will only be temporary as technology and human uses advance and change over the decades. The biome should be a concept restricted to nature in the first instance. By continuing to do so, we can use the biome concept to assess the degree and type of human alteration at a given site, simply by comparing it to the corresponding biome. This has also been argued in favour of the concept of Potential Natural Vegetation (PNV: Loidi and Fernández-González 2012). Therefore, for the definitions of biomes, the PNV should be taken as a leading feature (Navarro-Sánchez and Molina-Abril 2021). A biome must be defined and named according to its set of characteristic PNVs, as in the case of the tundra, the tropical forest or any other.

Another point is that biomes refer to zonal ecosystems. As these respond mainly to climatic conditions, the biomes will be distributed along climatic gradients. These gradients are manifested on two spatial scales: large regions and continents (geographical scale) and mountains (altitudinal scale). In the latter, a compressed climatic gradient occurs across a small territory, leading to a chain of different biomes or vegetation belts along the altitudinal gradient. Azonal ecosystems, either humid (such as wetlands), dry (such as rocky or shallow substrates), or saline (such as coastal marshes, etc.) are excluded in our classification and are assimilated to the zonal biomes of each territory. In this way, we intend to define the climatic envelope of the recognized physiognomic units and to use them to create a truly bioclimatic classification in a similar way as has been done by some authors (Box and Fujiwara 2005, 2013; Mucina et al. 2021; Navarro-Sánchez and Molina-Abril 2021), instead of defining climatic types and determining later the biological content that can be found within them.

## Biotic units classification

Similar to other proposals to frame all the ecosystems of the world (Walter 1985; Schroeder 1998; Faber-Langendoen et al. 2016; Keith et al. 2020), we propose a classification system of units basically supported by the earth's broad climatic zones. Various terms and concepts have been used for them. Among them, the Zonobiome by Walter (1977, 1979, 1985) and Breckle (2002) is the most similar to ours from the conceptual point of view. However, we adopted a hierarchical approach for global zonal ecosystems establishing the following categories:

**Biotic unit.** A generic concept which encompasses all existing biota living in a terrestrial ecological and geographical space. As indicated above, it is a large-scale container concept that includes all biotic components: biota, species assemblages, and ecological processes occurring within the ecosystems.

Biotic units are basically determined by a climatic definition. There are biotic units of four different ranks: domain, ecozone, biome and subbiome. In some other approaches, such units could be also defined by edaphic or other conditions of high relevance. A biotic unit is not defined by the taxonomic composition of its flora, i.e., it is not a biogeographic unit. A biotic unit can occur in multiple distant areas where floristic differences are substantial. As an integrative concept, biotic units should be primarily defined by natural features: natural biota (flora, fauna, etc.), natural ecosystems, natural landscapes. "Natural" means that the human influence is less apparent at the level of noticeable ecosystem modification.

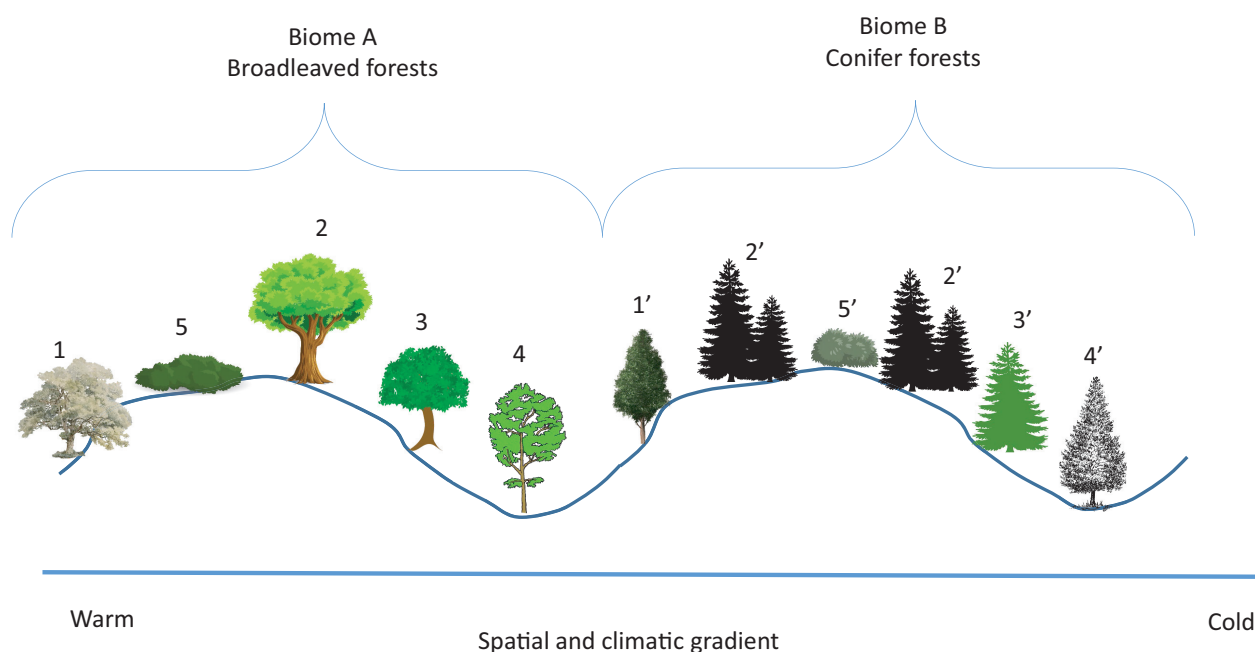
**Domain.** This is the largest division in the biotic units. It is characterized by broad climatic conditions (temperature and aridity) manifest in the four main belts of the earth: A. Severe cold around the poles and in the high mountains – cryocratic (governed by the cold); B. Thermic seasons in the intermediate belt between the Tropics and the cold areas, one cold and another warm – mesocratic (governed by the intermediate conditions); C. An aridity belt in the subtropics where the scarcity of moisture is the main determinant factor for living beings – xerocratic (governed by aridity); D. Absence of cold and of thermic seasons between the Tropics – thermocratic (governed by the warmth).

**Ecozone.** Inspired by Schultz (2005), this is the second rank category of the biotic units, which results from splitting the domains into units characterized by seasonality, either in rainfall (dry vs. wet season) or in temperature (cold vs. warm season). We recognize seven terrestrial ecozones in the world.

**Biome.** This is the third rank within the biotic units. Biomes are determined by the physiognomy of the zonal potential natural vegetation matching with specific climatic conditions, according to the traditional use of this term (Hunter et al. 2021). We recognize nine terrestrial biomes in the world, and the limits of a given biome in comparison with neighbouring biomes (Figure 4) are given by:

- Physiognomy or dominant life-forms; e.g., deciduous forests vs. evergreen forests, steppe vs. desert, etc.
- Regional climate or climatic zone; e.g., Ever rainy tropical vs. seasonally rainy tropical, boreal vs. temperate, summer rainy vs. winter rainy, etc.
- Ecological factors; e.g., Soil fertility, natural disturbance regime, etc.

**Subbiome.** This is a subunit of the biome that is also characterized by physiognomic and climatic features, but with higher resolution. Subbiomes also occur in several continents, but in a few cases, they have a regional distribution in only one continent due to the particular climatic circumstances prevailing. Such is the case for the *Patagonian shrubland* (5.c) in South America and the *Conifer coastal forests* (4.b) in North America. We recognize 20 subbiomes in the world.



**Figure 4.** A biome is replaced by a neighboring one when the climate undergoes a substantial change. Sigmata representative of neighboring biomes A and B. 1 and 1'. Dry and warm biotope. Xerothermophilous. 2 and 2'. Average biotope. Climatophilous. 3 and 3'. Cool and humid biotope. Ombrophilous. 4 and 4'. Riverine biotope. Edafoxerophilous. 5 and 5'. Seral stage.

### Bioclimatic classification

Any climatic classification is an attempt to describe the patterns of spatial variation that underlie the mass of accessible climatic data. Each category or climatic type is defined by limits in thermometric and pluviometric values provided by meteorological stations and has a specific territorial expression; i.e., an area in which the values of the climatic factors are within a set of defining limits. If these climatic types are defined in relation to some characteristic flora, fauna or vegetation element, then we will have a *bioclimatic classification*; i.e., the climatic envelope is justified by or adjusted to the biological content. Likewise, if the climatic types are defined in relation to agricultural contents (viable crops), we will have an *agrocimatic classification*, and if they are defined in relation to types of soils, the classification will be *edaphoclimatic*. There are also climatic classifications that are not intended to fit specific content and are purely numerical. Plants are often considered the climatic indicators *par excellence* because of their sedentary nature and because they necessarily survive the whole series of weather situations that they experience throughout their entire lives. If so, this makes phytoclimatology synonymous with bioclimatology. This fact leads us to think that if we know the climatic limits of a species in a certain territory, we can extrapolate its climatic profile to other areas which are suitable for the survival of that species (bioindication). The first bioclimatic classifications of the 19<sup>th</sup> century corresponded to the so-called physiognomic plant formations, in which dominant vegetation types were defined by morphological features in large areas of the

Earth. Over time, these classifications have been refined and multiplied, and among them we can mention some that have had a greater relevance. An important bioclimatic classification was developed by the German-born Russian meteorologist W. P. Köppen during the first half of the 20<sup>th</sup> century, which found a notable acceptance (Köppen and Geiger 1954). Thornthwaite's climatic classification (1933) also had a notable influence. Among later approaches, Holdridge's classification (1967) represents an important effort to define climatic types in relation to some of the large biomes by defining life zones (vital zones). This classification has been widely used in the Americas and established ecologically homogeneous units by choosing climatic indicators of special significance for vegetation, such as potential evapotranspiration (ETP) or biotemperature (calculated taking into account the number of hours with temperatures between 0 and 30°C). Another study of certain relevance was the classification of the biomes of the Earth proposed by Whittaker (1970), in which he framed each biome in a segment of a two-dimensional climatic space. This model shows great simplicity and is very easy to understand, but poorly defined and the validity of its envelopes have been questioned (Bond 2005). More recent and widely considered approaches have been those of Box (1981) and Box and Fujiwara (2005, 2013) which are based on a great amount of climatic data, and that of Botti (2018) which encompass only the European area.

The types defined in an integrative way by a small number of climatic parameters lead to inflexible systems, in which either the climatic envelope encompasses an often heterogeneous vegetation content, or vegetation entities do not

have a corresponding climatic type. For this reason, multidimensional bioclimatic classifications are more practical and more realistic, in which climatic parameters are considered separately, just like the vectors of a vector system.

In the world there are three main **geographic belts or zones** in each hemisphere: Polar, Temperate and Tropical, separated by the two Polar Circles (66°43'36"N and S) and the two Tropics (23°26'14"N and S). Between Temperate and Tropical, a fourth Aridity Zone is inserted which extends to the center of the continents from their western side.

### Adopted general bioclimatic classification of the world

Our proposed classification is inspired directly from that of Rivas-Martínez (Fernández-González 1989; Rivas-Martín-

ez and Loidi 1999; Rivas-Martínez et al. 2011) with some modifications intended to make it simpler. This classification is based on four groups of parameters that we consider to have the most important influence on the distribution of vegetation and terrestrial ecosystems: (1) thermometric or temperatures, (2) pluviometric or rainfall, (3) seasonality of the rainfall and (4) seasonality of temperatures or continentality. With these parameters we can build a bioclimatic classification system, as summarized in Table 1. The bioclimatic types match with the biotic units, as expected from a true bioclimatic classification (Table 2).

The thermometric values specify the thermal regime of the locality, as a result of its latitudinal and altitudinal position and the intensity of the solar radiation received. Rain gauge measurements provide the estimates of water availability, basically in the form of liquid water, although in many areas these precipitations are in solid form (snow,

**Table 1.** Seasonality, ombrotypos and thermotypes occurring in the different bioclimatic types with approximate threshold values of some climatic parameters. Tp: positive temperature; Pp: positive precipitation (see also Table 5).

Bioclimatic types		Seasonality		Ombrotypes lo = Pp/Tp							Thermotypes						
Macrobioclimates	Bioclimates	Precipitations: difference between dry and wet season	Temperatures: difference between cold and warm season (Continentality)	Hyperarid < 0,4	Arid 0,4-1	Subarid 1-2	Dry 2-3,6	Subhumid 3,6-6	Humid 6-12	Hyperhumid > 12	Infra	Termo	Meso	Supra	Oro	Crioro	Icy
Warm Tp >2000	Pluvial BIO15 < 60	low	null						+	+	+	+	+	+	+	+	+
	Pluviseasonal BIO15 > 60	high	low			+	+	+	+	+	+	+	+	+	+	+	+
Arid lo < 1	Warm-Temperate nfd < 40	low	low – high	+	+	+					+	+	+	+	+		
	Cold nfd > 40	low	high	+	+	+											
Mesic Tp 1000 – 2000	Aridiestival (Mediterranean s.l.) dws < 1	high	low – high			+	+	+	+	+	+	+	+	+	+	+	+
	Pluviestival dws > 1; BIO7 < 300	low	low – high			+	+	+	+	+		+	+	+	+	+	+
	Steppic BIO7 > 300	low	high – very high			+	+	+					+	+	+		
Cold Tp <1000	Tundral-Boreal	low	low – very high			+	+	+	+	+					+	+	

**Table 2.** Correspondence between biomes and bioclimatic types (for names of subbiomes, see Table 7).

Domains and biomes											
Cryocratic	1. Tundra									1a + 1b + 1c	
	2. Boreal forest							2a + 2b			
Mesocratic	3. Temperate deciduous forests							3a			
	4. Pluvial evergreen forest and shrublands							4a+4b+4c			
	5. Sclerophyllous-microphyllous evergreen forests and shrublands					5a + 5b + 5c					
	6. Steppe				6a + 6b						
Xerocratic	7. Deserts and semi-deserts of arid regions					7a					
				7b							
				7c							
Themocratic	8. Tropical pluviseasonal forestst and shrublands	8a + 8b									
	9. Tropical rain forests	9a									
		Pluvial	Pluviseasonal	Warm	Temperate	Cold	Steppic	Aridiestival	Pluviestival	Boreal-Tundral	Bioclimates
		Warm		Arid		Mesic		Cold		Macrobioclimates	

hail). Water inputs due to fog condensation, which is substantial in some mountainous areas, are often hidden in the pluviometric data (cryptoprecipitations). Seasonality affects the regular oscillation in the increase and decrease of one or the other according to the seasons of the year. Therefore, there will be a seasonality of rainfall that will be determined by the latitudinal displacement of the aridity and rainfall belts throughout the year, and another of the temperatures, which will be accentuated by the latitude and by the distance from the influence of the seas and oceans.

The system is organized hierarchically, using the factors that exert the greatest influence on the distribution of terrestrial ecosystems. Thus (and adopting the Köppen criterion), a first division is made into four large types or macrobioclimates, reproducing the great climatic belts of the planet that determine the main groupings of ecosystems in the world. From the poles to the equator we distinguish: I. The cold macrobioclimate, II. The temperate macrobioclimate, III. The arid macrobioclimate and IV. The warm macrobioclimate.

### I. Cold Macrobioclimate (Cryocratic)

This type is dominated by the low temperatures which fall below zero for at least 4 to 5 months, causing severe limitations to the development of life and enforcing strong adaptation of living organisms to low temperatures. There are two bioclimates within this macrobioclimate. *I.a. Tundral*. The highest latitudes, oscillating between 55° and 70°, are covered by tundra vegetation in which the trees do not develop due to the short duration of the period of plant activity in the short summers and due to the existence of permanent ice on the ground (permafrost). Permanent ice occupies large areas, especially in Antarctica and Greenland. Continental and oceanic versions can be distinguished. *I.b. Boreal*. This type occupies the latitudes above a border that oscillates between 40° and 66° depending on the marine currents, where winters are long and cold, and summers are short and rainy. Depending on the amplitude of the seasonal variation of temperatures, oceanic and continental versions can be distinguished. In general, the territory is dominated by cold-resistant coniferous forests, which are accompanied by some deciduous trees, such as birch, willow and aspen. In both cases, there are high elevation versions in the mountains of the temperate and tropical zones.

### II. Mesic Macrobioclimate (Mesocratic)

This is the most climatically diverse and the one that hosts the greatest diversity of terrestrial ecosystems. Its lower latitude limit oscillates between 25° and 30°, bordering the warm and arid bioclimates. Its entire area is subject to a thermal seasonality, with a clearly differentiated winter and summer; the more pronounced the greater the latitude and the distance from the influence of the seas. In addition to this, the seasonality of rainfall, basically determined by the polar front, plays an important role in differentiating the bioclimates: *II.a. Temperate ombroestival* (summer-rainy), occurs in latitudes immediately higher than the tropics and

in contact with them. These areas are influenced by the polar front dragged by the westerlies, trade winds and even the monsoonal regime, ensuring summer rainfall in sufficient quantity. There are very oceanic areas, in the regions close to the coast, and others more continental, in which winter rainfall is lower than in summer due to the influence of high polar pressures and, in East Asia, due to the effect of the winter monsoon. It spans Europe, eastern North America, and eastern Asia in the Northern Hemisphere (hereafter NH), while in the south it is found in southern Chile, southeastern sides of Australia and Africa, and New Zealand. The dominant vegetation is temperate deciduous forests and non-sclerophyllous evergreen temperate forests. In the tropical zone, mountains above 1000 to 1500 m asl have a cooler climate and higher precipitations, and thus their climatic conditions approach rainy temperate. *II.b. Temperate aridiestival* (summer-dry or Mediterranean s.l.), located in the latitudinally lower fringe of this zone (subtropical), between 25° and 45°, on the western sides of the continents and in contact with the extratropical deserts. In the summer there is an intense drought of at least two consecutive months caused by the strengthening and expansion of the subtropical highs, while the winters are under the influence of the polar front that moves towards lower latitudes. The countries bordering the Mediterranean Sea and Middle East, the central-southern area of California, central Chile and Argentinian Patagonia, the Cape region and the south and southwest of Australia correspond to this variant, where the typical plant response is the evergreen sclerophyll-microphyll, both wooded and shrubby. There is a more continental variant of this type extended across central western North America and West-Central Asia. *II.c. Temperate steppic*, spread over the interior regions of the great continental masses, subject to strong thermal seasonality and low rainfall throughout the year. The powerful winter anticyclones that form on these continents limit the rains, which are somewhat more abundant in summer when there are sporadic incursions of maritime air masses. This climatic variant extends mainly through the interior regions, strongly continentalized, of the great land masses of the Northern Hemisphere (NH), such as that spanning from eastern Central Europe to western China and Mongolia, as well as the interior regions of North America (Great Plains). Its characteristic vegetation is the steppe, formations dominated by grasses, either in mosaic with scattered forest patches (forest-steppe) or without them (grass-steppe).

### III. Arid Macrobioclimate (Xerocratic)

This is characterized by climatic aridity and appears in regions with very low rainfall (Ombrothermic Index *I<sub>o</sub>* (Rivas-Martínez et al. 2011) lower than 1, exceptionally 2; see below). The response of the vegetation is a desert due to dryness, with a notable presence of succulents in certain regions, with a scattered distribution, low cover, and little biomass. They can be found in a wide latitudinal range between 10° and 45°. Depending on its temperature and rainfall regime, we can distinguish three main

bioclimates: *III.a. Continental cold desertic*, in mid to high latitudes of the central areas of the large NH continents, North America and Eurasia, where thermal seasonality is very marked in the innermost regions and in higher latitudes. *III.b. Temperate desertic*, in mid-latitudes above the tropics in which there is a seasonal variation in temperatures, or in the highlands of some tropical desertic areas where temperatures are lower. Sporadic rains occur in the winter solstice in latitudes above tropics and are caused by sporadic entries from the polar front. These extratropical deserts extend through the interior regions of the great continents (Eurasia, Africa, North America, Australia), due to the decrease in rainfall caused by the distance from the seas and by rain shadow phenomena generated by mountain systems. *III.c. Warm desertic*, in low latitudes around the tropics and where temperatures are higher and do not show a notable annual oscillation. In this case, the scarce rainfall will fall in the months close to the summer solstice, as it is in the tropical zone, and will be caused by the sporadic approach of the Intertropical Convergence Zone (hereafter ITCZ), which will contribute to them. The deserts of the southern Sahara, Arabia and South America can be included in this variant.

#### IV. Warm Tropical Macrobioclimate (Thermocratic).

This roughly encompasses the regions between the Tropics of Cancer and Capricorn (intertropical), with some subtropical extensions in certain lowlands influenced by warm ocean currents. Within the intertropical zone, all its points receive solar rays with an inclination of 90° twice a year. Therefore, it is the area that receives the most solar energy and is the warmest on the planet, not being subjected to thermal seasonality, although it is to the rainfall seasonality in many of its parts. As for its bioclimates, we distinguish two. *IV.a. Tropical pluvisesional*, in which there is a clear seasonality in the rains, which fall mainly in the summer months, leaving a dry season for the remainder of the year, in which the temperatures often reach very high values. It occupies the bands between 5° to 10° and 20° to 25°N and S, to which ITCZ moves on the spring equinox to cause seasonal rains. From the autumn equinox, the movement is towards the opposite hemisphere and the strip comes under the dominion of the high subtropical pressures, giving rise to the dry season. The monsoon regime is also the cause of this climatic variant in the regions where it operates and the trade winds spread this climatic type along the eastern sides of the continents. Vast tropical territories of the Americas, Africa, Asia and Australia are under this variant, where deciduous or evergreen-sclerophyll formations predominate, adapted to survive a hot and arid season. *IV.b. Tropical pluvial*, in which the rains are abundant for the whole year (aseasonal). It occupies the latitudes closest to the equator, between 10°N and S and is under the permanent influence of the ITCZ, registering high amounts of precipitation and notable thermal uniformity throughout the year, with little or moderate seasonal variation. Its characteristic biome is the tropical rainforest and the typical regions are the Amazon, the Congo basin and the Indo-Pacific archipelagos.

#### Ombrotypes and thermotypes

Another set of categories, which we call thermotypes and ombrotypes, can be superimposed on this primary classification, in response to the variability caused by the topographic relief within each macrobioclimate and bioclimate described above, particularly accentuated in the case of the mountains. To account for this variability, a series of thermal and ombric types are distinguished separately, following the criterion that was initiated by the French geobotanical school for North Africa (Emberger 1955). The ombrotypes reflect the differences in water availability between different regions, including those caused by phenomena such as orographic precipitation and rain shadows. Seven ombrotypes are recognized: **hyper-arid**, **arid**, **sub-arid**, **dry**, **sub-humid**, **humid** and **hyper-humid**. This typology is common to the entire earth and its calculation is made by means of the quotient between positive rainfall and positive temperatures, **Io**, which are those taking place in the months suitable for vegetative growth; that is, with temperatures above 0°C (Table 3). The thermotypes are calculated basically by means of the positive temperature **Tp** (Table 5) and reflect the thermal differences due to latitude, occurring zonally from the equator towards the poles, and those due to altitude occurring from the low to the high areas, as we can see in the case of the mountains. Six thermotypes are recognized: torrid, warm, temperate, cool, cold and very cold, which can also be named **infra**, **thermo**, **meso**, **supra**, **oro** and **cryoro** (Table 4). These types will occur in different bioclimates depending on the existence of mountains and in more or less rainy areas.

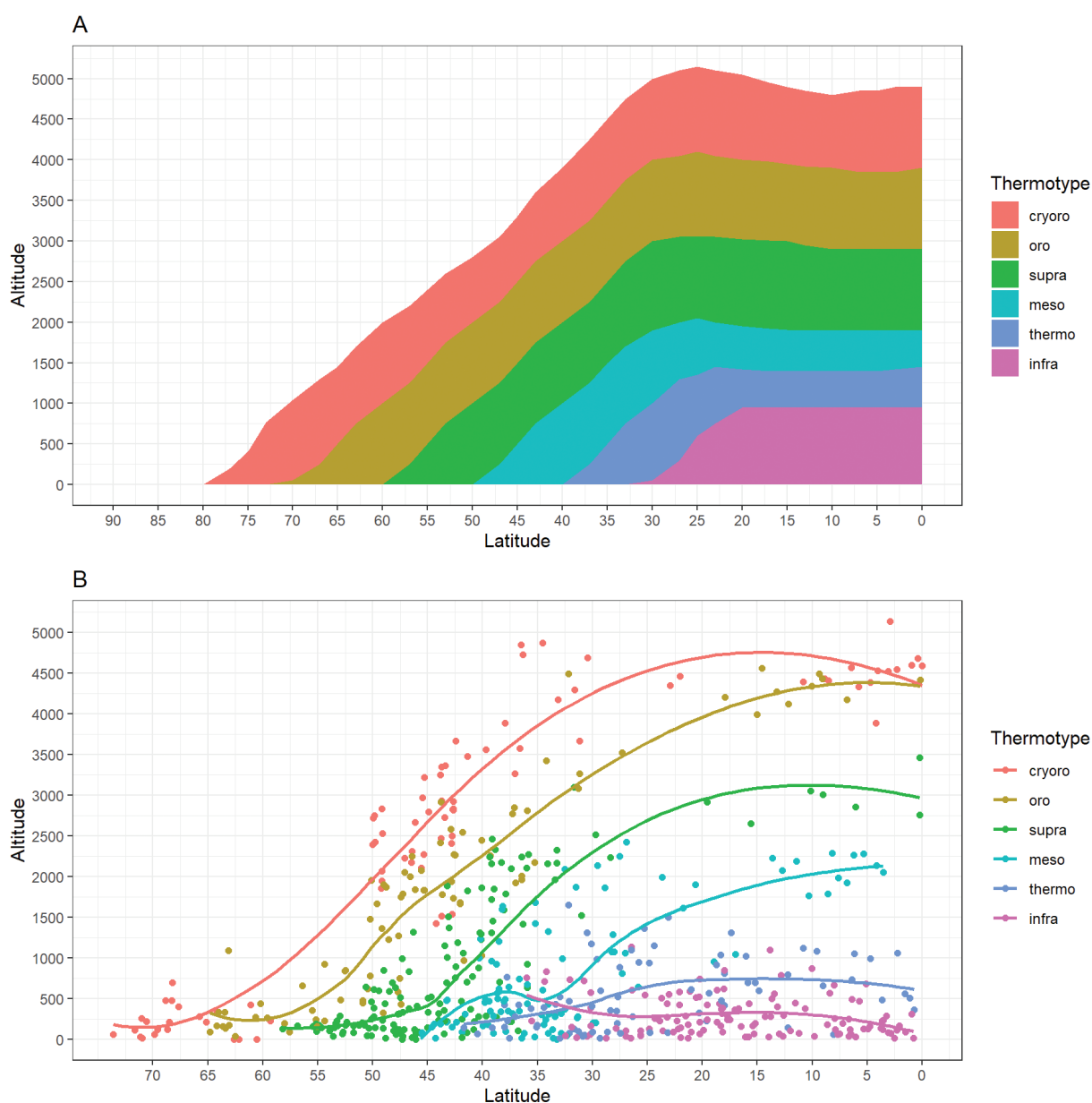
**Table 3.** Values of *Io* (ombrothermic index, quotient between positive precipitation *Pp* and positive temperature *Tp*) for the ombrotypes.

a) Ombrotypes of the World	
Ombrotype	$Io = Pp/Tp$
hyper-arid	< 0.4
arid	0.4–1
sub-arid	1–2
dry	2–3.6
sub-humid	3.6–6
humid	6–12
hyper-humid	> 12

**Table 4.** Values of *Pt* (positive temperature) for the thermotypes at different latitudes.

b) Thermotypes of the world						
Latitude	Infra	Thermo	Meso	Supra	Oro	Cryoro
00–10°	>2900	2900–2300	2300–1700	1700–950	950–450	450–100
10–20°	>2900	2900–2300	2300–1700	1700–950	950–450	450–100
20–30°	>2400	2400–2100	2100–1500	1500–900	900–450	450–100
30–40°	>2400	2400–2100	2100–1500	1500–900	900–450	450–100
40–50°		2350–2000	2000–1400	1400–800	800–380	380–100
50–60°				1400–800	800–380	380–100
60–70°					800–380	380–100
70–80°						280–100
80–90°						



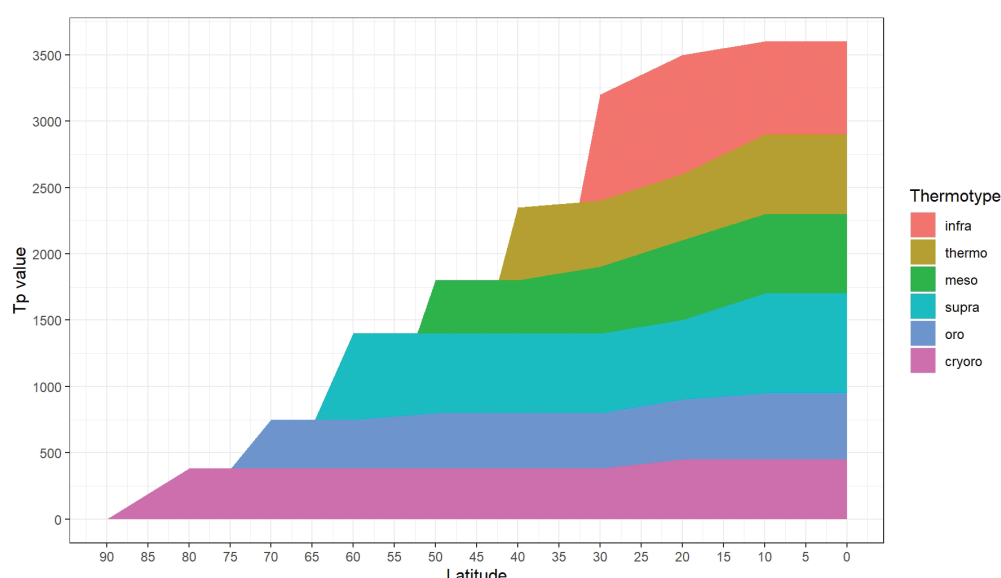


**Figure 5.** Thermotypes altitudinal ranges across latitude. **A** Theoretical representation; **B** Real representation of the 610 selected locations classified after thermotypes plotted against altitudes. In the latter, an anomaly is shown in the Infra curve which reaches higher elevations than Thermo and Meso in latitudes between 32 and 36°, meaning that there are locations which are Infra at higher elevations than others which have  $T_p$  of Thermo. This can be explained by the deserts occurring in these latitudes, which are subjected to extremely hot summers and enhancing high  $T_p$  values.

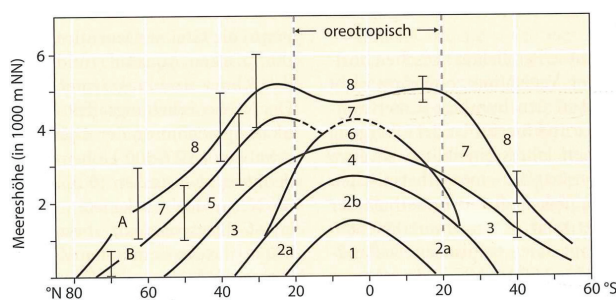
37°N, the cryoro is found above the 3500 m asl, whereas in similar latitudes in Europe, as in Sierra Nevada (Spain) it starts regularly above 2800 m asl (Fernández Calzado and Molero Mesa 2011).

The change of the thermal definition of the thermotypes. The thermotypes are basically defined by the  $T_p$  (positive temperature, Table 5). Along the latitudinal gradient, as a general pattern, the  $T_p$  range of the thermotypes changes, being lower towards the poles, and highest at latitudes near the equator (Figure 6). This effect is more pronounced in the warm thermotypes than in the colder ones. The reason for this changes is that plants need a minimum period of high temperatures to complete their

vegetative and reproductive cycle, an essential condition for their intergenerational survival. In a seasonal climate, the long and warm summer is sufficient to allow these cycles to complete, no matter how cold the winter is. In a non-seasonal climate, where winter is similar to summer, to reach the survival conditions of the plants it is necessary that the temperature values are high enough all along the year, winter and summer, as the difference between both seasons is small or null. This results in higher annual total values. For this reason, the limit values of  $T_p$  between thermotypes become lower the closer we get to the poles. Areas within the same latitudinal zone, thermal seasonality (i. e. continentality) strongly influences the altitudinal



**Figure 6.**  $T_p$  limits of thermotypes across latitude. As a general pattern, thermotypes shift towards colder limits at higher latitudes, as shown mostly in the Infra, Thermo, Meso and Supra thermotypes. This means that they occupy relatively higher elevations in low latitudes. They also vanish at certain latitudes: above 30° the Infra starts vanishing, above 40° the Thermo, above 50° the Meso, above 60° the Supra, above 70° the Oro and the Cryoro can surpass that latitude, always considering low elevations.



**Figure 7.** This is a model by Pfadenhauer and Klötzli (2014) of the altitudinal and latitudinal distribution of the world's broad vegetation units. The upper limit line of the Alpine Tundra draws an oscillation in the Equatorial zone, where this limit is lower than in the tropics. In addition, the maximum of the Tropic of Cancer is at a higher latitude than that of the Tropic of Capricorn.

belts zonation. If seasonality is low (very oceanic areas), the cold thermotypes are very wide and their limits with those immediately below are in lower elevations, while if the thermal seasonality is accentuated (continental areas), the warmer thermotypes expand to higher altitudes.

In short, the proposed system provides a typology in which the macrobioclimates reflect the general conditions of the great climatic zones of the earth, the bioclimates the seasonal regimes, the thermotypes the temperature regime (which will depend on the latitude and the elevation of the land above sea level), and the ombrotypes the abundance of rainfall and water availability, which are the climatic patterns determined by the General Circulation Model and the elevation of the terrain.

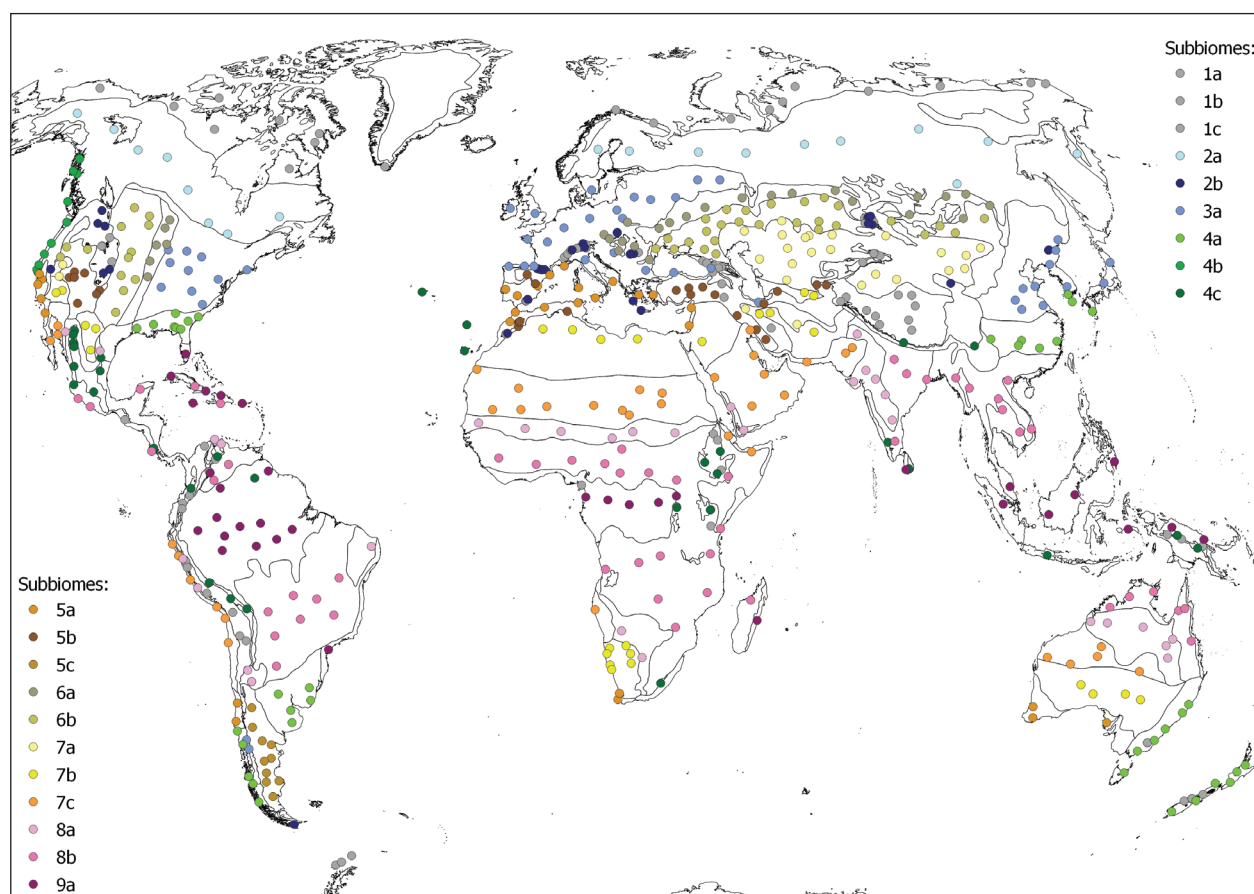
The climatic parameters and indices used are indicated in Table 5.

## Material and methods

The bioclimatic typology is inspired by that of Rivas-Martínez (Fernández-González 1989; Rivas-Martínez and Loidi 1999; Rivas-Martínez et al. 2011), using the terms ‘macrobioclimates’ for the highest units and ‘bioclimates’ for the lower ones, and distinguishing ‘ombrotypes’ and ‘thermotypes’ in a similar way as these authors and the used climatic typology was also established by them. The domains ‘ecozones’, ‘biomes’ and ‘subbiomes’ are inspired by the contributions of several authors (Walter 1985; Schroeder 1998; Pfadenhauer and Klötzli 2014), combined with the author’s expert knowledge.

The climatic data were extracted from Chelsa Climate database (Karger et al. 2017, 2018), using 616 locations over the emerged lands of the Globe, in a regularly distributed pattern over the described bioclimates, biomes and subbiomes, encompassing their recognized variability and representing their geographical distribution (Figure 8) according to the literature sources and expert knowledge. Thus, mountain areas concentrate more locations in order to represent the small areas in which orophytic versions of the biomes occur. An initial matrix of the selected climatic data and parameters (Table 5) was compiled and used for the analyses. The additional variables were calculated in R (R Core Team 2021) using the package *raster* (Hijmans 2020).

The data of the 616 locations are shown in the table in Suppl. material 1. By using the package *climatol* (Guijarro 2019) we built the Walter-Lieth diagrams (climagramms) for each locality, which are shown in Suppl. material 2. To disentangle the climatic envelope for the biomes, we applied Principal Component Analysis (PCA). Based on



**Figure 8.** Distribution of the 616 localities from which climatic data have been obtained by means of CHELSA. The colors of the dots correspond to the 20 subbiomes and the lines are subbiome boundaries: 1a Polar tundra, 1b Tundras of the temperate mountains in cryo belt, 1c Tundras of the tropical mountains in cryo belt, 2a Lowland boreal Taiga, 2b Forests and shrublands of the temperate oro belt, 3a Temperate deciduous forests, 4a Lauroid evergreen forest of the lowlands, 4b Conifer coastal forests, 4c Tropical montane cloud lauroid and conifer evergreen forest, 5a Oceanic sclerophyllous-microphyllous evergreen forests and shrublands (Mediterranean), 5b Continental scrub and woodlands, 5c Patagonian shrubland, 6a Forest-steppe, 6b Grass-steppe, 7a Cold deserts and semi-deserts, 7b Temperate deserts and semi-deserts, 7c Warm deserts and semi-deserts, 8a Tropical xeric shrublands and woodlands, 8b Tropical pluviseasonal forests and woodlands, 9a Tropical rain forests.

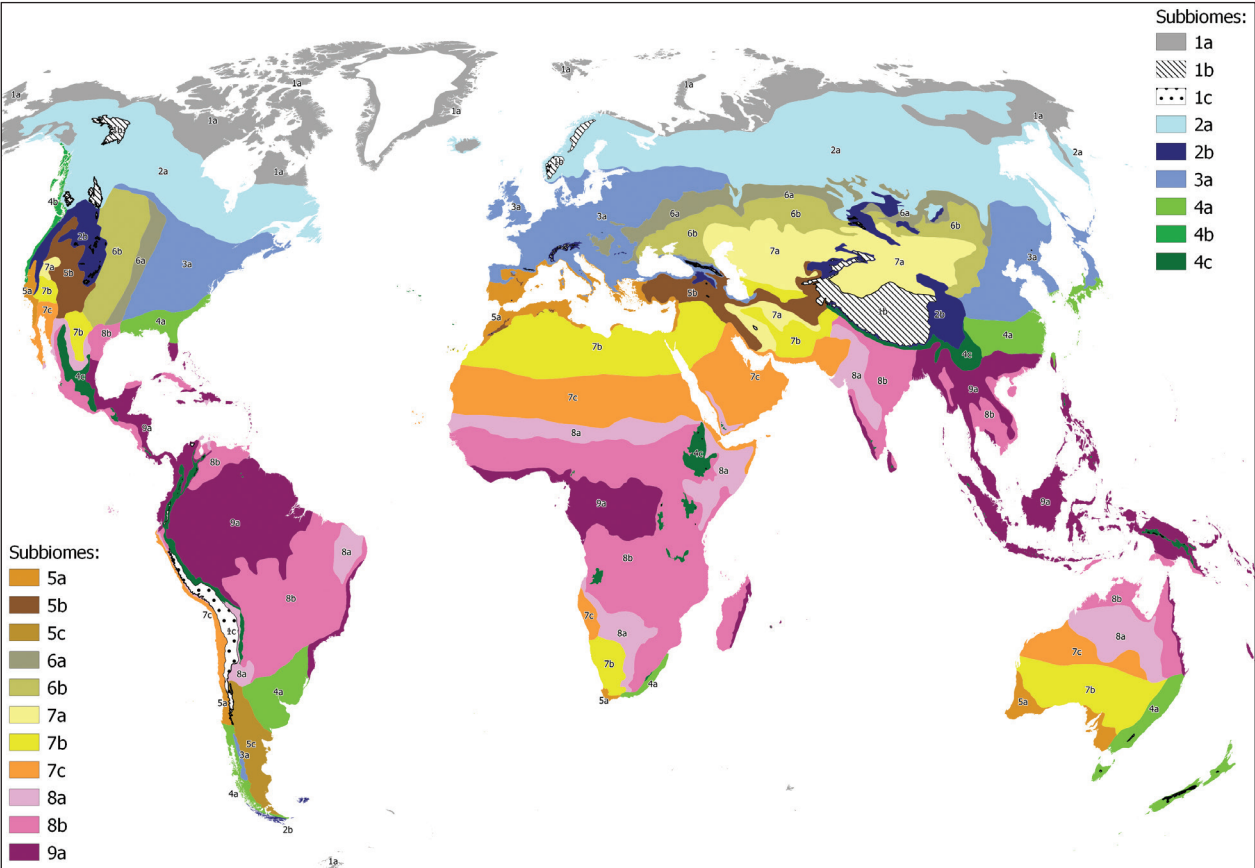
the results of PCA, and depending on the membership of localities to one or another biotic unit, we adjusted the boundaries between the biomes and prepared a map using QGIS 3.16 software (QGIS Development Team 2009). Additionally, all the localities were classified according to their thermotypes and ombrotypes (Rivas-Martínez et al 2011). Boxplots of Suppl. material 4 summarize the climatic definition of the biotic units at their four levels.

## Description of the world biomes

### General patterns of distribution

A summary of the adopted biomes typology is shown in Table 7 and the occurrence of the thermotypes in each of the climatic zones is shown in Table 8. The world distribution of the subbiomes is represented in Figure 9. This distribution is mainly determined by climate and it is intended to represent the biomes at a continental scale.

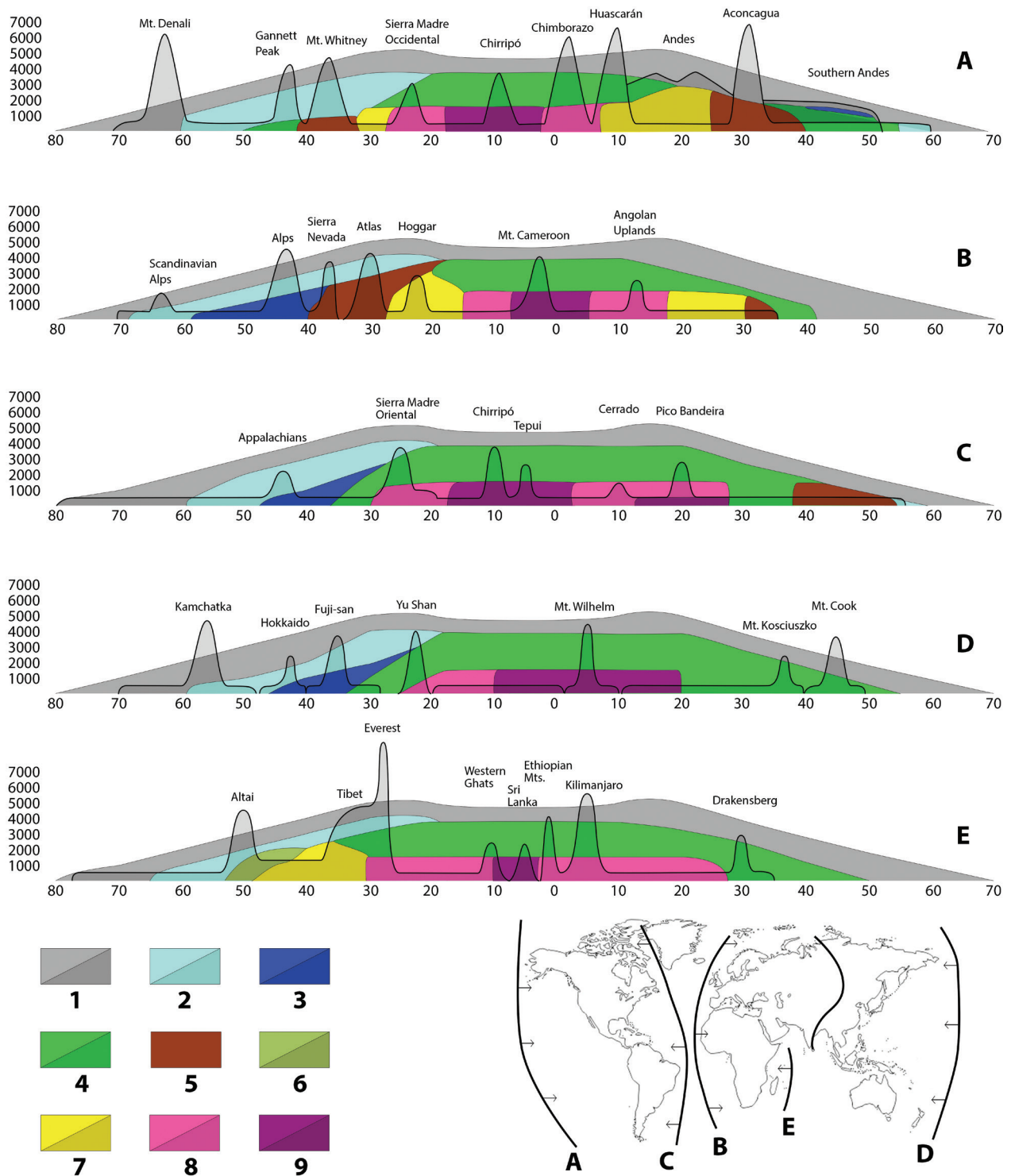
More detailed maps are offered in the folder of Suppl. material 3. The profiles of Figure 10 are inspired by those in Schroeder (1998). There are five profiles of the continental masses relative to their coastal borders. The latitude ranges of the continents are compared and the mountains are much exaggerated, but their relative altitudes are represented. Profiles A and B correspond to the western side of the continents while C and D represent the eastern side; the E profile includes a central transect across the Asian continent. There is a clear difference between eastern and western sides due to the occurrence of drought driven biomes in the latter. Additionally, the biomes have their real and virtual areas, the former on land and the latter in the air, in a way initially inspired in Troll (1948) and later in Schroeder (1998) and Pfadenhauer and Klötzli (2014), attempting to relate the latitudinal expression with the altitudinal occurrence. It is important to notice that the asymmetry of both hemispheres is revealed in these schemes; the northern has important areas with biomes 6, 2 and 3, while the southern has only a scarce representation of the



**Figure 9.** Distribution of the 20 subbiomes across the world. 1a Polar tundra, 1b Tundras of the temperate mountains in cryoro belt, 1c Tundras of the tropical mountains in cryoro belt, 2a Lowland boreal Taiga, 2b Forests and shrublands of the temperate oro belt, 3a Temperate deciduous forests, 4a Lauroid evergreen forest of the lowlands, 4b Conifer coastal forests, 4c Tropical montane cloud lauroid and conifer evergreen forest, 5a Oceanic sclerophyllous-microphyllous evergreen forests and shrublands (Mediterranean), 5b Continental scrub and woodlands, 5c Patagonian shrubland, 6a Forest-steppe, 6b Grass-steppe, 7a Cold deserts and semi-deserts, 7b Temperate deserts and semi-deserts, 7c Warm deserts and semi-deserts, 8a Tropical xeric shrublands and woodlands, 8b Tropical pluviseasonal forests and woodlands, 9a Tropical rain forests.

**Table 7.** Domains, Ecozones, Biomes and Subbiomes of the Earth.

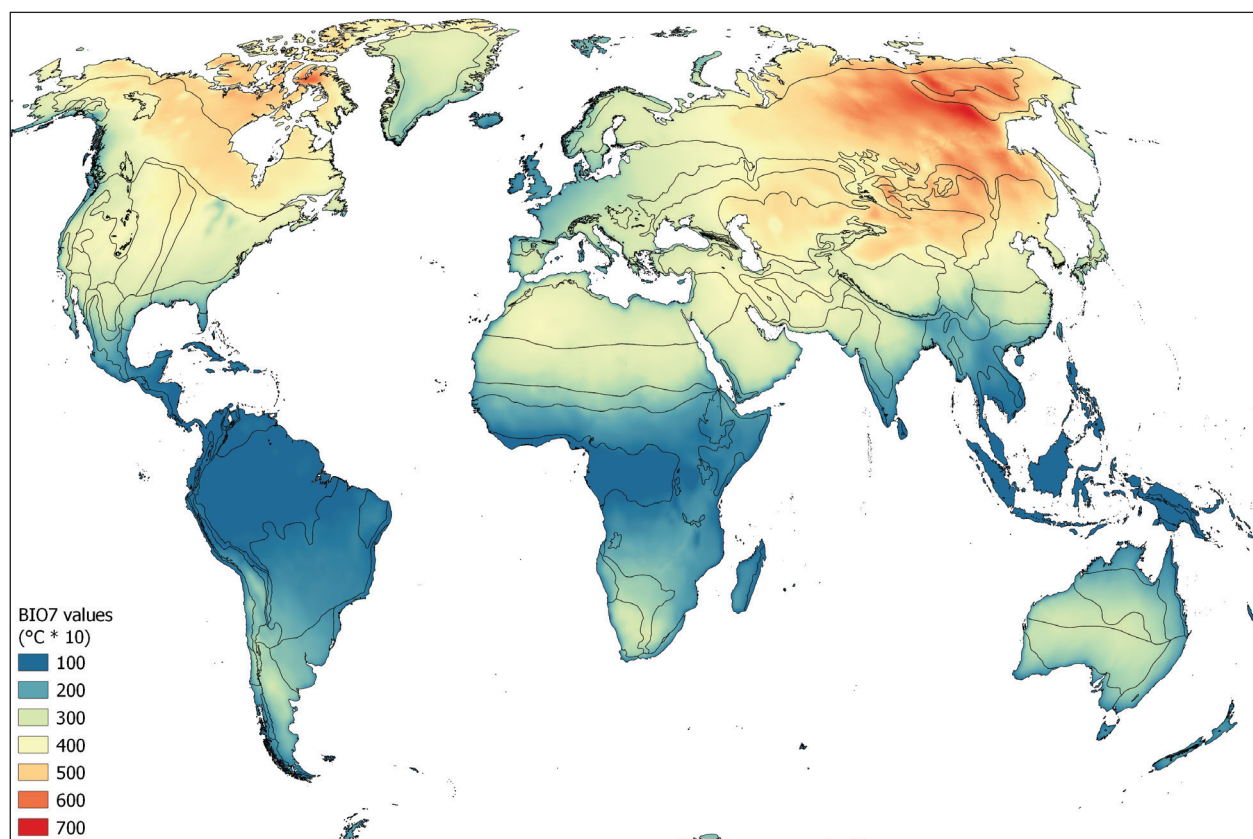
Domains	Ecozones	Biomes	Subbiomes
A. Cryocratic Domain of the cold climates	AA. Polar and boreal ecozone	1. Biome of the tundra	1a. Polar tundra
			1b. Tundras of the temperate mountains in cryoro belt
	BB. Temperate ariadiestival ecozone	2. Biome of the boreal forest	1c. Tundras of the tropical mountains in cryoro belt
			2a. Lowland boreal Taiga
B. Mesocratic Domain of the temperate climates (incl. tropical mountains)	BA. Temperate ombroestival ecozone		2b. Forests and shrublands of the temperate oro belt
		3. Biome of the temperate deciduous forests	3a. Temperate deciduous forests
		4. Biome of the temperate pluvial evergreen forest, shrublands and grasslands	4a. Lauroid evergreen forest of the lowlands
	BB. Temperate ariadiestival ecozone		4b. Conifer coastal forests
		5. Biome of the temperate ariadiestival evergreen forests and shrublands	4c. Tropical montane cloud lauroid and conifer evergreen forest
	BC. Temperate hypercontinental steppic ecozone	6. Biome of the steppe	5a. Oceanic sclerophyllous-microphyllous evergreen forests and shrublands (Mediterranean)
C. Xerocratic Domain of the arid climates	CA. Ecozone of the deserts and semi-deserts of arid regions		5b. Continental scrub and woodlands
		7. Biome of the deserts and semi-deserts of arid regions	5c. Patagonian shrubland
			6a. Forest-steppe
	DB. Tropical pluvial, rainy all the year round ecozone	8. Biome of the steppe	6b. Grass-steppe
D. Thermocratic Domain of the warm climates	DA. Tropical pluviseasonal, rainy and dry seasons		7a. Cold deserts and semi-deserts
		9. Biome of the deserts and semi-deserts of arid regions	7b. Temperate deserts and semi-deserts
			7c. Warm deserts and semi-deserts
E. Thermocratic Domain of the warm climates	DA. Tropical pluviseasonal, rainy and dry seasons	8. Biome of the tropical pluviseasonal forests and shrublands	8a. Tropical xeric shrublands and woodlands
		9. Biome of the tropical rain forests	8b. Tropical pluviseasonal forests and woodlands
F. Thermocratic Domain of the warm climates	DB. Tropical pluvial, rainy all the year round ecozone		9a. Tropical rain forests



**Figure 10.** Representation of real and virtual areas of the 9 biomes across latitude and altitude in profiles of the continents. **A** and **B** are North South profiles from the western side of the continents (**A** The Americas from the Pacific; **B** Europe and Africa from the Atlantic), and **C** and **D** are profiles from the eastern side (**C** The Americas from the Atlantic; **D** Asia and Australasia from the Pacific). **E** Represents a transect in the middle of the Asian continent, continued with the profile of Africa from the Indian Ocean. Inland the colors are darker than in the air, where they only represent a virtual area. 1 Tundra; 2 Boreal forest; 3 Temperate deciduous forest; 4 Temperate pluvial evergreen forest, shrublands and grasslands; 5 Temperate arid/steppe evergreen forests and shrublands; 6 Steppes; 7 Deserts and semi-deserts of arid regions; 8 Tropical pluviseasonal forests and shrublands; 9 Tropical rain forests.

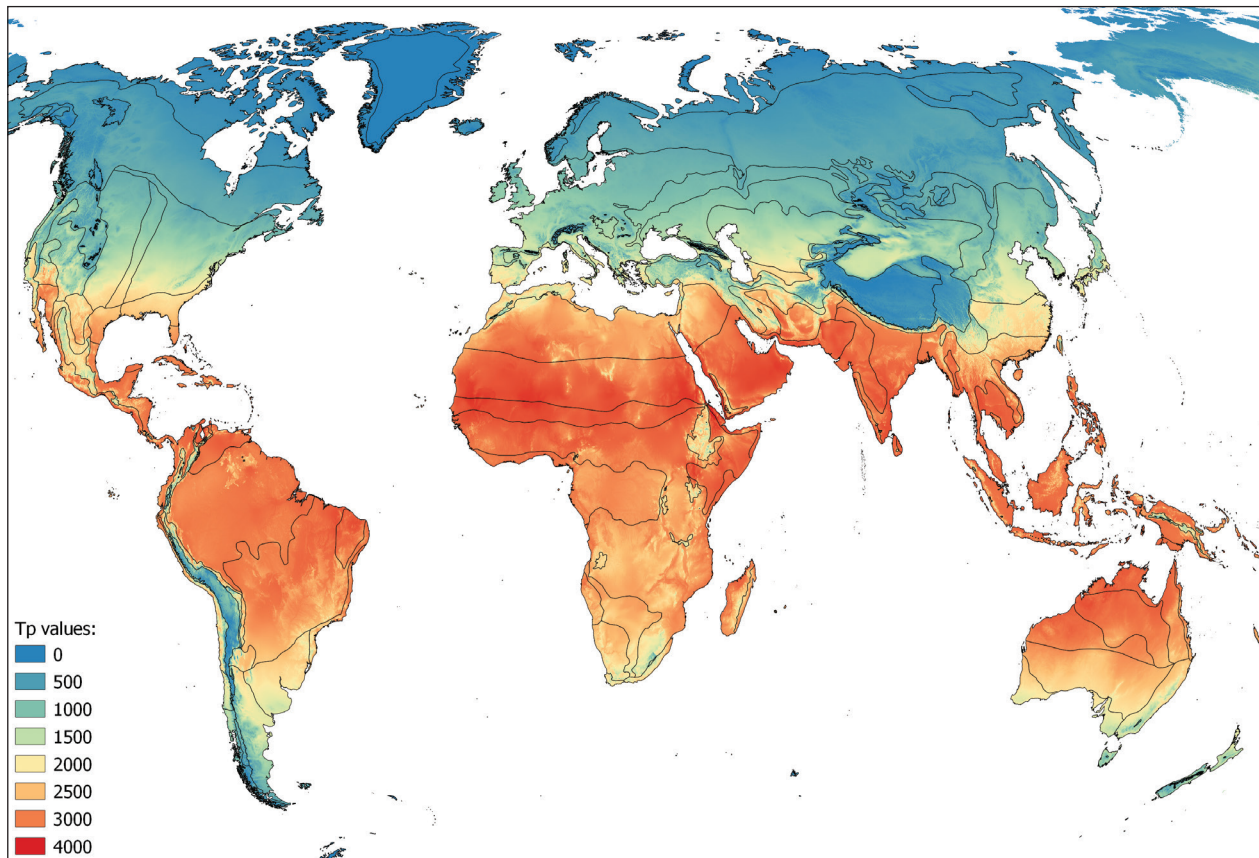
**Table 8.** Subbiomes of the Earth with their corresponding thermotypes.

Macrobioclimates Thermotypes	Cold		Mesic				Arid			Warm			
	Cryoro	Oro	Cryoro	Oro	Supra-Meso	Termo-Infra	Cryoro	Oro	Supra-Infra	Cryoro	Oro	Supra	Meso-Infra
<b>Subbiomes</b>													
1a. Polar tundra	X												
1b. Tundras of the temperate mountains in cryoro belt			X										
1c. Tundras of the tropical mountains in cryoro belt										X			
2a. Lowland boreal Taiga		X											
2b. Forests and shrublands of the temperate oro belt				X									
3a. Temperate deciduous forests					X	X							
4a. Laurid evergreen forest of the lowlands						X							
4b. Conifer coastal forests					X						X	X	
4c. Tropical montane cloud laurid and conifer evergreen forest					X							X	
5a. Oceanic sclerophyllous-micrphyllous evergreen forests and shrublands (Mediterranean)					X	X							
5b. Continental scrub and woodlands					X			X					
5c. Patagonian shrubland					X								
6a. Forest-steppe					X								
6b. Grass-steppe					X								
7a. Cold deserts and semi-deserts								X	X				
7b. Temperate deserts and semi-deserts								X	X				
7c. Warm deserts and semi-deserts								X	X				
8a. Tropical xeric shrublands and woodlands													X
8b. Tropical pluviseasonal forests and woodlands													X
9a. Tropical rain forests													X

**Figure 11.** Distribution of the BIO7 (annual temperature range) values across the world with subbiome boundaries.

latter two. This is due to the much higher continentality of the former. Conversely, biome 4, which is linked to a more oceanic climate, has a much wider amplitude in the south as is shown in Figure 11 with the distribution of the continental-oceanic gradient (BIO7) across the world. It is also remarkable that the highest altitude for biome 1

(tundra) is not reached in the equatorial zones (somewhat below 5000 m) but in latitudes around the tropics (little above that level); this likely related to the extreme oceanicity and higher cloudiness in the equatorial band. This suggest that the highest thermic regime is reached in these bands (Figure 12), but with a certain asymmetry between



**Figure 12.** Distribution of the Tp (positive precipitation) across the world with subbiome boundaries.

hemispheres, ranging between 20° and 30° in the NH and between 10° and 20° in the SH. This difference can also be attributed to the higher continentality of NH, which favors thermicity in the warm season. The distribution of the water availability is shown in Figure 13, where the arid areas are clearly visible. Other patterns to be observed are the differences between the eastern and western sides of the continental masses. The western sides have representations of biome 7 (deserts) and biome 5 (temperate arid/steppe or Mediterranean s.l.), which are lacking in the east. Only the Argentinian Patagonia has biome 5 due to the rain shadow of the southern Andes. In the D transect-profile are shown the high continental biomes-subbiomes such as 6 (Steppe), 5.b and 7.a, only represented in the highly continental land masses of the NH.

### A. Cryocratic Domain of the cold climates

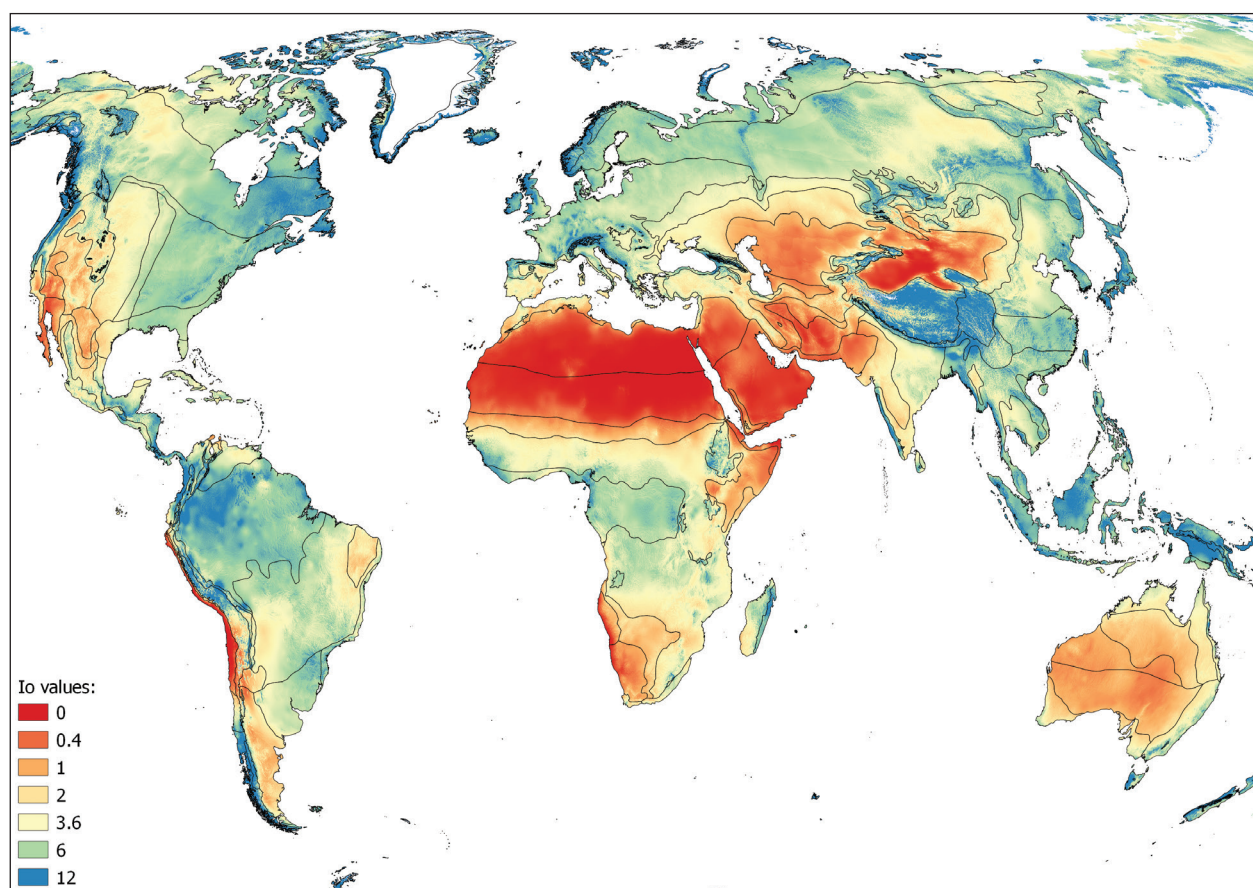
The climate of this domain is governed by the clearly negative radiative energy balance, with more radiation issued than received. This entails the permanence of the polar high pressures, which diffuse extremely cold air masses causing low temperatures and long frost periods in the higher latitudes of the Planet, mostly above 60°N and S. The long cold periods alternate with brief and cool summer seasons which can be longer and warmer in the case of the boreal forest. As a general rule, the values of Tp units rarely exceed 1000. In the case of the tundra, summers are practically non-existent since the temperature does not exceed 10°C on average in the warmest month, being also short

but mild in the case of the taiga. The differences between winter and summer are extreme, with very long daylight in the central days of summer, which lasts up to 24 hours on the corresponding days in the latitudes above those of the Arctic and Antarctic Polar Circles, while in winter the situation is the inverse. There is a great difference between the seasons regarding the solar radiation received.

The vascular vegetation of this domain presents the entire syndrome of adaptations to low temperatures. Its origin is quite recent (Brochmann and Brysting 2008) since it is estimated that it was forged throughout the Pleistocene (Tallis 1991) in favor of the general cooling of the Planet and the elevation of the current mountain ranges. This vegetation probably differentiated in the adjacent mountainous areas and expanded through the polar regions in the warm stages, in a repeated cycle in line with the glacial-interglacial cycles. For this reason, the vegetation of the tundras and boreal forests have clear homologies with those of the alpine (cryoro) and subalpine (oro) levels of the mountains, particularly of the NH areas.

### AA. Polar and Boreal ecozone

This is the only ecozone of the domain and it can be split into the tundra and the boreal forest biomes. They both present clear relationships with the high elevations of the temperate and tropical mountains, which are also under the dominance of the low temperatures and are considered a part of this ecozone and its corresponding biomes.



**Figure 13.** Distribution of Io (ombrothermic index) across the world with subbiome boundaries.

## 1. Biome of the tundra.

The term derives from the Russian тундра, which is applied to a plain area without trees, because it is a biome devoid of trees and constituted by a continuous, dense and evergreen vegetation layer formed by a combination of bushes, herbaceous vascular plants (often grasses and sedges), bryophytes and lichens; the low temperatures prevent the development of trees. It is the biome with the greatest adaptation to cold climate, both in latitude and altitude. Temperatures remain above freezing for only 2 to 6 months, during which the probability of frost does not disappear. The average temperature of the warmest month does not generally exceed 10°C. Ocean influences determine the span of temperature seasonality, being much higher in continental regions. In addition to the Arctic and Antarctic tundra, the cryoro (alpine) belts of the world's mountains above the forest level are considered to have tundra vegetation due to similarly low temperatures and the morphologic analogies with them. The upper limit of the polar tundra is marked at 380 units of positive temperature (Tp) and 450 in the case of tropical and Mediterranean alpine tundras.

### 1.a. Polar (Arctic and Antarctic) tundra.

This extends through the territories closest to the poles above a border that oscillates between 65° and 70° (exceptionally it can go down to 56°) of latitude, depending

on the continentality and the marine currents, following more or less the isotherm of 10°C of the month of July (January in the SH). It spans vast peri-arctic territories in the northernmost fringes of North America (Alaska, Canada, and Greenland) and Eurasia. In the SH there are few emerged lands in those latitudes but it is recognized in the extreme north of the Antarctic peninsula and in the small islands that surround that continent.

Due to the low temperatures and its recent release from the ice cover since the last glacial maximum, the soils of the tundra are poorly developed. In polar tundras the characteristic soil is *permafrost*, which freezes completely in the long winter and thaws only on its surface (mollisol) in the short summer, always leaving a permanently frozen layer of soil below 25 to 30 cm, which can reach a remarkable depth (pergelisol). Permafrost is one of the elements that limit the growth of trees by preventing the development of their root system. In the domain of the tundra there are the so-called *polygonal soils*. These are formations of geometric cellular figures of different sizes, with circular to hexagonal contours, formed by the accumulation of larger particles displaced by the freeze-thaw cycle.

In Arctic tundras rainfall is low, of the order of 200 mm per year or even less, and is mostly in the form of snow, so that a layer of snow forms lasting all winter. With the spring thaw this ice melts and in the short summer there is abundant availability of liquid water. The wind is responsible for an uneven distribution of the snow on the surface, so that

it accumulates in the hollows and is swept from the ridges. This is of great importance in the distribution of the mosaic of tundra communities, as the most protected areas will be in the troughs and the most exposed at elevation.

Because of the extreme specialization required to survive in such an extreme habitat, tundras are generally species poor. The Arctic tundras support approximately 900 species while the cryoro (alpine) tundras are more diverse as they have numerous endemics typical of the mountains. Woody species of the genera *Arctostaphylos*, *Betula* (*B. nana*), *Cassiope*, *Dryas*, *Empetrum*, *Ledum*, *Salix*, *Silene acaulis*, *Vaccinium* etc., herbs of the genera *Carex*, *Deschampsia*, *Saxifraga* (*S. oppositifolia*) or *Silene* are frequent in the Arctic tundras. Non vascular plants are abundant such as the bryophytes *Hylocomnium splendens* and *Polytrichum juniperinum* or fruit lichens such as *Cetraria nivalis*, *Cladonia gacilis* or *Cladina mitis* (Klein 1970; Bliss et al. 1973).

In Antarctica, tundra vegetation has a modest representation in the Antarctic Peninsula area with only two vascular species: *Colobanthus quitensis* and *Deschampsia antarctica* (Smith and Poncet 1987), and a much larger number of lichens and briophytes.

#### 1.b. Tundras of the temperate cryoro (alpine) belt.

In the tundras of the cryoro (alpine) belt of the mesic (temperate) zone, the thermic and luminic seasonality is lower than in the polar regions, reaching to nill in the tropical latitudes. In contrast, there is a strong daily temperature oscillation (diurnality) and a strong incidence of wind, with its intense, abrasive and drying effect upon the areas not sheltered by the snow cover. As a result, the cryoro tundras have a less severe winter and in general receive higher rainfall due to the orographic precipitations effect. Permafrost is thinner in the cryoro tundras, disappearing in the mid latitudes where permanently iced soils are lacking. In the cryoro belt tundras, periglacial phenomena associated with movements caused by the daily cycle of melting-freezing of soil water, such as cryoturbation and solifluction, are frequent, as well as the fragmentation of rocks due to freezing of water: gelifraction (Körner 1995).

In the alpine (cryoro) tundras, rainfall can be very variable oscillating between low and very high values, depending on the climatic regime of the mountain system in question and the accumulation of snow as redistributed according to relief by the strong winds.

As the cryoro tundras are at higher elevations as latitude decreases, uv radiation increases, favouring the differentiation of new species and endemics. Thus, cryoro tundras have a particular flora resulting from the evolution of the low elevation local floras drawn by the adaptation to high mountain environments created during mountain uplift. This is particularly relevant in the mid and lower latitudes, such as the Mediterranean climatic area. In the higher latitude mountains, there is a strong participation of polar tundra flora which merge with the local mountain flora, due to migrations that took place in the Pleistocene ice ages, when the alpine tundras contacted with the polar

tundra in the mid elevation mountains of the high latitudes, allowing floristic exchange between both elements (Comes and Kadereit 2003). In these cryoro tundras of the temperate latitudes, the herbaceous element increases to become dominant with the addition of representatives of *Festuca*, *Carex*, *Oxytropis* and others.

In the SH there are fewer mountains bearing cryoro tundras in temperate latitudes. We can mention the Southern Andes, above the tree line, where there is vegetation of dwarf scrubs and herbs, with species such as *Gaultheria mucronata*, *Gunnera magellanica*, *Hamadryas magellanica*, *Marsippospermum grandiflorum*, *Oreopolus glacialis*, etc. (Galán de Mera 2005). In areas of the highest mountains of SE Australia there is also alpine vegetation above the tree limit, which develops cushion-shaped plant communities with species such as *Baeckea gunniana*, *Ewartia meredithae*, *Podocarpus lawrencei* or *Pterygopappus lawrencii* and some others (Beadle 1981). New Zealand has an important representation of subalpine and alpine vegetation as the tree limit lies at quite low elevations, between 900 and 1600 m asl. Above that, a subalpine scrub vegetation develops in which *Coprosma cheesemanii*, *Dracophyllum uniflorum*, *Gaultheria crassa*, *Podocarpus nivalis*, etc. thrive. Above the shrub belt, alpine grasslands occur in which *Chionochloa* species dominate, with *C. crassiuscula*, *C. oreophylla*, *Poa colensoi*, etc. The grassland is dotted by cushion plants such as *Haastia pulvinaris* or *Raoulia eximia*, and others such as *Aciphylla simplex* or *Celmisia viscosa* (Wardle 1991).

#### 1.c. Oro-Cryoro Tundras of the tropical mountains.

The tropical mountains show a high uniqueness because their floristic lineage is different from that of the cryoro tundras of the extratropical mountains (Rundel et al. 1994) which are more closely related to the polar tundras, particularly in the NH. Above the forest limit, in the tropical mountains there is a scrub floor or level formed by *Ericaceae* (*Erica*, *Rhododendron*, *Vaccinium*), *Protea*, *Kniphofia*, *Gaultheria*, *Ribes* or *Hypericum*. In South America, this level is occupied by a short woodland-shrubland, basically formed by species of *Gynoxys* (*Asteraceae*), *Polylepis* (*Rosaceae*), *Clusia*, *Gaultheria*, *Escallonia* and *Podocarpus*. It forms the upper part of the tropical mountain forest, constrained by the genuine tropical oro-cryoro tundra-like formations of the Andes: the *puna* or the *páramo*. In the northern Andes (Venezuela, Colombia, Ecuador), where rainfalls occur throughout the year, it develops the páramo, while in the central Andes (Perú, Bolivia, Northern Chile and Northern Argentina), where the rainfall annual regime has a dry season, there is the *puna*. In the Andean páramo, also recognized in the high mountains of Central America, there are plant species of the genera *Coespeletia*, *Espeletia*, *Espeletiopsis*, *Hypericum* or *Puya* (Rangel et al. 1997). In Africa the homologous ecosystem carries *Dendrosenecio*, *Helichrysum* (*Asteraceae*) and *Lobelia* (*Campanulaceae*), while in Indonesia *Anaphalis* appears and in New Guinea *Leucopogon suaveolens*. All of them have a

particular biotype formed by a stem that emerges up to half a meter, at the apex of which the leaves crowd, forming a rosette that protects the growth bud from the sudden and extreme cold that occurs in the tropical mountains at these altitudes. Separation from the floor can be a strategy to mitigate the low temperatures by covering the buds with the leaves and to separate them from a permanently soaked soil. In the puna, grass pastures (pajonales) predominate, with genera such as *Agrostis*, *Deyeuxia* (*D. vicunarum*), *Festuca* (*F. dolichophylla*, *F. ortophylla*), *Poa* or *Stipa* (*S. ichu*). These are Holoarctic lineages (genera) that testify to their ancestry as migrants from North America who traversed the dorsal mountains on the South American continent and reached the southern latitudes far south of the equator (Navarro-Sánchez and Molina-Abril 2020). These grasslands occupy large areas subjected to cryoturbation by the daily freeze-thaw cycle and alternate with abundant peaty fens (bofedales). In New Guinea the cryoro tundras are represented by grasslands with *Deschampsia klossii*, *Festuca papuana*, *Gleichenia vulcanica*, *Papuapteris linearis* and *Poa callosa* (Paijmans 1976; Gressitt 1982; Mangen 1993).

## 2. Biome of the boreal and austral forest

This biome is often known by the name of *taiga*, from Russian тайга, being a biome dominated by conifer forests, mostly perennial but which also include some deciduous broadleaved trees such as birches, aspen and willows. It is subjected to a shorter freezing period than the tundra, having a frost-free season of a certain duration which allows the soils to thaw at least partially and permit trees to establish. Temperatures reach very low values during winter, often lower than in the tundra, due to the high continentality of some of the areas occupied by this biome (Walter 1979). The Boreal forest biome is mostly spread in the NH, having a modest representation in the SH (southern Argentina; Tierra del Fuego), because there are very small areas in the latitude range of this biome. Tropical mountains also lack this biome as they have a much reduced temperature seasonality, and do not have cold winters. In the mountains of the temperate areas of the northern hemisphere, this biome can be recognized in the oro (subalpine) belt, between the cryoro tundra and the supra (montane) in which the biomes 3, 4 or 5 occur.

The typical zonal soil of the taiga is the podzol, which is created by the acid organic matter (mor) produced by the conifers and ericoids which grow under these climatic conditions and on acidic siliceous bedrock. On other substrates, such as volcanic rocks, andosolic podzols will be found.

### 2.a. Lowland boreal taiga.

The boreal taiga forest is predominantly a conifer forest, with some broadleaved trees, ericoid shrubs and an herb layer with sedges and grasses as well as bryophytes and lichens. Mycorrhization is widespread due to the soil

poverty. The boreal taiga develops in areas of higher thermic conditions and in lower latitudes than the Arctic tundra. It expands uninterruptedly across the NH lands both in Eurasia (Fennoscandia and northern Russia including large areas in Siberia) and North America, mostly in Alaska and Canada, in latitudes oscillating between 42° and 72°N. The climate is cold with a high temperature seasonality having long and cold winters in which temperatures reach extreme negative values, particularly in some areas as Eastern Siberia (Yakutia); there are at least 120 days where temperatures are < 10°C. On the other hand, the short summers can have 30 to 120 days in which temperatures are above 10°C, and with some days of remarkable length (Grishin 1995). The plant growth period oscillates here between 130 to 150 days. Precipitations are usually higher than in the Arctic tundra, oscillating between 500 mm and over 1000 mm in some coastal areas, occurring mostly in summer. This rainfall concentration in the warm season, added to the snowmelt of the springtime, determines that there is no drought in the summer season (Pfadenhauer and Klötzli 2014).

In **north Europe** the most frequent boreal forests conifers are *Larix decidua*, *Picea abies* and *Pinus sylvestris*, being accompanied by the broadleaved *Betula pubescens* and *Populus tremula*. In **east Siberia** *Abies sibirica*, *Larix gmelinii*, *L. sibirica*, *Picea obovata*, *Pinus pumila* or *P. sibirica* are found, often with the broadleaved trees *Betula ermanii*, *B. dahurica* and *B. platyphylla*. South of the taiga, in some areas of Europe and East Asia conifers mix with deciduous temperate tree species resulting in a transitional forest zone called hemiboreal (Hytteborn et al. 2005).

The boreal forest of northwestern **America** is formed by conifers such as *Larix laricina*, *Picea glauca*, *P. mariana* and *Pinus banksiana*, while in the northeast *Abies balsamea*, *Betula occidentalis*, *B. papyrifera*, *Populus balsamifera* and *P. tremuloides* form the broadleaved element.

The understorey flora is formed by species of the genera *Arctostaphylos*, *Empetrum*, *Ledum*, *Rhododendron*, *Vaccinium*, *Pyrola*, *Linnaea*, *Lycopodium*, *Trientalis* and several orchids such as *Corallorhiza trifida*. Bryophytes and lichens are abundant (Weber and van Cleve 2005).

### 2.b. Forests and shrublands of the temperate zone oro (subalpine) belt.

In the oro (subalpine) belt of the mountains of the temperate geographic zone, below the cryoro (alpine) level, this biome can be recognized as a mountain variant or subbiome dominated by conifers (Tallis 1991) and in the aridiestival mountains of Mediterranean character by a scrub of cushion shaped shrubs. They experience a lower seasonality as they are at lower latitudes, but at higher elevations, low temperatures are comparable to those of the Boreal taiga. Concerning the relationship of this subbiome with the lowland taiga, there is a parallel situation to that of the polar and cryoro tundras.

For the conifer forests of the European mountains, we can mention *Larix europea*, *Picea abies*, *Pinus cembra*, *P. mugo*

and *P. uncinata* for the temperate pluviestival regions, while in Mediterranean latitudes *Pinus nigra* subsp. *salzmanii* and *P. sylvestris* (several varieties), as well as *Cupressus sempervirens*, *Juniperus hemisphaerica* and *J. sabina*, are typical (Timbal et al. 2005). In the north American mountains, the Rocky Mountains support *Abies lasiocarpa*, *Larix occidentalis*, *Picea engelmannii*, *Pinus albicaulis*, *P. contorta*, *P. ponderosa*, *Pseudotsuga menziesii*, etc., while in the Appalachians *Tsuga canadensis* and *Pinus strobus* are frequent (Powers et al. 2005). In East Asia the subalpine forests have *Abies mariesii*, *A. veitchii*, *Picea jezoensis*, *Pinus koraiensis*, *Tsuga diversifolia*, etc. (Nakamura and Krestov 2005).

In the mountains of the temperate aridiestival areas (Mediterranean), oro (subalpine) levels are often occupied by a thorny cushion shaped shrubland in which several spiny legume species of *Astragalus*, *Echinopartum*, *Erinacea* and *Genista* dominate. In some territories, this shrubland is dotted with scattered populations of pines, cypresses or junipers.

In southern Tierra del Fuego, a small area is subjected to a climate corresponding to that of the Boreal forest biome – in a very oceanic variant – where the vegetation is dominated by broadleaved *Nothofagus* species (Magellanic forest) combined with dwarf conifers of the genera *Araucaria*, *Austrocedrus*, *Fitzroya*, *Pilgerodendron* or *Podocarpus*, in a mosaic with extensive moss-mire areas. This unit has been named the Magellanic Antiboreal Evergreen Forest (Luebert and Plischoff 2022). This modest area, in spite of being a lowland territory, fits climatically better in the 2.b subbiome than in 2.a due to its markedly oceanic character.

## B. MESOCRATIC DOMAIN OF THE TEMPERATE CLIMATES

The temperate zone of the earth extends between the high latitude zone dominated by cold polar air masses and the intertropical zone where solar radiation is maximum. In it, the thermal seasons are clearly distinguished between a hot summer and a colder winter, which coincide with the contribution of major-minor radiation throughout the year. This seasonality diminishes in the vicinity of the tropics (subtropical areas), particularly in terms of the rigors of winter. Within this temperate zone, the climatic regime is governed by the influences of the Polar Front, the Subtropical Highs and the Trade Winds depending on the regions. All these regimes are subject to seasonal latitudinal displacements, so that in the winters of the NH there is a displacement of the whole set towards the south, and in summers it is the other way around. This temperate zone is subject to an extreme diversity of climatic situations, particularly in the NH, where there is a large extension of landmass compared to the SH. The northern land masses (Eurasia, North America, North Africa) cover a substantial part of the total area and are traversed by many mountain ranges permitting the effect of continentality to play a significant role in the central regions of these continents. We include in this domain the areas that register an *Io* index above 1 and a positive temperature *Tp* ranging between 1000 and 2000 units approximately, where the vegetation

can develop up to a complete coverage of the ground surface, leaving the areas below that level in the desertic area of the arid climates. In the tropical latitudes, similarly to the cryocratic domain, the mountains replicate the mesocratic conditions above 1500 m of altitude due to the decrease in temperatures (meso-supra levels). For that reason, the ecosystems that inhabit areas above that altitude can be included in this domain since the decrease in temperatures is accompanied by the existence of many extratropical lineages, both of Holarctic and Gondwanan origin. The vegetation consists of a variety of forests, groves, bushes or grasslands, depending on regional conditions.

### BA. Temperate pluviestival ecozone

The summer season is critical in this domain because is the period in which plants can grow and reproduce. There is a phenological adjustment to seasonality of the entire ecosystem. Thus, the availability of moisture permits intense development and growth providing favorable conditions for high biomass production. In this category could also be included temperate rain forests as have been mentioned in the literature particularly for the Pacific coast of the Americas (Alaback 1991; Pew and Larsen 2001; Grubb et al. 2013). To separate this ecozone from the temperate aridiestival, the summer should have less than two months in which  $p < 2t$ , i.e., only one month with precipitations lower than double the temperatures.

### 3. Biome of the temperate deciduous forest.

Rainy summers in combination with a clear thermic seasonality, with well differentiated summer and winter seasons, allow the dominance of deciduous woody plants which shed their leaves in the severely cold season (criodeciduous).

#### 3.a. Temperate deciduous forests.

This represents the only subbiome of this biome. The climatic conditions for this biome-subbiome are well represented in the main three areas of the NH continents: East Asia, East North America and Western Eurasia. In the literature, this biome-subbiome has been also called the *nemoral forest* (Walter 1977, 1979, 1985; Breckle 2002). In the SH there are much smaller areas occupied by this biome-subbiome as the appropriate climatic conditions are less frequent (Loidi and Marcenò 2022).

The **eastern North American** region is favored by the rainfall linked to the maritime Atlantic air masses brought mostly by the northern Trade Winds. The vast area covered by this biome in **North America** spans between the Canadian areas of the St. Lawrence river and the Great lakes to the southern Appalachians, and from the east coast to the middle Mississippi basin, between 32° and 45°N latitude and 70° to 98°W longitude (Greller 1988). Some of the most representative species are *Acer sachharum*, *Castanea dentata*, *Carya* ssp., *Fagus grandifolia*, *Liriodendron tulipifera*, *Liquidambar styraciflua*, *Quercus alba*, *Q. rubra* and many others.

In temperate **East Asia**, this biome is widespread from northeastern China to the southern sectors of the Russian Far East, including most of both the Korean peninsula and the Japanese archipelago (Nakamura et al. 2007) between the latitudes 30° to 50°N and longitudes 123° and 103°E. The maritime air masses that favor this biome in that region come from the Pacific being drawn by the summer monsoon dominant in East Asia. The richness in species number of trees in this region is much higher than in the other two, and this is explained by the particular conditions that existed here in the Pleistocenic glaciations which permitted the survival of many taxa (Davis 1983). Some of the most relevant species are *Acer mono*, *Davidia involu-crata*, *Diospyros kaki*, *Fagus crenata*, *F. japonica*, *Pawlonia tomentosa*, *Quercus crispula*, *Q. mongolica*, *Q. serrata*, etc.

In **Western Eurasia** this biome covers a large area encompassing most of Europe, a strip in central-western Siberia, the Caucasus piedmonts and the eastern and southern coastal fringe around the Black Sea (Euxinian) and south Caspian Sea (Hyrcanian), a vast area limited by the boreal forest in the north and the Mediterranean and stepic regions in the south (Jahn 1991; Loidi et al. 2021). The summer rains are provided by the westerlies coming from the Atlantic, which drag a succession of lows with fronts, which form part of the Polar Front system. Particularly in Euxinian and Hyrcanian areas, local rains are due to the northern and northwestern winds which are reloaded with moisture when they cross adjacent water bodies. The most relevant species are *Acer campestre*, *Fagus orientalis*, *F. sylvatica*, *Fraxinus excelsior*, *Quercus petraea*, *Q. pubescens*, *Q. robur*, *Tilia cordata*, *T. platyphyllos*, *Ulmus glabra*, *U. minor*, etc. Within this biome, as result of human induced transformations, there are abundant several types of evergreen grasslands (hay and grazing meadows), spiny shrublands and the heathlands in the western part.

In the SH there are only a few scarce relictual representations of this biome. This is likely due to the lower continentality of the SH emerged lands in comparison to those of the north (Box and Fujiwara 2015). The only representation of this biome in the SH is a narrow strip in the southern Andes at altitudes between 900 and 1600 m asl in which several species of deciduous *Nothofagus* constitute forests: *N. antarctica*, *N. alessandri*, *N. alpina*, *N. glauca*, *N. macrocarpa*, *N. obliqua* and *N. pumilio* (Luebert and Pliscoff 2022), and a small area at the highest elevations of western Tasmania in Australia where it occurs with the deciduous *Nothofagus gunni*. Its small extent prevent it from being represented in the accompanying map.

#### 4. Biome of the temperate pluvial evergreen forest, shrublands and grasslands.

This biome encompass highly diverse forms of dominant vegetation formed by broadleaved evergreen species as well as conifers and grasslands. It is often formed by perennial evergreen forests, with leaves of varied texture and size, often coriaceous with shiny surfaces, called lauroid (laurisilvae), but also conifers of various taxa. This biome

is a complex and diverse one as it is represented in a variety of territories across the temperate and tropical latitudes of the world in both hemispheres.

In the temperate zone, it occupies the space between the tropics and the nemoral deciduous forest areas, under high to mid oceanic conditions entailing moderate winters and high summer precipitations. In the tropics it is also represented at the mid-elevations (meso-supra) of the mountain systems where temperatures are colder than in the lowlands. Due to orographic precipitations and frequent fogs, tropical mountains support this biome under several variants (Afro-montane, American Monteverde, etc.). In spite of such a diversity and broad geographic distribution, there are sufficient features to recognize a certain unity in physiognomy and origin between them. There are three subbiomes to be distinguished within it. In some coastal areas of the western side of the continents, particularly in Chile and in northwestern North America (British Columbia and Alaska), local conditions related to the persistence of westerlies allow the subsistence of this biome in lowlands or low elevation ranges in latitudes up to 55 and 60° respectively. In Western Europe, it may be expected to find such a biome in the comparable latitudes of some coastal areas, but it is not present. This absence may be due to the extinctions that happened during the Pleistocenic ice ages.

##### 4.a. Lauroid subtropical evergreen forest of the lowlands.

This subbiome can be found in a zonal position in the lowlands of the coastal or ocean influenced areas of the extratropical continental land masses. In the eastern side of the continents, the summer low pressure in mid latitudes circulates oceanic air masses towards the continent in a monsoonal regime causing abundant summer rains coincident with high temperatures. Winters are relatively dry and cold as the situation is inverse and land air dominates causing relatively low temperatures and scarce precipitation. Nevertheless, temperatures remain above 5°C in the coldest month. These formations have received several names such as *subtropical Lobeerwald* in German, *temperate broad-leaved evergreen forests* in English (Pfadenhauer and Klötzli 2014) or *Lucidophyll Forest* (Kira 1977).

In the Northern Hemisphere:

**Eastern Asia** is the most extensive area occupied by this subbiome, between 25° and 35°N latitude. Occupies the major part of Eastern continental China and the island of Formosa (Taiwan), penetrating to the west over the ranges connecting with the Tibetan Plateau and the arid regions of Central Asia, being limited by the 99° and 123°E longitude. Northwards, it reaches the southern areas of the Korean peninsula and the Japanese archipelago, in the coastal districts of the islands of Kyushu, Shikoku and southern Honsu (Yong-Chang and Liang-Jun 2016). In the south, it is constrained by the tropical rain forest (biome 9) in a transitional fringe north of Guangzhou (Canton) and connects to the west with the long narrow zone which

occupies the southern humid mid-elevation slopes of the Himalayas (Sekar and Srivastava 2010).

This region is subjected to a monsoonal regime with warm humid air masses coming in summer from the east (Pacific, Seas of China) and to winter invasions of cold air from the center of the Asian Continent originated by the strong Siberian high, which are responsible for brief cold episodes that can cause snow events.

The forests in this region have been dramatically reduced by human pressure, but do survive in some areas and support a high number of tree species of families such as *Fagaceae* (*Castanopsis*, *Cyclobalanopsis*, *Lithocarpus*, *Quercus*), *Myrsinaceae* (*Ardisia*), *Lauraceae* (*Cinnamomum*, *Machilus*, *Persea*), *Magnoliaceae* (*Magnolia*, *Michelia*), *Symplocaceae* (*Symplocos*), *Theaceae* (*Camellia*) etc. In spite of anthropogenic reduction, these forests are substantially more diverse in their tree flora compared with the eastern North American and Western Eurasian homologous portion (Latham and Ricklefs 1993). This richness is a result of the more mesic conditions that were dominant compared with Europe or North America during Pleistocene ice ages. Gymnosperms are also numerous, with representatives of *Cupressaceae* (*Fokienia hodginsii*, *Cryptomeria japonica*, *Cunninghamia lanceolata*, *Metasequoia glyptostroboides*), *Pinaceae* (*Pseudolarix amabilis*), *Podocarpaceae* (*Podocarpus macrophyllus*) or *Taxaceae* (*Cephalotaxus harringtonia*, *C. fortunei*, *Pseudotaxus chienii*). Some of these are old taxa, particularly *Ginkgo biloba*, and additionally bamboo-type grasses of the genus *Phyllostachys* are also frequent.

**Southeastern North America** is another of the regions where this subbiome is zonal, occupying a vast area in the USA between SW Texas and North Carolina, encompassing southern Louisiana, Mississippi, Alabama, Georgia, northern Florida and South Carolina. This area is under the influence of the Gulf Stream which flows across the Gulf of Mexico and the Atlantic coast and is associated with summer precipitations brought by the eastern trade winds. The forests of this region are substantially poorer than the homologous forests of East Asia, likely due to the higher intensity of the Pleistocene extinctions that took place in North America. This relative poverty can be also related to the lower precipitations occurring in this region (Kira 1991). A number of evergreen species, such as *Magnolia grandiflora*, *Myrica cerifera*, *Persea borbonia*, *Quercus hemisphaerica*, *Q. virginiana* or the palm *Sabal palmetto*, combine with deciduous species of wider distribution such as *Fagus grandifolia*, *Liquidambar styraciflua* or *Liriodendron tulipifera* (Greller 1988). An important part of this territory is currently covered by secondary pine forests (*Pinus elliotii*, *P. palustris*, *P. taeda*), which occupy the sandy soils of the coastal plain (Christensen 1988).

In the Southern Hemisphere:

The **South African southeast**, also called “Southern African Afrotropical Forest” (Mucina et al. 2021), is under the influence of the humid trade winds from the Indian

Ocean and the warm currents of Agulhas and Mozambique, having thus a temperate humid oceanic climate. It spans from Western Cape along the southern extreme of the continent across Eastern Cape and KwaZulu-Natal, being the only zonal representation of this biome in the African continent. It occupies the southern and western slopes of the Great Escarpment (including Drakensberg). Some of the species are *Afrocarpus falcatus*, *Cola greenwayi*, *Canonia capensis*, *Curtisia dentata*, *Faurea macnaughtonii*, *Ilex mitis*, *Leucosidea sericea*, *Nuxia floribunda*, *Ocotea bullata*, *Olea capensis* subsp. *macrocarpa*, *Olinia ventosa*, *Platylophus trifolius*, *Podocarpus latifolius*, *Pterocelastrus tricuspidatus*, *Rapanea melanophloeos* and *Widdringtonia schwarzii*. Among the tree-ferns we can mention *Alsophila* (*Cyathea*) *capensis* and *A. dregei*.

The region of **Southeastern Brazil and the Pampas** expands between 23° and 39°S latitude, on the Atlantic side of the South American continent encompassing the adjacent countries of the Río de la Plata estuary including southeastern Brazil (Paraná, Santa Catarina, Rio Grande do Sul), Uruguay and Northeastern Argentina. It is the SH counterpart of SE USA. The southern part of this territory is occupied by the Pampas, from Rio Grande do Sul, Uruguay to NE Argentina. It is a vast area which is currently almost entirely occupied by grasslands and crop fields; the arboreal vegetation is thus restricted to marginal positions. The anthropic origin of these grasslands has been previously discussed, as this area experiences completely different climatic conditions to those of the steppes. The overwhelming dominance of the grasslands indicate that the environmental conditions are optimal for them (Cabrera 1971; Oyarzábal et al. 2018); however, it is evident that the human influence with the pressure of grazers has favored them by reducing the cover of woody vegetation. In any case, it is likely that the influence of large grazing mammals present before humans appeared in this region led to the development of these Pampas grasslands.

The remnants of forest in these areas are formed by some species of regional distribution such as *Acacia bonariensis*, *Cassia corymbosa*, *Baccharis articulata*, *Colletia paradoxa*, *Ocotea acutifolia*, *Sambucus australis*, *Schinus longifolius*, *Scutia buxifolia* and particularly the ombú or *Phytolacca dioica* and the palm *Butia yatay*. Other species of broader distribution are *Acacia caven*, *Aloysia gratissima*, *Baccharis tandilensis*, *Celtis ehrenbergiana*, *Jodina rhombifolia*, *Prosopis alba*, *Zanthoxylum fagara*, *Margyricarpus pinnatus* etc.

The grasslands are dominated by grasses of the genera *Andropogon*, *Aristida*, *Briza*, *Bromus*, *Eragrostis*, *Melica*, *Panicum*, *Paspalum*, *Piptochaetium*, *Poa* and *Stipa*, which share their dominance with other herbaceous and woody plants of other families such as *Adesmia*, *Alicropsis*, *Aster*, *Baccharis*, *Berroa*, *Chaptalia*, *Heimia*, *Margyricarpus*, *Oxalis*, *Vicia*, etc.

This region is continued with the mid elevation areas of Paraná and Santa Catarina in south Brazil, where *Araucaria angustifolia* and *Podocarpus lambertii* occur with *Dicksonia sellowiana* in the understorey, being included in

this subbiome due to the subtropical climatic conditions dominant in these territories (Rizzini 1997).

In **Southeastern Australia**, this subbiome is represented in the coastal strip of land east of the Great Dividing Range, which crosses the eastern side of the continent and separates the arid regions of the interior from the moist coastal areas that are affected by the humid air masses from the Pacific Ocean. The southern stretch of this strip, which extends from the Rockhampton district to the southeastern tip of the continent and the island of Tasmania, is covered by this unit. The climate is humid all the year round and winters are mild. A high representation of species of the genera *Acacia* and *Eucalyptus* is present, some of them of great size such as *Eucalyptus globulus*, *E. obliqua* and *E. regnans*, reaching 100 m in stature. Other taxa are *Atherosperma moschatum*, *Doryphora sassafras*, *Ceratopetalum apetalum*, and conifers such as *Athrotaxis laxifolia*, *Phyllocladus aspleniifolius* and the endemic *Wollemia nobilis*, as well as several species of *Callitris*, *Macrozamia* and *Podocarpus*. Some Antarctic remnants are present such as *Nothofagus cunninghamii*, or the tree ferns *Cyathea australis* and *Balantium (Dicksonia) antarcticum* (Beadle 1981).

The **New Zealand** archipelago is located in a position where abundant rainfalls occur all year round, particularly on the western side of the islands. This entails a high oceanicity which permits the existence of evergreen temperate forests in the whole archipelago lowlands and midlands. The lower levels are occupied by a conifer/broad-leaved forest: among the conifers we can mention *Agathis australis*, *Dacrycarpus dacrydioides*, *Dacrydium cupressinum*, *Libocedrus bidwillii*, *Phyllocladus trichomanoides*, *Podocarpus totara*, *Prumnopitys ferruginea* and others, while among the broadleaved there are *Laurelia nova-zelandiae*, *Metrosideros umbellata*, *Weinmannia racemosa*, *W. silvicola* and the palm *Rhopalostylis sapida*. Several species of tree-ferns of the genera *Cyathea* and *Dicksonia* occur in the understory. The evergreen southern beeches (*Nothofagus*) occupy higher elevations than the conifer/broad-leaved forest with species such as *Nothofagus fusca*, *N. menziesii*, *N. truncata* or *N. solandri* (Wardle 1991).

**Southern Chile.** In the temperate southern part of Chile, around the 38°S, the climate shifts from arid to pluvial under the influence of the westerlies of the South Pacific. This region extends to Tierra del Fuego at 54°S, because conditions remain extremely oceanic all along the strip. Only in the southwesternmost strip of the area will occur boreal conditions (called antitropical by local authors such as Luebert and Plischoff 2022). The forests in this area (Valdivian and Magellanic) are evergreen with many lauroid species such as *Drimys winteri*, *Eucryphia cordifolia*, *Gevuina avellana*, *Laurelia sempervirens*, *Luma apiculata*, *Nothofagus betulodes*, *N. dombeyi*, *Persea lingue* and bamboos such as *Chusquea quila* (Grau 1992). In the cooler areas of the montane levels, conifers such as *Araucaria araucana*, *Fitzroya cupressoides* and *Pilgerodendron uviferum* become dominant. As mentioned in biome 3, at mid elevations there is a level of deciduous southern beech forests occupying a narrow strip in the western slopes of the southern Andes (Luebert and Plischoff 2022).

#### 4.b. Conifer coastal forests.

This subbiome is also zonal and differs from the previous one in that it presents a high dominance of conifers although there are always a significant presence of evergreen hardwoods. It can be recognized in northwestern North America, where it is known as the Pacific Northwest Forest (Franklin 1988), and occupies a 60–120 km width strip along the coast from central-northern California to southern Alaska, up to 60°N latitude. Tree species, either conifers or broadleaved, are adapted to a mild, moist, maritime climate with high oceanic influence in the form of frequent fogs. In the southern part of its area (mostly in California and Oregon), a clear summer drought is observed, as a result of the influence of the North Pacific High, but this drought is offset by the frequent summer fogs coming from the Pacific Ocean. Conifers, many of them of large size, combine with evergreen and deciduous hardwoods. Some important tree and shrub species are *Abies procera*, *Arbutus menziesii*, *Chamaecyparis lawsoniana*, *Chrysopsis chrysophylla*, *Libocedrus decurrens*, *Notolithocarpus densiflorus*, *Pinus lambertiana*, *P. radiata*, *Pseudotsuga menziesii* var. *menziesii*, *Quercus chrysopsis*, *Q. garryana*, *Q. sadleriana*, *Rhododendron macrophyllum*, *Sequoia sempervirens*, *Umbellularia californica* etc. Other species reach higher latitudes along the Pacific coast such as *Abies amabilis*, *Taxus brevifolia*, *Thuja plicata* or *Tsuga heterophylla* (Powers and Fiske 2005).

#### 4.c. Tropical and subtropical montane cloud lauroid and conifer evergreen forest and shrublands.

This subbiome can be recognized in the mid elevations of the tropical and subtropical mountains above 1000–1500 m (meso, and supra, humid and hyperhumid). They are evergreen forests formed by broadleaved trees and conifers which receive high amounts of moisture in the form of rain and fog. Conifers and broadleaved trees are both almost always present but they alternate in dominance, mostly depending on the historic evolution of the area. In any case, the broadleaved trees often have coriaceous and shiny leaves (lauroid) while the conifers often bear larger and softer leaves than in other biomes.

**The Macaronesian archipelagos: Azores, Madeira and Canaries.** Fragments of this subbiome (monteverde) are found in the north Atlantic volcanic archipelagos (Macaronesia), west to the Eurasian continent, being dispersed across most of its islands. Due to the influence of the Azores High, this area is overall subjected to a climatic dynamism in which summer is the driest season. This can be locally offset by orographic precipitations and, above all, through the cryptoprecipitations that take place due to the condensation of the fogs accumulating in the mid elevations of the windward slopes facing the trade winds (sea of clouds). Rain increases northwards and westwards so that the Azores are the most humid and the Canaries the driest, being the monteverde generally in the former and restricted to the north facing slopes in the latter. This

monteverde or laurisilva (Fernández-Palacios et al. 2017) has a certain relic character as it is considered the remnant of the Tertiary lauroid forests which covered the adjacent continental regions Eurasia and North Africa.

Trees are all perennial, with *Apollonias barbuja*, *Clethra arborea*, *Heberdenia bahamensis*, *Ilex canariensis*, *I. perado*, *Myrica faya*, *Laurus azorica*, *L. novocanariensis*, *Ocotea foetens*, *Persea indica*, *Picconia excelsa*, *Prunus lusitanica* and *Visnea mocanera* being the most relevant among others. Some of the noteworthy ferns are *Culcita macrocarpa*, *Davallia canariensis* and *Woodwardia radicans*.

The **southern slopes of the Himalayas** are covered by this subbiome at mid-elevations between 1000 m and 2500 m, above the tropical foothills that precedes the Indo-Gangetic plain covered with biomes 8 and 9, and below the subalpine conifer forest of 2.b thriving in the upper altitudes. This territory forms a long and narrow zone that spans along the southern slopes of the Himalayas, receiving the copious rains of the summer monsoon. This strip is thought to be the original area of the tea plant (*Camellia sinensis*) and is characterized by rhododendron forests, of which there are several tree species. Among them, *Rhododendron arboreum*, the national flower of Nepal, stands out, but also can be mentioned *R. barbatum*, *R. campanulatum* or *R. lepidotum* (Sekar and Srivastava 2010). These forests are rich in bamboo and *Araceae* and cover a wide stretch of the southern slope of the mountain range, from Kashmir to the mountains of the Chinese provinces of Yunnan and Sichuan.

**Afromontane forests** occur at elevations above 1000 m asl, where rainfall usually exceeds 1200 mm and fogs are frequent throughout the year. Their distribution is discontinuous being found in the long mountain chain crossing eastern Africa (Aerts et al. 2006), with the northernmost extreme in the highlands of Yemen. It occupies large areas in the many ranges and high plateaus of Ethiopia (from which the coffee tree, *Coffea arabica* originates), crosses Kenia, Ruanda, Burundi, Congo and Tanzania and reaches Malawi and Zambia, to finally connect with the South African southwest (Drakensberg). In the Equatorial latitudes the fragments of this subbiome occupy the belt between 2000 m and 4000 m asl, benefited by the fogs that accumulate in these altitudes favored by the trade winds from the Indian Ocean. There are other African mountain areas in which this subbiome is found, such as the highlands of Angola, the mountains of Cameroon, Nigeria and even the island of Bioko in the Gulf of Guinea. Some species of this Afromontane forests are *Balthasaria schliebenii*, *Barbeya oleoides*, *Chrysophyllum gorungosanum*, *Entandrophragma excelsum*, *Ficalhoa laurifolia*, *Hagenia abyssinica*, *Hypericum revolutum*, *Juniperus procera*, *Kiggelaria africana*, *Myrianthus holstii*, *Ochna holstii*, *Ocotea usambarensis*, *Olea europea* subsp. *cuspidata* (= *O. africana*), *Pouteria adolfi-friedericii*, *Prunus africana*, *Tabernaemontana stapfiana* and *Xymalos monospora*.

In the **Indo-Malesian** region, in the mountains of **Borneo, Java, Sumatra** and other islands, the flora is derived from both Asian and Australian lineages of families,

such as *Araucariaceae*, *Clethraceae*, *Ericaceae*, *Fagaceae*, *Lauraceae*, *Myrtaceae*, *Podocarpaceae*, *Symplocaceae* and *Theaceae*. They are very rich in epiphytes and forbs in the understory, with genera such as *Begonia*, *Cyrtandra* and *Musa*. Some species of this SW Asian region are *Agathis dammara*, *Dacrycarpus imbricatus*, *Castanopsis buruana*, *Lithocarpus celebicus*, *Magnolia carsonii*, *Myrsine affinis*, *Pinus kesya*, *Prunus mirabilis* etc. (Edwards et al. 1990; Kiatayama 1992; Buot 2002).

In the mountains of **New Guinea**, there are up to 14 species of *Nothofagus* which comprise forests from the mid elevations up to 3000 m (Robbins 1961; Pajmans 1976; Manger 1993; Read and Hope 1996). *Fagaceae* and gymnosperms are frequent in these forests, with species such as *Agathis spatulata*, *Araucaria hunsteinii*, *Callitris neocaledonica*, *Castanopsis acuminata*, *Dacrydium novoguineense*, *Dacrycarpus compactus*, *Libocedrus papuana*, *Lithocarpus megacarpus*, *Nothofagus carriei*, *N. flaviramea*, *Papuacedrus papuana*, *Phyllocladus hypophyllus*, *Podocarpus brasii*, *Prunus pullei* etc.

The island of **New Caledonia** is a fragment of Gondwana which has migrated northwards, entered into the intertropical zone and currently is immersed in a tropical climate. However, the indigenous flora is largely derived from the temperate Gondwanan and retains up to five species of *Nothofagus* and numerous gymnosperms (Read and Hope 1996). The mountain range that runs through the island along its length, crowned by elevations of modest altitude (1500 m), receives abundant rainfall from the east and in its upper section there is a montane forest with numerous gymnosperms such as *Araucaria humboldtensis*, *A. montana*, *A. laubenfesii*, *A. schmidii*, *Agathis montana*, *Podocarpus longifolius*, *Dacrydium lycopodioides*, *Libocedrus chevalieri*, *Retrophyllum comptonii*, *Acropyle pancheri* as well as other broadleaved such as *Metrosideros elegans*, *Nothofagus aequilaterialis*, *N. balansae* and several species of *Quintinia*, *Weinmannia* etc.

In the **Indian subcontinent**, these forests are recognized in the mountains of the south of the country, in the chain known as the Western Ghats, between the states of Kerala and Tamil Nadu (Greller et al. 2016). Some species are *Cullenia exarillata*, *Dyospiros barberi*, *Garcinia rubro-echinata*, *G. travancorica*, *Guta travancorica*, *Knema attenuata*, *Mesua ferrea*, *Palaquium ellipticum*, as well as the podocarp *Nageia wallichiana*. In the island of **Ceylon** (Sri Lanka), there is a significant representation of these mountain lauroid forests above 1000 m asl (Greller et al. 2016), which are under the influence of constant fogs in the massifs of the south-central part of the island. The famous Ceylon tea is grown in its territory. The arboreal rhododendron stands out, having an endemic subspecies for the island, *Rhododendron arboreum* subsp. *zeilanicum*. Additionally, *Palaquium rubiginosum*, *Stemonoporus cordifolius* and *S. rigidus* can be mentioned. There are also several arboreal ferns such as *Cyathea hookeri*, *C. sledei* and *C. sinuate*, while in the understory several *Strobilanthes* species are found.

In **Meso and South America** there are important areas with montane forests where temperatures are lower than

in the lowlands, precipitations higher and fogs frequent. In Meso- and Central America there are the Mexican Sierra Madre Oriental and Occidental, as well as the Mountains of Central America. In the Mexican sierras, above 1500 m asl of elevation, precipitations increase and are concentrated in the central months of the year (summer). There thrive evergreen lauroid forests, in particular the locally called *Mesophyllous Montane Forest* (Miranda and Sharp 1950), with trees such as *Clethra mexicana*, *Fagus grandifolia* subsp. *mexicana*, *Meliosma alba*, *Quercus ocoteifolia*, *Q. xalapensis* and many others. Under basically similar climatic conditions extend a major part of the *encinares*, or evergreen oak forests, with a high number of species of *Quercus* such as *Q. durifolia*, *Q. microphylla*, *Q. obtusata*, *Q. rugosa*, or *Q. sideroxylla*. As they occupy similar elevations and receive higher rainfall, they are assimilated to this subbiome too. The *pinares*, conifer forests with a high number of pine species such as *Pinus montezumae* or *P. teocote*, are subjected to a similar pattern of annual rainfall and can also be included in this subbiome (González Medrano 2004; Rzedowsky 2006). Southwards rises the Talamanca range (Costa Rica-Panamá) where *Quercus copeyensis*, *Q. costaricensis* and *Ilex pallida* appear, as well as other lauroid species such *Drimys granadensis* and *Weinmannia pinnata*, the tree fern *Cyathea fulva* and bamboos of the genus *Chusquea*, forming the luroid montane forest locally called *Monteverde*.

The **Guiana Shield** reaches elevations of ca. 3000 m asl in the Guiana Highlands, forming a mountainous area known as the *Tepuys*, which is covered by a vegetation very rich in endemics. Some frequent species are *Catostemma durifolius*, *Pouteria rigida*, *Protium neglectum*, etc. There are also several species of *Bonnetia*, such as *B. roraimae*, *B. steyermarkii* or *B. tepuiensis*, living above 2000 m asl (Delgado et al. 2009; Lozada et al. 2014).

In the **northern Andes**, in Ecuador, Colombia and Venezuela, the montane forests have species such as *Aegiphila bogotensis*, *Cecropia telenitida*, *Quercus humboldtii*, *Saurauia ursina*, *Vallea stipularis*, *Weinmannia tomentosa*, and several species of the genus *Cinchona*, such as *C. calisaya*, *C. macrocarpa*, *C. officinalis*, *C. pubescens* etc. (Rangel et al. 1997). The **central Andean** eastern slopes receive the wet air masses from the Atlantic drawn by the trade winds. At mid elevations, the cloud montane forest called *Yunga* or Andean Brow Forest occupies a narrow zone between 600 m and 2500 m asl between northern Peru and northern Argentina, crossing Bolivia. It occurs under extremely rainy and foggy conditions and is formed by a dense canopy up to 30 m high, which creates a humid and dark understory where a mass of shrubs, epiphytes, herbs and lianas live. Some of the trees are *Alnus acuminata*, *Escallonia myrtilloides*, *E. paniculata*, *E. pendula*, *E. resinosa*, *Podocarpus parlatorei*, *Polylepis pepeii* or *Sambucus peruviana*. In the southernmost stretches appear *Blepharocalyx salicifolius*, *Cedrela angustifolia*, *Cynnamomum porphyrium*, *Duranta serratifolia*, *Fuchsia boliviana*, *Ilex argentina*, *Juglans australis*, *Ocotea porphyria*, *Polylepis australis* and *Schinus gracilipes*, and the bamboo *Chusquea lorentziana*, among others (Cabrera 1971; Oyarzábal et al. 2018).

## BB. Temperate aridiestival ecozone

Unlike the previous ecozone, if the summer is dry (at least 2 months) the ecosystem is subjected to double stress, that of cold in winter and drought in summer, severely limiting biomass production and inducing adaptations to drought in the traits of plants. This summer aridity is due to the fact that in that season these areas are under the influence of the subtropical highs, since they are in the vicinity of the domain of arid climates and desert biomes, in the zonal scheme, or are in rain shadow during the summer season.

### 5. Biome of the temperate aridiestival evergreen (Mediterranean) forests and shrublands.

This biome lives under Mediterranean climatic conditions (s.l.), and the vegetation is formed by trees, shrubs and scrub with reduced and hard leaves (Tomaselli 1995). This sclerophylly, combined with microphyllly in the leaves and other photosynthetic organs, is an adaptation to survive under the arid conditions of the summer months. There are also an abundance of ephemeral therophytes which present a life cycle adapted to this type of climate.

#### 5.a. Oceanic sclerophyllous-microphyllous evergreen forests and shrublands (Mediterranean s.str.).

The territories which are under oceanic conditions, not distant from the seashores, are those which are considered as genuine Mediterranean. There are five areas in the world which can be included in this subbiome: the Mediterranean coastal countries of Europe, Near East and North Africa, the central and southern Californian area, the central Chilean region, the fynbos in the Cape province of South Africa, and the southwestern Australian territories.

The **Mediterranean Basin** territories extend along the shores of the Mediterranean Sea encompassing relevant areas in southern Europe, from Portugal to Greece, northern Africa (Magrebian countries and Cyrenaica), the Middle East from Anatolia to Siria and Palestine to the Gaza Strip and all the islands within that sea. The territory is covered by sclerophyllous-microphyllous vegetation (Quézel and Barbero 1982) dominated by forests (*Quercus ilex*, *Q. suber*, *Q. calliprinos*, *Pinus halepensis*, *P. pinea*), shrublands (maquis, high matorral; *Quercus coccifera*, *Pistacia lentiscus*, *Rhamnus alaternus*, *Juniperus phoenicea*) and scrub (garigue, low matorral, phrygana; *Rosmarinus officinalis*, *Thymus vulgaris*, *Sarcopoterium spinosum*) having a particular flora with a high endemic component (Quézel 1995).

Central and southwestern **California** is another region where this subbiome can be recognized, having a clear summer drought that is responsible for sclerophyll vegetation types. These forests are usually formed of oak and pine species such as *Quercus agrifolia*, *Q. chrysolepis*, *Q. douglasii*, *Q. dumosa*, *Q. wislizenii*, *Pinus sabiniana* and others, and the shrublands, locally called chaparral, have a high number of species of *Arctostaphylos* (manzanita) and *Ceanothus*, as well as *Adenostoma fasciculatum*, *Rhamnus*

*californica* and others. In this region, fire plays a relevant role in the ecosystem and the chaparral is closely associated with it. The abundance of serpentines shapes a substantial number of vegetation types. In the coastal strip, the sagebush formation with several *Salvia* species is also characteristic (Barbour et al. 2007).

In South America there is a region under similar Mediterranean climatic conditions in **Central Chile**, between 31 and 38°S. In this area thrive evergreen sclerophyllous forests with *Cryptocarya alba*, *Jubaea chilensis*, *Lithraea caustica*, *Peumus boldus* and *Quillaja saponaria*, which are replaced by a shrubland (matorral) when disturbance occurs, with *Adesmia microphylla*, *Bahia ambrosioides*, *Fuchsia lycioides* and other species (Grau 1992).

The small Cape region in **South Africa** is covered with the shrubby evergreen vegetation called fynbos, which is comprised of sclerophyllous small-leaved scrubs of an extremely high variety of species, with high endemism (Mucina and Rutherford 2006). This subbiome is adapted to extremely nutrient-poor soils and to frequent fires. With very few exceptions (*Protea nitida*), all the species of the fynbos are scrubby, many of them belonging to the *Erica* genus, as well as species of *Proteaceae*, *Asteraceae*, *Rhamnaceae*, *Thymleaceae* and *Restionaceae*.

**Southwestern Australia** is another of these “Mediterranean” regions having precipitations concentrated in the winter season and a low continentality (Beard et al 2000). The region stretches along the southern fringe of the continent, occupying the western side of its two main salients, where the main cities of Perth and Adelaide are located. Southwestern Australian flora is extremely rich, with a high number of endemics (Beard 1975; Beard et al. 2000) and forms several types of forests in which *Eucalyptus* species are dominant: *Eucalyptus* (*Corymbia*) *calophylla* (mari), *E. diversicolor* (jarrah), *E. marginata* (karri), and many others. Other outstanding plants are *Anigozanthus manglesii* (kangaroo paw), *Banksia attenuata* or *Xanthorrhoea preissii* (black boy). Additional to forests, there are shrub formations such as that of the *kwongan* (Mucina et al. 2014), rich in endemic species as *Banksia formosa*, *Hakea victoria* etc., and mallee, formed by shrubby eucalypts with many stems arising from a lignotuber (Beadle 1981).

#### 5.b. Continental scrub and woodlands.

Related to the previous subbiome, when continentality increases due to altitude or distance from the oceans and winter temperature descends frequently below zero, sclerophyllous-microphyllous broadleaved woody plants decrease and there is an increase in conifers and deciduous tree species. Conifers belonging to *Juniperus* or *Pinus* genera form a vegetation of open woodland with a scrub covering the floor. There are several regions with this subbiome, all of them in the NH: western United States, Central Asian highlands and the Zagros range, as well as the highlands of the southern Atlas ranges in North Africa. In North America it is represented by the Pinyon-Juniper Woodland (West 1988) with relevant species such as *Juniperus monosperma*, *J. osteosperma*, *Pinus edulis* and *P. monophylla*.

In the central Asiatic areas of this subbiome there are several *Juniperus* species comprising this unit (*J. excelsa*, *J. polycarpus*, *J. seravschanica*, etc.), which often combine with some broadleaved trees such as *Pistacia atlantica* or *Prunus scoparia* and with *Quercus brantii* particularly in the Kurdo-Zagrosian area (Zohary 1973). In central Spain there is a small area that can be attributed to this subbiome with *Juniperus thurifera* as one of the main species (Peinado et al. 2017). In the highlands surrounding the mid elevations of the Atlas ranges, in Morocco and Algeria, continentality increases and woodlands of *Juniperus africana* and *Cupressus atlantica* thrive (Taleb and Fennane 2019; Rivas-Martínez et al. 2020).

#### 5c. Patagonian shrublands.

Due to the coincidence of particular geographic and orographic conditions, this subbiome is only found in the Argentinian Patagonia, on the eastern side of the southern Andean Range. It is a very unique unit from both the climatic and floristic-vegetation point of view. It is a region with pronounced summer aridity due to the rain shadow of the Andes combining with the southern westerlies coming off the Pacific. However, temperatures and precipitations are quite low, but the ombrothermic index (*Io*) is not so low to be considered as a true desert. This results in a cool and dry climate where summer is dry matching the aridiest conditions in the broad sense. Due to the maritime influence, the annual temperature range is low. The vegetation is a grassy shrubland formed by species with clear drought adaptations such as spiny aphyllous or cushion dwarf shrubs. Some species are: *Chuquiraga rosulata*, *C. avellaneda*, *Ephedra ochreatea*, *Grindelia anethifolia*, *G. chilensis*, *Malguraea tridens*, *Larrea ameghinii*, *L. nitida*, *Mulinum spinosum*, *Nardophyllum bryoides*, *Nassauvia glomerulosa*, *Prosopis denudans*, *Prosopidastrium globosum*, *Retanilla patagonica*, etc. Grasses are common, with species such as *Festuca argentina*, *F. pallens*, *Pappostipa humilis*, *Poa alopecurus* etc. There are some species in common with the Central Chilean region, such as *Lycium chilense* or *Mulinum spinosum*, showing the climatic proximity of western Patagonia with central Chile (Cabrera 1971; León et al. 1998; Oyarzábal et al. 2018).

#### BC. Temperate hypercontinental steppe ecozone

Low levels of precipitation throughout the year, accompanied with a high annual temperature variation range (continentality or *BIO7* > 300), produce a type of vegetation often dominated by turf-grasses in which other growth forms are less abundant. The extreme cold of the winter combined with a not so low summer rainfall are the conditions of the steppes persisting in the central areas of the big continents of the NH. In North America, these occupy a vast extension in the center of the continent, where the Rocky Mountains buffer the influence of the Pacific Ocean and are separated from the east coast and the influence of the Atlantic Ocean by the wide rainy regions of the east and the Appalachians.

ans. Though some authors recognise similar biotic units in the SH like the Patagonian steppe and grasslands in South America (Luebert and Plischoff 2022), in our scheme they are not presented at all due to the lower levels of continentality which, we believe, are crucial for their development.

## 6. Biome of the steppe.

The steppes form a zonal biome whose dominant vegetation is made up of grasses and grass-like plants that constitute the dominant element mixed with a large number of herbs and a mixture of chamaephytes. The main climatic characteristic of the steppe is continentality; that is, the high annual temperature range, which implies usually very cold winters. The precipitations are generally moderate or low, taking place mainly in summer; in winter they are scarce and are produced mainly in the form of snow. Usually, the summer coincides with the peak of rains, leading to no or moderate drought in the growing season. Thus, winters are dry and windy, while summers are relatively rainy except in the driest versions in which a certain summer aridity is manifested. Such a climate, a combination of a cold or very cold dry winter and a growing season with sufficient rainfall or moderately dry, cannot support the development of taller and more closed woody vegetation than that of a grassland or dwarf-shrubland (Wesche et al. 2016). These conditions are combined with the frequency of natural fires and the existence of large browsers and wild herbivores, adding difficulties to developing larger woody vegetation (Sims 1988). The soils typically belong to the chernozem type with their thick, blackish surface layers rich in organic matter.

### 6.a. Forest-steppe.

In **Eurasia**, this subbiome covers a large extent between eastern Central Europe and East Asia, occupying an intermediate spatial position between the closed forests (taiga or Temperate nemoral forests) and the treeless steppes, under transitional climatic conditions. It is formed by a typical pattern of mosaic of forest and grassland vegetation (Lavrenko 1970; Erdős et al. 2018). It is under the influence of the huge Mongolian winter anticyclone where high pressures determine low temperatures and precipitations over a vast area across the Central Eurasian area.

The most common trees in this subbiome are those present in the nearby forest areas, such as *Betula pendula*, *B. pubescens*, *Pinus sylvestris*, *Populus tremula*, *Quercus robur*, *Ulmus pumila*, etc. In the eastern territories there are also *Betula platyphylla*, *Larix sibirica* and others. The grasslands are dominated by grasses such as *Festuca valesiaca*, *Koeleria macrantha*, *Stipa capillata*, *S. pennata*, *S. tirsia* and herbs such as *Fragaria viridis* and *Filifolium sibiricum*.

In **North America**, this subbiome can be roughly recognized in the tallgrass prairie that extends in a north-south strip in the eastern side of the biome as a transition to the temperate deciduous forest. Accordingly, this subbiome is moister than the following one, likely enabling it

to bear a tree component. It has a scattered-tree overstory of *Quercus marilandica* and *Q. stellata* with an understorey of *Andropogon gerardii*, *Panicum virgatum*, *Schizachyrium scoparium*, *Sorghastrum nutans*, etc. (Bailey 1998).

### 6.b. Grass-steppe.

When climatic conditions are more extreme, i.e. lower precipitations and colder and longer winters, the trees become scarce, or even disappear, and we have the true grass-steppe which form a grassy treeless landscape. It occupies the temperate areas subjected to higher continentality, both in North America and in Eurasia.

In **central Eurasia** this subbiome covers a large extent between the northern Black Sea and East Asia, in a fringe south to the forest-steppe. The southern fringe of this area usually has a drier climate and a “desert-steppe” is recognized locally. Species are numerous, many of them grasses but also other herbs. We can mention some as *Agropyron cristatum*, *Allium strictum*, *Bothriochloa ischaemum*, *Cleistogenes squarrosa*, *Krascheninnikovia ceratoides*, *Salvia nutans*, *Sisymbrium polymorphum*, *Stipa glareosa*, *S. lessingiana*, *S. zaleskii*, *Veronica spicata*, *Scorzonera austriaca*, etc. (Hurka et al 2019; Liu et al. 2022).

The **North American** grass-steppe zone comprises the so-called “short-grass prairie” and the “mixed-grass prairie” (Sims 1988). It occupies the central-western belt of the prairies in central North America, receiving less precipitations than the forest-steppe. Common grasses in this region include *Andropogon gerardii*, *Bouteloua gracilis*, *Buchloe dactyloides*, *Eragrostis trichodes*, *Panicum virgatum*, *Schizachyrium scoparium*, *Sorghastrum nutans*, *Sporobolus compositus* and others. Although perennial grasses are dominant, forbs supply the majority of the plant diversity: *Amorpha canescens*, *Ambrosia psilostachya*, *Aster ericoides*, *Chenopodium belandieri*, *Echinacea atrorubens*, *Helianthus hirsutus*, *Lesquerella ovalifolia*, *Liatris punctata*, etc.

## C. XEROCRATIC DOMAIN OF THE ARID CLIMATES

The most decisive climatic characteristic of this domain is the extreme aridity, which is mostly due to the predominance of permanent subtropical highs (Logan 1968; Mares 1999). There are areas in which its influence is constant throughout the year and other areas in which there are some short periods in which some irregular rainfall occurs, both in the post-solstice period in the areas surrounding the temperate zone, as in the post-equinox in those closer to the tropical domain. In any case, deserts and semi-deserts occur when the *Io* index is generally lower than 1, with arid and hyper-arid ombrotypes, and vegetation is reduced to only partially cover the ground and very rarely to develop large trees or even shrubs. This formation can receive the names of desert and semi-desert, depending on the coverage and the meaning that these words have in the different languages.

### CA. Deserts and semi-deserts of arid regions ecozone

This is the only ecozone recognized in this domain.

## 7. Biome of the deserts and semi-deserts of arid regions

This is the only biome recognized in this ecozone.

### 7.a. Cold deserts and semi-deserts.

In **central Asia**, there is a vast arid territory from the eastern shores of the Caspian Sea to southern Mongolia and northeastern China, encompassing southern Kazakhstan, vast portions of Uzbekistan and Turkmenistan, Dzungaria as well as the Taklamakan and the Gobi Deserts. Aridity, measured by *Io*, keeps usually below 1 but due to altitude in some areas exceptionally increases near to 2. This huge continuous arid territory is created by the rain decrease due to distance from the oceans and several mountain ranges rising around. It still receives scarce winter and spring precipitations of Atlantic origin in its western part, whereas its eastern part is under the influence of the monsoonal regime, receiving some rains from the Pacific in summer (Walter 1977). These arid areas include many patches of saline soils due to topography and climate, which are populated by a halophytic usually succulent vegetation. Some of the relevant species in these regions are *Artemisia lerchiana*, *A. terrae-albae*, *Potania mongolica* or *Stipa tianshanica* as well as some *Anabasis*, *Zygophyllum* and *Peganum* (Pfadenhauer and Klötzli 2014). In **North America** some areas in the Great Basin Desert in the US can be included in this subbiome, with species such as *Artemisia tridentata*.

### 7.b. Temperate deserts and semi-deserts.

These occur in arid areas in which thermic seasons are clearly distinguished with a winter in contrast to a warm and hot summer.

The deserts and semi-deserts of **western North America** occupy the depression between the Rocky Mountains and the Sierra Nevada-Cascades range, which create a strong rain shadow between them. The Mohave Desert, dominated by *Larrea tridentata* (creosote bush) is included in this category, and in Mexico the Chihuahua desert, confined to the depression between Sierra Madre Occidental and Oriental, penetrating much to the south. In spite of its low latitude, this desert is relatively cool and rainy (*Io* between 1 and 2) due to its high altitude, with elevations mostly between 1100 m and 1500 m. The Neotropical flora is dominant with a high proportion of succulents such as *Agave* (*A. lechuguilla*), *Yucca* (*Y. torreyi*) and cacti species (MacMahon 1988; Rzedowski 2006).

In **Australia** the temperate arid regions extend across the southern half of the central areas of the continent, bearing a semi-desert with a number of shrubby species such as *Acacia aneura* (mulga). There are also several species of spiny grasses of the genera *Triodia* (*T. basedowii* and others) and *Plectrachne schinzii* called spinifex grasses (Walter 1977) as well as *Crotalaria cunninghamii*, *Zygichloa paradoxa* and *Atriplex vesicaria* (Beadle 1981).

In the **Old World**, the temperate deserts have a large representation which includes the northern half of the

**Desert of the Sahara**, the northern part of the **Arabian Peninsula**, **Mesopotamia** with **Iraq**, **Jordan** and **Siria**, as well as central **Iran** and **Afghanistan**, and western **Pakistan**. They are under extremely arid conditions with a marked thermic seasonality and rains falling in winter. Some relevant species are *Aristida acutiflora*, *Calligonum polygonoides*, *C. comosum*, *Zilla spinosa* and *Calotropis procera*, whereas in the western areas close to the Atlantic coasts, *Euphorbia* stem-succulents appear such as *Euphorbia echinus* (Quézel 1965).

In **southwestern Africa** there is an important region of aridity formed by the coastal Namib desert, the Karoo, the Succulent Karoo, Nama-Karoo and the Kalahari towards the inland (Mucina and Rutherford 2006). In general, the aridity is due to the dry air masses provided by the South Atlantic Subtropical High, which is a result of the descending arm of the Hadley cell in that area, in combination with the rain shadow created by the South African Great Escarpment range which dries up the SE humid trade winds from the Indian Ocean. The coastal Namib desert strip is influenced by the Benguela current in which cold waters favour the formation of frequent fogs. These areas are mostly included in the temperate deserts as they are influenced by the cool waters of the Benguela current in the coastal areas and the highlands in inland, which attenuate the high temperatures. The vegetation varies from the coastal desert where *Aloe dichotoma* is found, to the Succulent Karoo with great diversity and abundance of succulent *Aizoaceae* and *Crassulaceae* as well as *Asteraceae* and geophytes. *Acacia mellifera* subsp. *detinens* and *Lycium cinereum* inhabit more in inland districts.

### 7.c. Warm deserts and semi-deserts.

The arid regions within the tropical climatic latitudes, i.e. with a reduced thermic seasons, post equinox precipitations and expanding in lowlands, are included in this subbiome. In **Tropical America** there are two areas in which these deserts can be recognized, the Sonoran desert in North America and the Pacific Coastal Desert in South America. The Sonoran Desert occupies an area south of the Mojave Desert, from southern California and Arizona extending to the Mexican territories of coastal Sonora and most of Baja California. The vegetation is dominated by a high number of cacti as well as some *Fouquieria* (ocotillo) and *Parkinsonia* species (palo verde). The Pacific Coastal Desert occupies a narrow strip between the Andes range and the Pacific shores, from northern Peru to mid Chile spanning between 6° and 27°S latitude. This arid strip is a result of the rain shadow created by the high Andes against the southeastern trade winds, which is enhanced by the cold waters of the Humboldt stream. The vegetation is very sparse and there are communities of *Tillandsia* which survive by taking the humidity from the frequent coastal fogs (garúas), and some cacti (*Neoraimondia*, *Armatocereus*, etc.) in inland sectors (Galán de Mera 2004; Galán de Mera et al. 2009).

The **southern Sahara** desert is continued in the Arabian Peninsula and southern **Iran** and **Pakistan** until

the **Indian Sind-Thar**. This vast strip is under tropical climatic influence and the rainfalls occur in the summer months. Some species of this territory are *Acacia senegal*, *Aristida pungens*, *Cornulaca monacantha*, *Indigofera oblongifolia* or *Neurada procumbens* (Quézel 1965) as well as *Euphorbia caducifolia* and *Prosopis cineraria* in the eastern stretches (Enright et al. 2005).

The northern section of the western **South African** deserts, in the coastal regions of northern Namibia up to southern Angola, can be included in the category of the warm deserts. It is well known that *Welwitschia mirabilis* is a remarkable element in the flora of this area.

The **tropical Australian desert** occupies the northern fringe of the arid region of the continent where the rainfalls are received predominantly in summer (Beadle 1981). Some species are several mallee form eucalypts including *Eucalyptus brevifolia*, *E. microtheca* or *E. odontocarpa* as well as *Acacia shirleyi*, *A. pachycarpa*, shrubs like *Hakea subarea* and spinifex grasses such as *Triodia pungens* or *T. wiseana* among others (Beard 1990).

#### D. THERMOCRATIC DOMAIN OF THE WARM CLIMATES

This domain is extended through the lowland areas spanning approximately between both tropics, receiving the maximal amount of solar radiation and having a positive radiative balance. Thus, *Pt* is usually over 2000 units. Thermic seasons are not distinguishable in this tropical zone because the solar radiation falls on the earth almost vertically all year round, and there are at least two days each year in which the sun rays are perpendicular to the ground. Seasonality, when it exists, is due to yearly rainfall distribution. Precipitations can be continuous all year in the areas influenced by the ITCZ, or seasonal in the areas more separated from the lowest latitudes and subject to a monsoonal regime. In the last case, the rain season occurs in the "summer" (post-summer equinox) months. Vegetation is adapted to these thermic and pluviometric circumstances and phenology does not follow the mandatory concentration of flower and fruit production of the temperate world but only the rain seasonal regime.

Mountains rising within this tropical zone reproduce tropical versions of the biomes of the mesocratic and cryocratic domains in their vegetation belts, which are formed partially by local lineages combined with others migrated from higher latitudes in different climatic episodes. In our classification, these mountain formations will be explained within the biomes of the mesocratic and cryocratic domains as the lower temperatures of the higher elevations determine substantial convergences with them in terms of climate, growth forms and often biogeographical relationships. Thus, we will consider warm (tropical) biomes *stricto sensu* to those of the lowlands up to 1000–1500 m asl (infra and thermo).

#### DA. Tropical pluviseasonal ecozone

As indicated above, in the intertropical latitudes the major part of the rainfalls occur in the post-summer equinox (summer) months and if this entails a wet and a dry season, so we will find an important set of adaptations to the

drought. In many areas trees and shrubs become deciduous or semideciduous to prevent water loss. Woody plants often become spiny to prevent herbivory and the woody formations adopt a low density leaving room for many other smaller plants, like grasses and shrubs. Sclerophylly and evergreenness appears when soils are poor in nutrients.

#### 8. Biome of the tropical pluviseasonal forests and woodlands.

In general, the vegetation is adapted to pluvial seasonality and in the dry season there is a complete or partial shedding of the leaves. In some areas where soils are very poor, woody plants become sclerophyllous and evergreen, as in the Brazilian *cerrado* (Rizzini 1997) or the north of Australia (Beadle 1981). Within this biome are included the savannas (from *çabana*, a term taken from the taino natives of the island of Hispaniola and incorporated to the Spanish language; Oviedo 1535) meaning that the vegetation is formed by sparse trees including a substantial proportion of grasses.

##### 8.a. Tropical xeric woodlands and shrublands

This subbiome represents the transition from the warm desert (7.c) to the pluviseasonal areas with a longer rainy season and abundant precipitations, which in many cases follows a flat gradient which leaves substantial areas of dubious qualification. The seasonality of the precipitation becomes strongly unbalanced in favor of the dry season, which covers over 8 months of the year and with mostly arid and sub-arid ombrotypes. This results in a shrubby and spiny vegetation, often with many succulents.

In Africa, it is greatly extended in the Sahel, between Senegal and Sudan, in the **western African Horn** (Somalia and Masai areas) and in the transitional areas to the deserts of the southern part of the continent.

In the vast territories of the **Sahel** the vegetation comprises thorny shrubs or trees, mainly acacias, such as *Acacia nilotica*, *A. tortilis*, *Senegalia laeta* and *S. senegal*. Other tree species are *Balanites aegyptiaca*, *Boscia senegalensis*, *Commiphora africana* or *Faidherbia albida*. The grass layer is formed by annuals such as *Aristida stipoides*, *Cenchrus biflorus*, *Panicum turgidum* and *Schoenefeldia gracilis*, which dry up in the dry season when the trees and shrubs shed their leaves (Quézel 1965).

In the **southern African** territories covered by this subbiome, *Acacia erioloba*, *Colophospermum mopane* and *Terminalia sericea* with grasses of *Aristida*, *Eragrostis* or *Panicum*, are frequent (Mucina and Rutherford 2006).

In **tropical America**, it is dominant in the southern Chaco and Monte in Argentina and nerby countries, the Guajira in Venezuela and the Caatinga in Brazil. The **Guajira-Maracaibo** in northern Venezuela and Colombia occupies an area around the gulf of Maracaibo, with some relevant species including *Castela erecta*, *Cercidium praecox*, *Cesalpinia coriaria*, *Gyrocarpus americanus*, *Haematoxylon brasiletto*, *Myrospermum frutescens*, *Prosopis juliflora* and the cacti *Acanthocereus columbianus*,

*Cephalocereus russelianus* and *Ritterocereus griseus* (Mares 1999; Josse 2014; Morrone 2017; Navarro-Sánchez and Molina-Abril 2021).

Northeastern Brazil is occupied by the **caatinga**, a dry deciduous spiny vegetation rich in legumes with species such as *Auxemma onocalyx*, *Caryocar cuneatum*, *Caesalpinia bracteosa*, *Maytenus rigida*, *Mimosa caesalpiniiifolia*, *Piptadenia viridifolia*, *Ziziphus joazeiro* and others (Rizzini 1997).

In **India**, this subbiome ranges over a large area around the west of the Deccan plateau, including east of Rajasthan, south-west Punjab, Haryana, Gujarat and parts of Uttar Pradesh, Madhya Pradesh, Maharashtra, Telangana and Andhra Pradesh. The species of Indian distribution such as *Acacia planiformis* or *Azadirachta indica*, mix with others of broader range within this subbiome including *Acacia nilotica*, *Butea monosperma* or *Prosopis cineraria* (Greller et al. 2016).

In **Australia**, the distribution of the subbiome occupies a strip in the central northern regions, between the pluviaseasonal forest and the warm desert (Beard 1990). It occupies vast portions in north Western Australia, southern sections of the Northern Territory and southwest of Queensland. Some of the common woody species are *Acacia aneura*, *A. estrophiolata* and *A. kempeana*.

#### 8.b. Tropical pluviaseasonal forests

This subbiome corresponds to the mesic version of the biome and is formed basically by tree-dominated vegetation, often with a grassy (savanna) or scrubby understorey. Climatic conditions entail a dry season between 1–2 to 6–7 months, where double temperatures are higher than precipitation.

In **tropical Asia and Malesia**, the vast areas occupying most of the Indian subcontinent, as well as territories in Indochina and Malesia, are subjected to a tropical climate with a dry season, and a deciduous forest develops which corresponds to this biome. In it species such as *Anisoptera thurifera*, *Anogeissus latifolia*, *Areca catechu*, *Azadirachta indica*, *Bombax ceiba*, *Butea monosperma*, *Dalbergia sissoo*, *Diospyros melanoxylon*, *Ficus religiosa*, *Garuga floribunda*, *Haldina cordifolia*, *Intsia bijuga*, *Madhuca longifolia*, *Phyllanthus emblica*, *Protium macgregorii*, *Pterocarpus indicus*, *Schleichera oleosa*, *Senegalia catechu*, *Shorea robusta*, *Tectona grandis* and others can be found (Paijmans 1976).

In **tropical America**, this biome is widely represented all over the continent, from Mexico to the south American Paraná-Paraguay river basin, encompassing a range of more humid to more xeric variants. There are a couple of well defined regions which are occupied by this biome in their particular versions: In **Mesoamerica** (southern Mexico and Central America, as well as in the Caribbean islands), there are important areas occupied by this biome, particularly on the Pacific side, with deciduous trees such as *Swietenia humilis*, *Bombacopsis quinatum*, *Cedrela fissilis*, *C. mexicana*, *C. odorata*, *C. salvadorensis*, *Ceiba aesculifolia*, *Dalbergia retusa*; many legumes in-

cluding *Enterolobium cyclocarpum*, *Hymenaea courbaril*, *Cassia grandis*, *Platymiscium dimorphandrum*, *Samanea saman*; and the palms *Acrocomia aculeata*, *A. crispa*, etc. and succulents (*Cactaceae* and *Agavaceae*) (Miranda and Hernández 1963; Vargas Ulate 1997; Rzedowski 2006).

The area of the Orinoco watershed shared by Colombia and Venezuela, known as the **Llanos**, is a flat region which is influenced by extensive floods (Pantanal). In the non flooded areas a woody vegetation of evergreen semideciduous trees is established, with tropical American species such as *Bowdichia virgilioides*, *Brysonima crassifolia* or *Curatella americana*, which combine with other endemics such as *Borreria aristeguietana*, *Duguetia riberensis* or *Randia venezuelensis* (Galán de Mera et al. 2006).

The Brazilian **cerrado** occurs widely across central Brazil (Rizzini 1997) and western Bolivia, where it forms a mosaic with the Bosque Chiquitano (Chiquitania; Navarro-Sánchez 2011). It encompasses a more or less open woodland with sclerophyllous evergreen or semideciduous shrubs and trees such as *Aspidosperma tomentosum*, *Cavanillesia umbellata*, *Licania sclerophylla*, *Palicourea rigida*, *Qualea parviflora*, *Schinopsis brasiliensis*, *Terminalia actinophylla*, *Vochysia elliptica*, *V. thyrsoidea*, and many others, accompanied by dwarf palms of the genus *Allagoptera* and herbs such as several species of *Paepalanthus* with tropical grasses such as *Axonopus aureus*, *Trachypogon spicatus* which form a dense and continuous herb layer. The cerrado grows on siliceous poor substrata rich in free aluminium, being the sclerophyll-evergreenness of the woody plants an adaptation to these harsh edaphic conditions. Where substrates change to base-rich, the forests become deciduous.

The **Chaco** is a vast region extending along the plain east of the central Andes through southwestern Brazil, most of Bolivia and Paraguay and northern Argentina. It is occupied by a deciduous forest in which occur species such as *Aspidosperma quebracho-blanco*, *Ceiba speciosa*, *Piptadeniopsis lomentifera*, *Prosopis ruscifolia*, *Schinopsis balansae*, *S. cornuta*, *Sideroxylon obtusifolium*, *Ziziphus mistol* and others, with some grasses such as *Cenchrus pilcomayensis* and *Elionorus muticus* (Oyarzábal et al. 2018; Navarro-Sánchez et al. 2006).

In **tropical Africa** this subbiome occupies its largest extent, surrounding the tropical rain forest biome area and constrained by the 8.a subbiome (White 1983). It encompasses the vast territories of central, east and south Africa (Sudano-Zambesian territories) and most of Madagascar, which are covered by several forms of this subbiome, with trees of genera such as *Adansonia*, *Brachystegia* (miombo), *Combretum*, etc. and several *Bombacaceae*. Some frequent woody species are *Boscia angustifolia*, *Cussonia arborea*, *Daniellia oliveri*, *Erythrina abyssinica*, *Pterocarpus angolensis*, *Vachellia nilotica* or the palm *Borassus aethiopum*, while grasses of the genera *Hyparrhenia*, *Heteropogon* and *Anropogon* are frequent in the herb layer. In Madagascar, this subbiome occupies the entire central and western side of the island and there are many endemics in it, such as *Adansonia rubostipa*, *A. za*, *Givotia madagascariensis* or *Stereospermum euphorioides*.

In **Australia** this subbiome occupies a vast area encompassing the northernmost regions of the Continent such as the Kimberly Plateau, the area of Darwin and the Carpentaria Plains (south of the Gulf of the same name), most of the Cape York peninsula and other areas in the northeast. It occupies the landscapes between the shores of the Timor and Arafura seas and the xeric inland regions of the continent. The vegetation is dominated by woodlands formed by evergreen and hard-leaved eucalypts. This sclerophyllous evergreen life form is consistent with the poverty of the soils widespread on the Australian continent. Some important trees are *Acacia shyrleyi*, *Corymbia confertiflora*, *C. grandifolia*, *C. polycarpa*, *Eucalyptus brevifolia*, *E. dichromophloia*, *E. grandifolia*, *E. miniata*, *E. phoenicea*, *E. pruinosa*, *E. tectifera*, *E. tetradonta*, etc. Some other woody plants are *Acacia humifusa*, *A. mountfordiae*, *Hakea arborescens*, *Grevillea pteridifolia* or *Lysiphyllum cunninghamii* (Beadle 1981).

## DB. Tropical pluvial ecozone

In the tropical areas where rainfall persists all year round (Rainfall seasonality BIO15 < 60) in a sufficient intensity and frequency so that no or a very brief (1 month) dry season can be recognized, the tropical pluvial ecozone is established. Temperatures are high and present low daily and yearly oscillations, and precipitations rarely fall below 2000 mm per year and occur usually at zenital showers in the afternoon. The soils undergo an intense leaching leading to the formation of laterites.

## 9. Biome of the tropical rain forests.

This biome occurs where the tropical warm and moist forest thrives, usually called tropical rainforest or pluviisilva. It has a high number of vascular plant species, including trees, which bear particular adaptations to this favorable environment: thin barks, leaves with entire margins, guttation organs and other well documented features of this tropical rainforest (Schroeder 1998; Primack and Corlett 2011; Pfadenhauer and Klötzli 2014).

### 9.a Tropical rain forests

This is the only subbiome recognized within this biome.

In Tropical America, there are several areas occupied by this biome-subbiome:

In **Central- and Mesoamerica**, this biome-subbiome develops mostly in the Caribbean side, occupying the entire isthmus of Panamá and peripheral areas in the Antilles, including the southern half of the Florida peninsula.

The most important area is the vast **Amazonian plain** (the *hylea amazonica* of Humboldt and Bonpland 1805) which spans from the high Orinoco and the Guianas to the central regions of Brazil, southern Colombia, western Ecuador and Perú and northwestern Bolivia, i.e. all the area between the Atlantic coast and the Andean piedmonts, constrained by the drier regions to the north and the south. The vegetation is dominated by dense forests very rich in species

of plants, with many epiphytes and lianas, hosting most of the representatives of the genus *Hevea* (Rizzini 1997). Noteworthy is the high number of ant-pollinated species (myrmecophyllous) and the large extent of flooded areas by the regular oscillations in the level of water characteristic of the Amazonian drainage network. Among the overwhelming richness of the Amazonian tree flora, we can mention *Bertholletia excelsa*, *Calophyllum brasiliense*, *Caraipa grandifolia*, *Caryocar villosum*, *Clarisia racemosa*, *Clathrotropis macrocarpa*, *Clusia spathulifolia*, *Euterpe precatoria*, *Hevea brasiliensis*, *Hyeronima oblonga*, *Pterocarpus amazonum*, *Taralea oppositifolia* and many others (Josse 2014).

Another characteristic region is the **Darién-Chocó** in the Pacific coastal strip from southern Panamá to Colombia and Ecuador, which receives abundant precipitations from the east. The tropical rain forest of this area has many endemics and there are species such as *Billia columbiana*, *Exarata chocoensis*, *Guettarda crispiflora* subsp. *sabiceoides*, *Humiriastrum procerum*, *Virola dixonii* and others (Rangel 1997).

The low altitudes of the Atlantic coastal fringe of Brazil, spanning between Bahia and Santa Catarina are covered by this biome-subbiome. It is represented by the **Mata Atlântica** or **Floresta Atlântica**, a highly diverse tropical forest maintained by the moist trade winds of the south Atlantic, which provide abundant rainfall all year. Due to the higher latitudes and elevations in the mountains of the coastal range, the thermic regime has lower temperatures than in the Amazonian river basin. The natural forest is extremely rich in species, particularly epiphytes with many bromeliads, making each tree resemble a true garden in miniature (Rizzini 1997). Among the trees we can mention *Alseis involute*, *Astrocaryum aculeatum*, *Caryocar edule*, *Cordia taguahyensis*, *Ficus gomelleira*, *Lecitis pisonis*, *Licania salzmanii*, *Tabebuia obtusifolia*, *Virola oleifera*, etc., many of them growing also in the Amazonian river basin.

The **Guineo-Congolian** region is the most important of tropical Africa, encompassing the coastal strip of the gulf of Guinea from Sierra Leone to Nigeria and entering deep into the African continent in the Congo watershed until the chain of mountains and lakes crossing east Africa, including large parts of Cameroon, Gabon and Equatorial Guinea (White 1983). Some near-endemic species are *Azelia bipindensis*, *Pouteria altissima*, *Diospyros gabonensis*, *Garcinia punctata*, *Sterculia tragacantha*, *Syzygium owariense*, *Trichilia prieuriana* or *Xylopia aethiopica* (Sayer et al. 1992).

The **Madagascar** eastern coast is homologous to the Mata Atlântica region of Brazil. The flora is mainly African with a high number of endemics, among them *Ravenala madagascariensis*. (Moat and Smith 2007).

The **Indo-Malesian** region is a large territory encompassing south China, the Philippines, the islands of Malaysia (Java, Sumatra, Borneo, Celebes, Moluccas, etc.), the peninsula of Malacca, parts of Indochina and the gulf of Bengal to the piedmonts of the eastern Himalayas. For Malesia we can mention some species such as *Artocarpus elasticus*, *Macaranga hispida*, *Nephelium lappaceum*,

*Palaquium rostratum*, *Platea excelsa*, *Prunus arborea*, *Shorea leprosula*, *Trevesia sundaica* etc. (Edwards et al. 1990; Kitayama 1992).

The **Malabar-Ceylon** region lies along the southwestern coast of the Indian subcontinent, at the piedmonts of the Gaths range and the western half of the Sri Lanka (Ceylon) island.

The **Pacific Oceanic** region encompass the numerous islands widespread over the Pacific Ocean. The flora and vegetation of this immense number of islands is full of endemic species having originated from neighbouring continental Gondwanic islands (basically New Zealand and New Caledonia) and from tropical East Asia across the Malesian archipelagos. There are representatives of gymnosperms of the genera *Agathis*, *Dacrydium* or *Podocarpus* and some species of a more general distribution are *Calophyllum neoebudicum*, *Canarium vitiense*, several species of *Metrosideros* such as *M. collina*, among many others (Mueller-Dombois and Fosberg 1998).

The **Papuan-Australian** region includes the island of New Guinea and the northeastern extreme of the Australian continent. In Australia only a narrow area in Queensland can be assigned to this biome, in the eastern coastal strip of the **Cape York Peninsula**, bearing similarities with the near island of New Guinea. Some species are *Agathis microstachya*, *Balanophora fungosa*, *Balanops australiana*, *Cordyline canniifolia*, *Macaranga inamoena*, *Musa banksia*, *Pandanus monticola*, *Syzygium wilsonii* and others (Beadle 1981).

## Results and discussion

In this section, we will provide comment on the climatic characterization of the considered biotic units (domains, ecozones, biomes and subbiomes) by means of data from the 616 selected locations.

### Ordination diagrams

PCA ordination was performed for the selected locations and plotted along axis 1 and 2, which encompasses most of the variability of the data (40.1% for axis 1 and 29.7% for axis 2, Figure 14). Axis 1 relates to pluviometric parameters whereas axis 2 refers to thermometric ones. The PCA of Figure 15 shows the distribution of the domains, showing clear separation among them. In Figure 16, there are represented the biomes and subbiomes in the same PCA. The xerocratic (biome7), cryocratic (1 and 2) and thermocratic biomes (8 and 9) separate clearly to the periphery of the diagram whereas the mesocratic ones (3, 4, 5 and 6) overlap in the central area. We can focus on the subbiomes of the A domain (Cryocratic) in Figure 16A: 1.a (Tundra), 1.b (temperate cryoro tundra) and 1.c (tropical cryoro tundra) and the subbiomes 2.a (boreal forest) and 2.b (temperate oro forest). We see that those of biome 1 overlaps to a large extent, reaching 1.b relatively to dry positions and 1.c relatively to warm and humid ones, as can be expected for tropical

high mountains. Units 2.a and 2.b intermingle with those of biome 1 as they are subject to very low temperatures in the winter, even lower than those of 1.c. Unit 2.b (temperate oro forest) has a warmer position than 2.a because the coldest areas are in the high latitude regions suffer a very cold winter. The high mountain variants of the biomes of these cryocratic domains, i.e. 1.b, 1.c and 2.b, overlap with the mesocratic domain biomes, particularly with the steppic biome (6) due to the low temperatures they have in common.

In domain B, biome 4 occupies a central position (Figure 16B) and 4.a (lowland lauroid forest) and 4.b (coastal NW North American conifer forest) overlap to a great extent showing their strong climatic coincidence, while 4.c of the tropical and subtropical mountains occupies also some warmer and moister areas. Biome 5 of temperate arid/semi-arid ecosystems, is split into 5.a (sclerophyllous-microphyllous Mediterranean), 5.b (continental scrub and woodland) in colder positions and 5.c (Patagonian shrubland) in between. Steppic subbiomes 6.a and 6.b separate quite clearly.

In Figure 16C, the subbiomes of domain C are shown, with the subbiomes 7.a (cold deserts), 7.b (temperate deserts) and 7.c (warm deserts) separated along axis 2 following a temperature gradient.

In Figure 16D, the distribution of biomes of domain D, subbiomes 8.a (tropical xeric), 8.b (tropical pluviseasonal) and 9.a (tropical pluvial) clearly separate along the precipitation gradient.

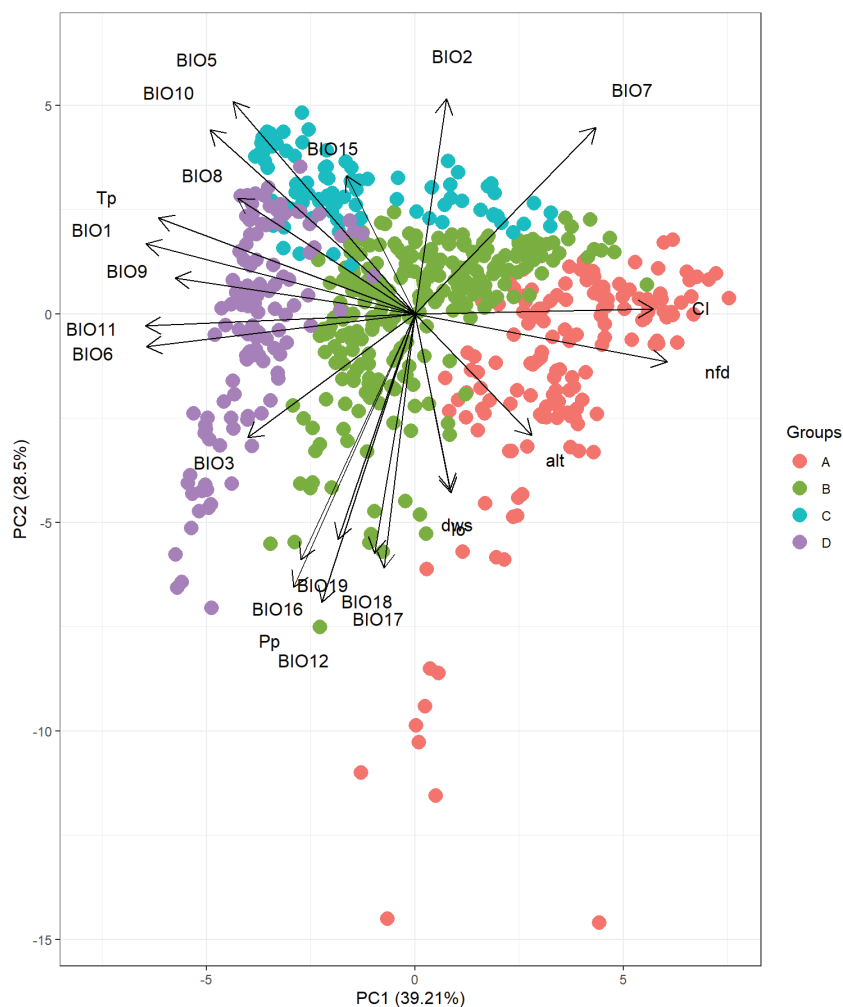
### Boxplots

In this section, the climatic parameters used for the PCA are examined separately in order to see the differences between the domains, ecozones, biomes and subbiomes (boxplots available in Suppl. material 4). The following comments will focus on the domains, biomes and subbiomes only.

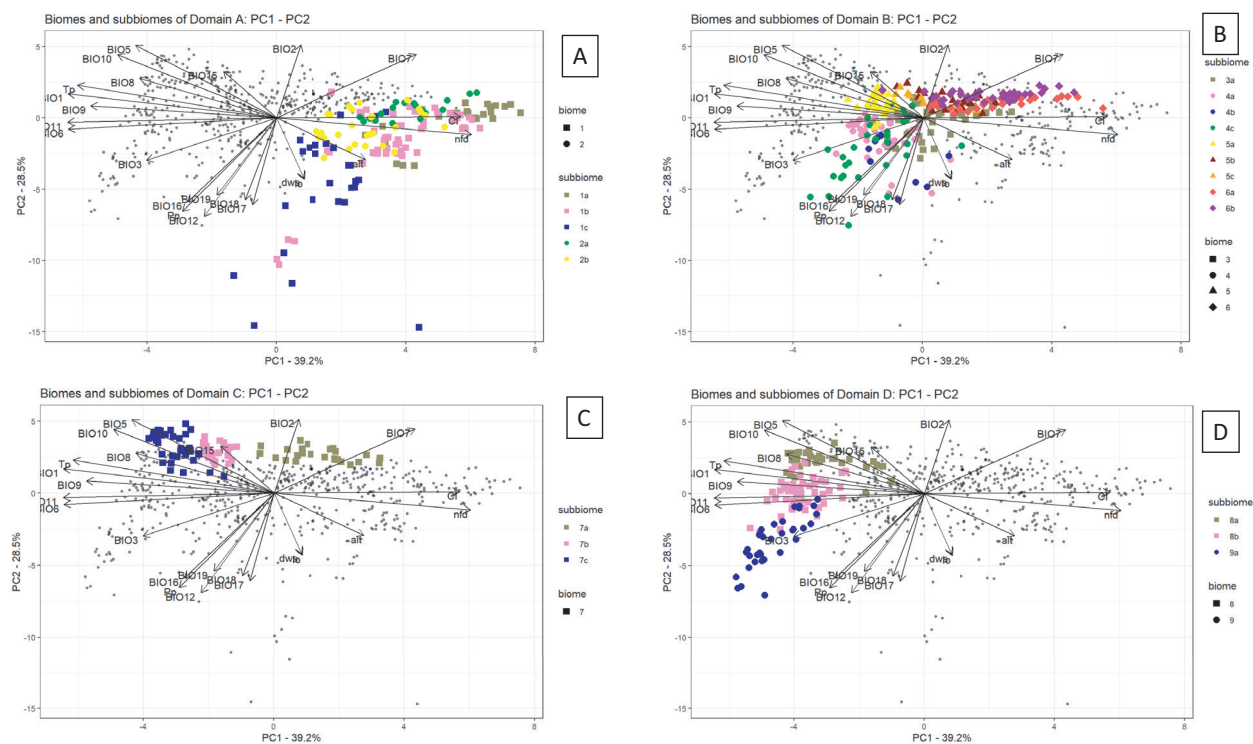
Concerning the domains, the thermometric parameters indicate a clear separation of the four domains in terms of mean annual temperature (BIO1, 6, 8, 9, 10, 11, *CI*, *nfd*, *tp*) and of isothermality (BIO3). The summer warmth intensity (BIO5) separates also the four domains with a clear increase in the case of the xerocratic deserts and arid areas. The temperature annual range (BIO7) in these large units only separates the thermocratic domain which have the lowest scores. The pluviometric parameters (BIO12, 13, 14, 16, 17, 18, *Io*, *Pp*) separate clearly the xerocratic domain from the other three. Other parameters (BIO15) are not discriminated at this level.

At the biome level, thermometric parameters (BIO1, 6, 8, 9, 10, 11, *CI*, *nfd*, *tp*), separate along a gradient from the colder ones to the warmest, but the steppes (6) fall down almost to the level of the boreal cold forest (2). The mean diurnal range (BIO2) also reveals high scores for the steppes and the lowest in the tropical rain forest (9), quite opposite to isothermality (BIO3). The summer warmth intensity is maximal in deserts and minimal in the tundra





**Figure 15.** PCA of 610 plots separating the four domains: A Cryocratic; B Mesocratic; C Xerocratic; D Thermocratic.



**Figure 16.** PCA with each of the four domains biomes and subbiomes highlighted.

continental temperate aridiestival subbiome (5.b). The degree of summer warmth is measured by BIO5 reaching the maximal values in the temperate and warm deserts (7.b and 7.c), and in the tropical xeric shrublands and woodlands (8.a), reflecting also the cooling effect of altitude (1.c and 2.b). The cold of the winter reflects a similar general pattern but the steppes (6.a and 6.b) as well as the cold deserts (7.a) are subjected to very cold winters. In particular, cold deserts (7.a) are separated from the other arid regions by their higher temperature seasonality with a very cold winter (BIO7, 11, *nfd*) and a substantially lower thermal regime (BIO1, 6, *Tp*). If we compare the temperatures of the wettest quarter (BIO8) with those of the drier one (BIO9), it is revealed that the arctic tundra (1.a), the boreal forest biome (2) and the steppic biome (6) undergo very low temperatures in their dry season, but are much milder in the wet season. A comparison of the temperatures of the warmest quarter (BIO10) with those of the coldest quarter (BIO11) again reveals the low values of the cold period in the steppes (6) and in the cold desert (7.a). The tropical cryoro tundra shows high stability in comparison with the other two tundra subbiomes (1.a and 1.b).

Pluviometric values are represented in BIO12, where the deserts (7.a, 7.b and 7.c) are the driest, followed by the Patagonian shrubland (5.c). On the opposite side, the tropical rain forest (9.a), the tropical cryoro tundras (1.c), the tropical montane forests (4.b) and the conifer coastal forest (4.c) receive the highest amount of precipitation, and these results are similar to those of *Pp*. Comparing the precipitation in the driest (BIO17) and the wettest (BIO16) month and quarter reveals that the difference between them is higher in the tropical cryoro tundra (1.c), in the tropical montane forests (4.b) and in the tropical pluviseasonal biome (8), where the wet season receives more rain. Precipitation seasonality (BIO15) is highest in the warm desert (7.c) and in the tropical pluviseasonal biome (8), being low in the Patagonian shrubland (5.c). The precipitation in the warmest quarter (BIO18), as an estimation of the intensity of the seasonal drought, is highest in the deserts (7) but also remarkable in the temperate aridiestival (Mediterranean s.l.) biome (5). Precipitation in the coldest quarter (BIO19) shows high scores for the tropical montane forests (4.b).

Other indices have also been used for the analysis. The *CI* (Kira's cold index) basically reproduces the pattern shown by BIO6 and BIO11 in relation to the temperatures of the coldest period.

The drought of the warm season (*dws*) distinguishes clearly the deserts (7.a, 7.b and 7.c) in a comparable position to the temperate aridiestival biome (5.a, 5.b and 5.c), highlighting the summer drought of the latter.

*Io* is a strong indicator of aridity in the xerocratic biomes (7), in the grass-steppe (6b), the Patagonian shrubland (5c), the tropical xeric shrublands and woodlands (8a), the temperate deciduous forests (3), and in the continental temperate aridiestival biome (5.b). Opposite to it, the tundra biome (1) and the tropical montane cloud lauroid and conifer evergreen forest (4c) reach the highest

values. Figure 13 shows this parameter across the world in combination with subbiome boundaries.

## Conclusions

Despite the great floristic diversity that exists across the different regions of the planet, a comprehensive bioclimatic scheme is presented for all the world's vegetation, which has been categorized into a small number of units with their distributions explained by climatic factors. The most notable conclusions that can be drawn from the application of this system can be summarized as follows:

1. There is homology between the latitudinal and altitudinal zoning of the ecosystems through this biome system.
2. There is asymmetry between the two hemispheres: Biomes 2 and 3 are overwhelmingly more abundant and diverse in the NH and biome 6 and subbiome 5.b are exclusive of it. This is a consequence of its higher continentality in the more extensive land masses covering extratropical latitudes. Conversely, biome 4 is more widely distributed in the SH.
3. There is asymmetry in the occurrence and latitudinal distribution of biomes along the continental masses: the western sides of continents are subjected to drought caused by subtropical high pressure systems determining the existence of biomes 7 and 5, which are lacking in the eastern sides. These biomes associated with aridity expand inland in the case of Eurasia due to the enormity of that continent.
4. For the climatic characterization of zonal biotic units, large sets of climatic parameters such as that provided by CHELSA should be used.
5. The climatic characterization does not provide sharp boundaries, as can be expected due to the transitional nature of the biotic units.

## Data availability

Used data are available in the Suppl. material 1–4.

## Author contributions

J.L. planned the survey, conducted the analysis and wrote the manuscript, G.N.-S. provided information on the tropical world, his vision on the typology in South America and revised the manuscript, D.V. performed all analyses, prepared the figures, provided his insight and knowledge on the steppes, and revised the manuscript.

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## Supplementary material

### Supplementary material 1

**table with the climatic data of the 616 selected locations.**

Link: <https://doi.org/10.3897/VCS.86102.suppl1>

### Supplementary material 2

**Climatic diagrams of the 616 selected locations.**

Link: <https://doi.org/10.3897/VCS.86102.suppl2>

### Supplementary material 3

**Supplementary maps and figures. S3.1 Importance of the selected variables in the PCA ordination axis 1 vs. 3; S3.2. Biomes and Subbiomes of Africa S3.3. Biomes and Subbiomes of Asia; S3.4. Biomes and Subbiomes of Australasia; S3.5. Biomes and Subbiomes of Europe S3.6. Biomes and Subbiomes of North America; S3.7. Biomes and Subbiomes of South America; S3.8. World distribution of ombrotypes; S3.9. World distribution of Io.**

Link: <https://doi.org/10.3897/VCS.86102.suppl3>

### Supplementary material 4

**Boxplots of the selected parameters for the domains, ecozones, biomes and subbiomes.**

Link: <https://doi.org/10.3897/VCS.86102.suppl4>