

# The Temperate Deciduous Forests of the Northern Hemisphere. A review

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**Abstract.** Temperate Deciduous Forests occur almost exclusively in the northern hemisphere and thrive under temperate climate with cold winter and warm-humid summer. They covered a continuous belt during most of the Tertiary across the continent Laurasia occupying a large area in higher latitudes. With the cooling of the Earth's climate and the appearance of the subtropical aridity areas, in combination with the separation of North America from Eurasia, this continuous area split into the three mainly existing now: Eastern North America, Western Eurasia and Eastern Asia. The tree flora reveals the common origin of the three current areas and the events causing more or less severe extinctions during the cold periods of the Pleistocene, in combination with the mountain uplift did happen since the Miocene affected differently to them. The basic features of the deciduous trait and its likely origin are discussed, as well as the ecologic implications of such a trait. For further research, the current possibilities provided by available vegetation datasets (EVA, sPlot) opens the possibility of using a large mass of vegetation plots data involving most of the vascular flora of these forests to find out insights about their origin and evolution over time as well as their links with current or past environmental conditions.

**Keywords:** Temperate forest biota, deciduousness, Arcto-Tertiary flora, evergreenness, Western Eurasia, Eastern North America, Eastern Asia.

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## 1. Introduction, the weight of history in the current state of temperate deciduous forest biotas and floras

Temperate Deciduous Forests (hereafter TDFs) are one of the most representative forest types of the Northern Hemisphere (hereafter NH), and one of the most characteristic in the mid-latitudes (Rübel, 1930; Pfadenheuer & Klötzli, 2014; Walter, 1985). They thrive under temperate climate (i.e., summer moist and pronounced seasonality with a cool to cold winter). There are three main areas in which they are the dominant forest type: Eastern North America (ENA), Eastern Asia (EA) and Western Eurasia (WEA). In the Southern Hemisphere, a smaller representation is found in the southern Andes and Tasmania (Figure 1a). All the NH TDFs areas present a common origin in paleo-historical terms, supported by the extant and fossil tree flora of both continents, as they dominated mid and high latitudes in early- to mid-Tertiary, forming a broad continuous belt that encompassed the entire Laurasia continent (Axelrod, 1983; Xing *et al.*, 2015). That area fragmented later due to late Tertiary and Pleistocene climatic oscillations (Wolfe, 1978) and continental drift, which, combined with decreasing global temperatures, ultimately resulted in the three large areas in which TDFs today occupy

a dominant position. The fact that most the tree genera are common to all three areas, either today or in the fossil record, makes it generally accepted that these areas have a common history of evolution and adaptation.

Temperate deciduous forests of the northern hemisphere (TDFNH) provide an opportunity to examine the extent to which physical events and biotic circumstances influence the current state of ecosystems and biodiversity in large regions or continents in comparison with historical drivers. As stated by Ricklefs & Latham (1999) and Latham & Ricklefs (1993a), this case is appropriate to test whether historical reasons are sufficient to explain the observed differences among continents and regions or whether physiographic differences alone are sufficient (Qian & Ricklefs, 2004).

We aim to illustrate one of the widely recognized biomes of the world by means of its main vegetation type, in order scientific community can reach to an agreement on its definition and concept for consistent use and provide a framework in which comparative research can be carried out, and their results can be compared. We describe the main features of this biome, summarize its origin and historical development, and propose some questions that could be addressed in future investigations.

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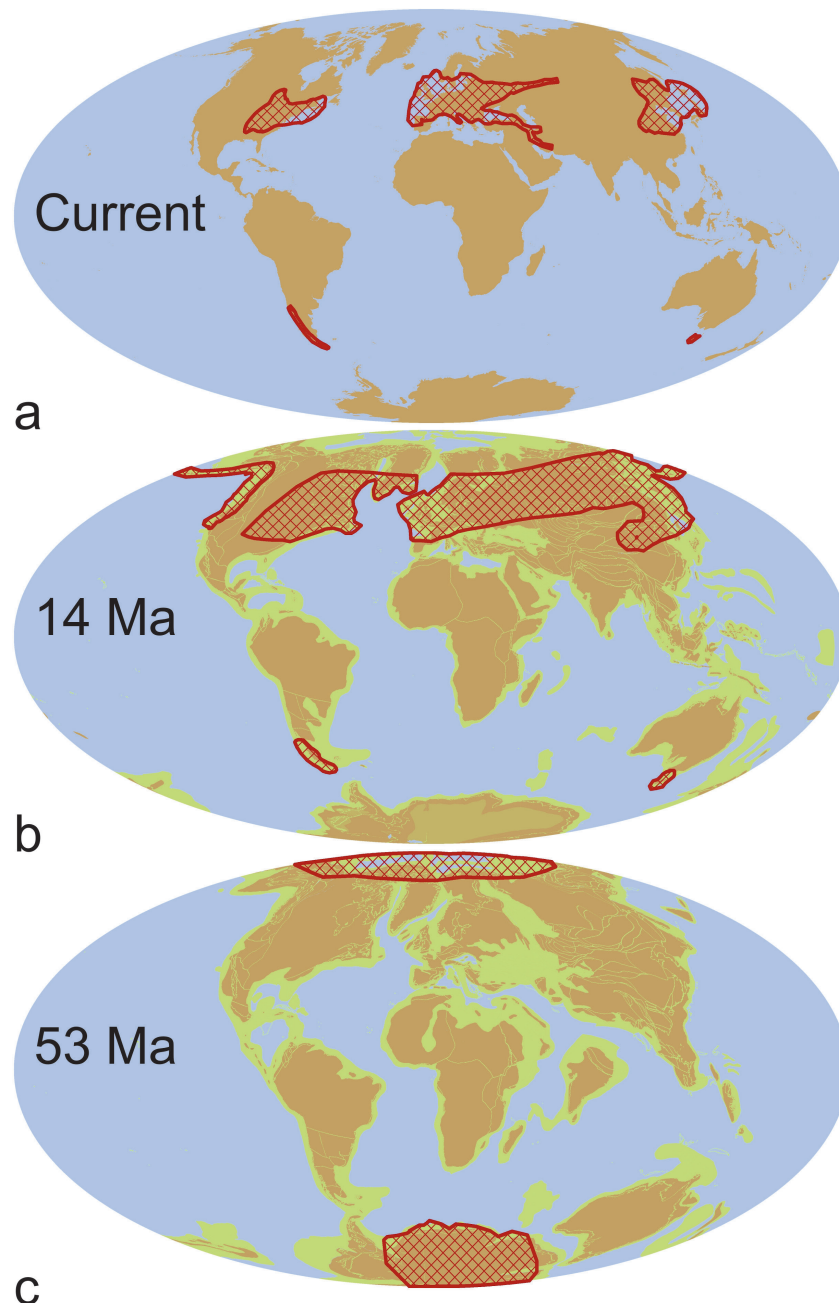


Figure 1. Distribution of the Temperate Deciduous Forests in the world in three moments: a, current distribution; b, middle Miocene (14 my ago); c, early Eocene (53 my ago). Data from Barron *et al.* (1980), Olson (1985) and Wolfe (1985).

## 2. Deciduousness. Historical evolution and adaptative issues

The deciduous character in trees and shrubs can be divided into summer deciduousness, adapted to a tropical pluviseasonal climate in which drought drives these plants to shed their leaves, and winter deciduousness, typically adapted to temperate climates in which the plant sheds the leaves to avoid low winter temperatures. Following this distinction, we could establish the terms *xerodeciduous* for the former and *cryodeciduous* for the latter.

Early in the 19<sup>th</sup> Century, it was discovered that a temperate hardwood flora populated high latitude regions, such as Spitsbergen, Iceland, Greenland,

Kamchatka, etc., during the Late Cretaceous and Paleogene (Gray, 1878), presumably under a climate similar to that of the current mid-latitudes. For that type of flora, Engler (1882) established the concept of “Arcto-Tertiary geoflora”, a concept which many other authors have used (Kryshstovovich, 1929; Wolfe, 1978; 1980; Axelrod, 1983; Mai, 1989; 1991; Röhrig, 1991a; 1991b; Tallis, 1991; Walther, 1994; Barrón, 2003; Barrón *et al.*, 2010; Utescher & Mosbrugger, 2007; Utescher *et al.*, 2007). This Arcto-Tertiary floristic element or geoflora is that group of woody plants formed by deciduous plants and conifers which populated high latitude lands (arctic areas of Eurasia and North America) during late Cretaceous and early Tertiary, where temperate and cold-temperate climatic conditions were dominant

in that time. It matches with the Northern hemisphere cluster described by Xing *et al.* (2015), reinforcing its common origin in the Cenozoic. With the climatic cooling of the late Tertiary, this Arcto-Tertiary flora was drawn southwards, invading mid-latitudes in Eurasia and North America (Tallis, 1991; Walther, 1994). This flora is the ancestor of the current deciduous and conifer elements which are currently inhabiting the boreal and temperate mid-latitude areas. South to the Arcto-tertiary geoflora, there was an “Arcto-Paleotropic geoflora, formed by macrothermic elements, which was dominant in the mid-latitudes of North America and Eurasia under moist subtropical conditions and formed by evergreen lauroid taxa. Since the Oligocene (Oligocene deterioration, Wolfe, 1971), the increase in climatic cooling and seasonality (continentalization, Bruch *et al.*, 2011) pushed these belts southwards, and the Arcto-Tertiary flora invaded lower latitudes at the expense of the Arcto-Paleotropic area, which had to withdraw from many regions, a retreat which was accompanied by regional extinctions and that left a number of relic populations in some environmentally favourable locations (Postigo Mijarra *et al.*, 2009; Barrón *et al.*, 2010; Jiménez-Moreno *et al.*, 2010; Ivanov *et al.*, 2011; Ivanov & Worobiec, 2017; Martinetto *et al.*, 2017). In the early phases of these migrations, connections between northern continents allowed interchanges of flora (North America with Asia and Europe), permitting this deciduous hardwood plus conifer flora to be connected (Graham, 1993) through the Beringia and the North Atlantic land bridges (Tiffney & Manchester, 2001). The expansion of mesothermal broad-leaved forests followed the decline of tropical elements in mid-latitudes of the NH. In the western sides of the continents, ecosystems had to adapt to the increasing summer drought was being established since the late Miocene (Mai 1989; Barron *et al.*, 2010; Ivanov *et al.*, 2011), as well as a cooling of the temperatures at the onset of the Messinian Salinity Crisis, (Jiménez-Moreno *et al.*, 2013) which lead to the disappearance of the European Tertiary laurel forest belt, with the extinction of almost all its laurophyll elements, of which only a few elements currently remain. These profound changes gave way to the appearance of the Mediterranean type xeromorphic vegetation, the highly continental formations in the interior landmass areas (Central Asia) and the post-Tertiary deserts existing today (Wolfe, 1985). As a result, lauroid evergreen forests, heirs of the Arcto-Paleotropic flora, practically collapsed in the western sides and central areas of both NH continents (Utescher *et al.*, 2007). This resulted in the contemporary Euro-African-Westasian Mediterranean and Western North American (Madrean) areas (Takhtajan, 1986), where the summer seasonal drought influences vast territories. Only in the eastern sides of the continents, this laurophyll vegetation has survived, thanks to the particular climatic conditions dominated by the oceanic trade winds and the monsoonal regime, as well as in some exceptional refuges in the west, such as the Macaronesian islands (Canary, Madeira and Azores) (Fernández-Palacios *et al.*, 2017). In addition, a few lauroid taxa in Atlantic SW

Europe and the Pontic region have survived as witnesses of the past occupancy of those territories by laurophyll forests. The microthermal conifer forests of higher latitudes and high mountains, together with the birch and poplar deciduous, endured in the regions where temperatures decreased more dramatically, forming the current taiga formations at the end of Miocene while the Tundra appears still later in the Pliocene (Wolfe, 1985; Graham, 1993). It is a story of the transition from a greenhouse to an icehouse world (Ivanov *et al.*, 2011).

Consistent with the evolution explained above, the most widely accepted hypothesis about the origin of deciduousness in the evolutionary history of the woody angiosperms is that posed initially by Axelrod (1958, 1966) and followed by other authors (Röhrig, 1991a), which supposes that deciduous character was established within recently originated angiosperms as an adaptation to slight to moderate seasonal aridity during Cretaceous. This is consistent with the tropical origin of flowering plants, which later expanded to higher latitudes. Deciduousness would initially originate from evergreenness (Bews, 1927; Axelrod, 1966; Takhtajan, 2009) in several lineages as an adaptation to moderate winter drought climate in lower-middle latitudes under subtropical conditions marginal to the tropical zone. Later the deciduous hardwoods originated as an adaptation to a cool and dry winter, migrated to higher latitudes where they occupied more seasonal climatic areas with a colder winter and, as they were already preadapted to a certain coldness and drought, they found a secondary niche in colder climates with more pronounced photoperiodicity (Axelrod, 1966). Thus, the deciduous habit may be regarded as a favorable preadaptation by which species initially originated under subtropical conditions were able to migrate to a new adaptive zone. Initially acquired as an adaptation to seasonal drought, the deciduous habit was now suited for adapting to a cooler season in higher latitude areas. Other authors (Zanne *et al.*, 2014; Edwards *et al.*, 2017) consider the TDFs to have evolved directly from evergreens as an adaptation to colder climates from several lineages independently. In any case, the drought preadaptation hypothesis entails a progressive expansion, along with upper Cretaceous and early Tertiary, of deciduous hardwoods from lower-middle latitudes, where they were originated, towards higher latitudes of more seasonal climate with cooler to cold winters. This means that after the long period of late Cretaceous and early Tertiary (Paleocene, Eocene), the evergreen forests covering the mid-latitudes were progressively replaced by deciduous hardwoods.

Consistent with this idea of the Arcto-Tertiary geoflora being originated in high latitudes of the NH, where a dark and long winter dominated, it has been suggested (Wolfe 1980; 1985; 1987; Cronquist, 1988) that deciduousness was really an adaptation to the long dark winter dominant in those polar and sub-polar latitudes. This deciduousness was combined with large leaf sizes, perhaps an adaptation to the low angle of solar radiation incidence during summer. The leaves could be large as there was no overheating problem, and the trees could afford to have deciduous leaves as they had a long

growing season. Such trait was also a preadaptation that later accommodated to the temperate seasonality, with a not so long but cold winter of the mid-latitudes we have today. If the initial angiosperms reached high latitudes in mid-Cretaceous, it is considered physiologically impossible that broadleaved evergreens can withstand such a dark winter as it is today in the arctic areas. Only a possible lessening of the inclination of the Earth's rotational axis could add more light to a polar-arctic winter and allow an evergreen forest under suitable temperatures, but this probably only happened during a limited time.

Between these two hypothetical origins, drought has been lately considered as the main factor in the origin of the deciduous habit for temperate trees and that moderate drought in the cool part of the year selected for deciduousness probably in moderately seasonal tropical climates in the Early Cretaceous (Wolfe, 1987). In any case, the expansion of TDFs in late Cretaceous mesothermal climates appears related to the advantage of shedding the leaves in plants of early successional stages; furthermore, deciduousness represented an additional advantage to the absence of winter light in high latitudes. Progressive evolution of climate along Tertiary towards lower temperatures and higher seasonality with cold winters expanded these forests towards mid-latitudes. Either as an adaptation to seasonal drought in subtropical latitudes or as an adaptation to winter darkness in arctic high latitude areas, winter deciduousness seems to be a preadapted trend to different conditions than those for which later was used by these woody plants.

## 2.1 Evolution of the TDF tree flora along the Tertiary and its distribution in the NH continents.

The NH temperate deciduous tree flora is the mixture of two sets of high-level taxa: one proper of the temperate regions of the NH, derived from the Arcto Tertiary geoflora (families like Aceraceae, Betulaceae, Cornaceae, Fagaceae, Juglandaceae, Rosaceae, Salicaceae, etc.), mostly represented in the northerly and central regions of that biome, and other composed by tropical families which are more frequent in its southern fringe (Bignoniaceae, Hamamelidaceae, Lauraceae, Magnoliaceae, etc.). In both sets, the differences in floristic diversity between regional floras reside at high taxonomic levels. Thus, such differences were established long ago. In both groups, the maximal diversity is found in East Asia, both in families and in genera. This continent had a continuous landmass connecting temperate and tropical latitudes in the Cretaceous. Late Tertiary and Pleistocene extinctions affected Europe and North America more than East Asia, which can be one reason for its higher diversity. However, there should also be a primary reason for this anomaly related to colonization episodes and differential production of new taxa by speciation in the three regions. Asia seems to have suffered more colonization episodes and has differentiated more new species than the other two regions (Latham & Ricklefs, 1993b). Such succession of

events has suggested the East Asian origin of a majority of the current NH temperate tree flora, particularly supported by the high diversity, including the genus and family levels, and the abundance of modern taxa in its fossil record. One example is the adaptative radiation that took place in the genus *Fagus* in the East Asian mountain ranges (Hukusima *et al.*, 2013)

Most of the angiosperms arose during Upper Cretaceous and Paleogene, under a relatively warm climatic period with few frost areas in the world. At the end of this period, modernization of this taxa happened parallel to its expansion over the world (Tiffney, 1985). Only East Asia had a continuous land connection between the tropics and the high latitudes during this period. The Tethys Sea and the waters that existed between both Americas limited southwards both the mid-latitude areas of Western Eurasia and North America. Furthermore, large inland seas were separating Europe from East Asia. Thus, the southern halves of the NH temperate zones were separated while its northern portions were (at least intermittently) connected through land bridges in the Ural, Greenland, Bering and mid-Canada (Tiffney, 1985). This seems to be when this temperate flora arose (Latham & Ricklefs, 1993b). When the cooling started in Oligocene, the frost area began to expand in the higher latitudes, and this flora migrated southwards. But this was still in a time in which North America and Europe were not yet connected to the southern continents as they are now, differently from East Asia, which had a continuous land corridor to the south which could act as an "escape route" in the cold periods (Huntley, 1993). This could explain the mentioned East Asian higher tree flora diversity.

## 2.2 Eco-physiological traits

The evergreen character of forest foliage can have diverse functioning patterns in the different biomes. For example, in an evergreen tropical rain forest, the vegetation always has green leaves, but each leaf has a short life (often less than one year). This is different to an evergreen lauroid forest or even to the Mediterranean or coniferous forest, where leaves live longer than one year, sometimes up to three or four years in a functional state, enduring adverse periods, as long as it is worth for the plant to keep the leaves alive for a longer time to offset the costs of having to build them up again.

Shedding the leaves (deciduousness) is one of the most important adaptations of woody plants to climates having an unfavorable period for growth, either because of drought combined with high temperatures or either because of low temperatures, which also use to combine with desiccation during freezing (Wolfe, 1987), in a strategy to prevent freezing and physiological drought (Parker, 1963). In any case, the growing season has to be long, warm and wet enough to produce all the photosynthates needed for the year's maintenance, growth and reproduction. Thus deciduous trees require medium to high levels of nutrient availability; deciduousness is only compatible with a very productive growing season. It occurs in areas where summer is



warm and rainy, and the soil provides sufficient humidity and nutrients (Barnes, 1991). An important part of the nutrients in the tree's biomass is returned to soils with the leaf fall, and an efficient and rapid recovery must offset that loss. Then, rapid decomposition of the litter is needed and prompts reabsorption of the nutrients. For that, the litter has to be easily decomposable, and the root system of the trees, aided by the mycorrhizae, has to be efficient in absorbing them

The distribution of dominance between evergreen and deciduous trees and shrubs in the NH and the tropics is quite satisfactorily explained by Givnish (2002) from the eco-physiological point of view. Evergreen and deciduous species have been competing for a long time and, as a result of such a concurrence, a tight adjustment has been established between both types. Evergreens have a longer photosynthetic season, and they need less nutrients as the plant does not need to replace the leaves so frequently. Thus, evergreenness is favored by climates with long growing seasons and by nutrient-poor substrata. On the other hand, the greater the difference between seasons in terms of temperature and rainfall, the greater is the dominance of deciduous plants because they reduce transpiration and respiration during the dry or the cold season. Soil infertility favors evergreens and sclerophylly by reducing the difference in net photosynthetic rates between seasons, which has a similar physiological effect to the low seasonality.

In Mediterranean climates, evergreens and deciduous woodlands have a similar efficiency in the assimilation of carbon under sufficient water supply; they both have similar ecological costs. As deciduous have a shorter growing season, they produce leaves with higher nitrogen content, enabling them to assimilate higher levels of carbon. Thus they compensate for the shorter growing season by having a greater capacity for assimilating carbon in the well-watered short spring season; they can assimilate six times more carbon than evergreens at saturating light levels in this period of the year (Balocchi *et al.*, 2010). In water shortage conditions, this strategy is no more valid and evergreens have a better adaptation for survival.

The climatic boundaries which conceal the broadleaved temperate deciduous forests for the NH were given by Wolfe (1979, 1987) and there is a limit of the coldest month (CM) mean of 1°C, above which evergreenness thrives. The upper limit with the boreal conifer forests is the warmest month mean, which has to be higher than 20°C. These boundaries were calculated basically for East Asia, where the seasonal temperatures range is high. But this climatic correspondence is not so exact in other geographic regions, particularly where continentality is lower than in East Asia, as it happens in Europe (Wolfe, 1987). Deciduous broadleaved trees are less adapted to extreme conditions than some conifers. The latter use to outcompete hardwoods in conditions of low temperature, short growing season, aridity, strong wind and low nutrient soils (Barnes, 1991). Additionally, conifers often represent secondary forests of TDFs, establishing after disturbance. This does not mean that the conifer life form is better adapted than

hardwoods to mesic conditions, as they are widespread in many lauroid forests across the world and in Europe some of them share climatic requirements and historical migrations with deciduous trees (Tinner & Lotter, 2006).

In terms of structure and ecological traits, these forests often bear a multilayered structure, with a closed canopy, sometimes covering a sub-canopy tree layer, one or two shrub layers and a herb layer. Vascular lianas also occur but are not numerous. Epiphytes are abundant, most of them bryophytes and lichens, and some vascular plants (usually ferns). The abundance of layers depends on the abundance of available nutrients and the humidity of the climate and the atmosphere, particularly for the epiphytes. In general, woody deciduous plants predominate in all the layers except in epiphytes, and frequent mesophytic affinities.

### 3. Deciduousness. The question of the Southern Hemisphere

The Southern Hemisphere (SH) pattern is entirely different from that of the NH. Relatively, evergreenness is much more widespread in SH than in NH non-tropical areas, or if we wish to express it in an opposite way, winter deciduous woodlands are much rarer in extratropical SH (modest representation in Southern Chile and Tierra del Fuego by seven *Nothofagus species* (*N. alessandri*, *N. alpina*, *N. antarctica*, *N. glauca*, *N. macrocarpa*, *N. obliqua* and *N. pumilio*), and in Tasmania by a single species (*N. gunni*). This point has been highlighted by several authors (Diels, 1918; Troll, 1948; Schimper & von Faber, 1935; Larcher, 1973; Axelrod *et al.*, 1991; Box, 2002; Box & Fujiwara, 2015) and has been related to the lower continentality of the SH, i.e. the lower difference between the summer and winter temperatures. Winter cold limits the evergreenness while the summer warmth enhances summer productivity and makes it possible to offset the energy loss due to the winter leaf shedding. The case of New Zealand is particularly illustrative as in this archipelago evergreenness dominates in forests under clearly temperate climate, quite comparable to areas in the NH (Europe and North America) where deciduous forests dominate; only in seral and forest marginal habitats are found some deciduous plants. This dominance of evergreens has been explained by McGlone *et al.* (2004) by the pronounced oceanic climate and the low fertility of the soils in SH temperate areas. Wolfe (1979) indicates that simply there are no landmasses in SH where the coldest month mean is <1°C and warmest month mean is > 20°C, being thus impossible the survival of temperate broadleaved deciduous forests. Others, such as Wardle (1991), support the idea that in New Zealand, deciduous habitat is poorly represented because of its long isolation, which prevented deciduous lineages from colonizing the islands (historic explanation). In any case, areas of similar soil poverty and highly oceanic climate are also found in western Europe and are entirely dominated by deciduous forests (Brittany, western British Isles, Galicia).

Axelrod (1966) has also commented on this issue, which highlights the independent forest evolution in the boreal and austral regions along the Cretaceous and Tertiary. The much lower landmass in the southern middle and high latitudes have probably been responsible for a highly oceanic climate, having given fewer opportunities to develop a deciduous hardwood flora adapted to more extreme seasonality. The more oceanic character of the temperate climates (very low seasonal ranges of temperature) in the SH compared to the NH, entails much less severe winters and high rainfall evenly distributed along the year. This long frostless period allows a longer growing season, better suited to an evergreen habit. In conclusion, current NH vegetation at mid-latitudes has a more “temperate” aspect than SH vegetation under comparable climates (Wolfe, 1987).

From the historical point of view, the currently SH existing TDFs in the southern Andes and Tasmania appear to be related to the deciduous forests that covered central Antarctica in the early Tertiary (Figure 1c), formed to a large extent by *Nothofagus* species (Dettmann, 1989), which were likely related with the more numerous evergreen lineages of the same genus. With the drop in temperatures throughout the Tertiary, the Antarctica ice cap began in the Oligocene, whose growth drove vegetation to the periphery of the continent, causing the extinction of these deciduous forests. The abundant Late Cretaceous and Tertiary *Nothofagus* fossil remains found in the southern part of South America (Tanai, 1986) suggest that the connection of Antarctic TDFs with those of the Patagonian area precedes the interruption of the land bridge that existed before the Oligocene (Lawver *et al.*, 1992) and, therefore, suggest an Antarctic origin of these forests (Figure 1b). The subsequent rise of the Andes, together with the establishment of the Humboldt Current, after 14 my bp, changed the general climatic conditions of the area (Le Roux, 2012), creating the enormous arid zone due to rain shadow in western Patagonia and reducing the suitable territory for deciduous *Nothofagus* species to the present strip they are found today, where they survive in the middle-high elevations of the windward side of the southern Andes. The remnant deciduous *Nothofagus* of Tasmania can be explained similarly.

#### 4. The different northern hemisphere TDFs regions.

The NH areas where TDFs are mostly distributed are three: Western Eurasia, Eastern North America and Eastern Asia (Figure 1a). As said above, they are the remnant territories in which this biome survived the climatic affairs of the late Tertiary and Pleistocene. In addition to them, there are some other smaller areas in central Eurasia and Western North America, which can be interpreted as residuals of the once largely expanded TDF biome of the early and mid-Tertiary. We will discuss in more detail each of these regions.

##### 4.1 Western Eurasia

It is the largest area potentially occupied by TDFs in the NH. Due to the influence of the Gulf Stream, these

forests reach 60° N on the coasts of Norway (Jahn, 1991) and North-central Portugal in the south, encompassing a broad zone in the Atlantic regions of Europe. The southern limits contact with the Mediterranean biome and are depending on the rainfall regime, being present in the rainy mountain areas of the southern peninsulas (Iberian, Italian and Balkans) till 38° N. They are also dominant in some peripheral territories such as the Euxinian (south and southwest coasts of the Black Sea), Hyrcanian (southern Caspian coasts) and Zagros regions, where they reach the lowest latitudes at about 33°N. To the East, they penetrate into the continent in a wedge-shaped area beyond the Urals until about 70° E, where they vanish between the boreal taiga and the central Asian steppe.

Deciduous forests, like evergreen forests, took refuge in some favorable locations mostly on the peninsulas of southern Western Eurasia during the Quaternary ice ages. After the LGM (Last Glacial Maximum), about 11,000 years ago BP, they began their advance northwards after the climatic improvement that took place in the Holocene. This process had different phases and was subject to accelerations and slowdowns, but a general pattern is recognized in its advance from south to north (Huntley & Birks, 1983; Lang, 1994; Ferris *et al.*, 1998; Petit *et al.*, 2002). A first wave is formed by conifers, birches, aspen and willows. Then the first temperate deciduous trees arrive, replacing the previous boreal ones, with hazel in the first wave and the oaks, elms and linden trees later. The latest additions are those of beech, hornbeam and fir. This pattern, driven by the climatic variations during the Holocene, seems to be reproduced in the previous interglacial periods, and this establishes a regularity in the migratory movements of the glacial cycle in this region (Iversen, 1958).

The most common tree species of the current TDFs are *Acer campestre*, *A. platanoides*, *A. pseudoplatanus*, *Alnus glutinosa*, *Betula pendula*, *Carpinus betulus*, *Corylus avellana*, *Fagus sylvatica*, *Fraxinus excelsior*, *Prunus avium*, *Quercus petraea*, *Q. robur*, *Tilia cordata*, *T. platyphyllos*, *Ulmus glabra*, *U. minor* and others. In the southern fringe of its area, forming a transitional band towards the Mediterranean sclerophyllous forest biome, a particular forest flora adapted to the sub-Mediterranean climatic conditions establishes. The main tree species are *Quercus faginea*, *Q. pubescens* or *Q. pyrenaica* in the west, and in the central-eastern sector *Ostrya carpinifolia*, *Quercus cerris*, *Q. frainetto* or *Q. trojana*. The southeastern external regions of the Black and Caspian Seas and the Caucasus have particular species such as *Fagus orientalis*, *Parrotia persica*, *Pterocarya fraxinifolia*, *Quercus brantii*, *Q. iberica*, *Q. libani*, *Q. macranthera*, *Zelkova carpinifolia*, etc. They have served as a refuge during the last ice ages for several cold-sensitive taxa, some of them evergreens such *Rhododendron ponticum* or *Prunus laurocerasus*. The oaks usually have hairy leaves and a marcescent habit in adaptation to the moderate summer drought. These Western Eurasian forests have a high number of shrub species and a rich herbaceous layer mostly formed by perennial herbs and geophytes (Röhrig, 1991b).

## 4.2 Eastern North America

The deciduous forests of Eastern North America occur mostly south of 48° N, in contact with the Coniferous Boreal Forest zone, and East of 95° W, in contact with the Great Plains Grasslands. The southern limit draws a line shifting between 33 and 37 ° N, which separates from the Mixed Evergreen forest of southeastern US, which spans between eastern Texas and southeastern Virginia. This vast area enjoys a temperate climate with rainy, warm summers and cold winters where precipitations are equally distributed along the year, ensuring a sufficiently humid summer.

Opposite to western North America, no uplift of huge mountain ranges took place in this side of the continent since late Tertiary, and there is not an everlasting high pressure in the subtropical latitudes. After the cold periods of the glaciations, in which cold-adapted biomes, such as Tundra and boreal forests, migrated deeply southwards, the ice retreat left vast areas to re-colonize by temperate ecosystems (Barnes, 1991). Only modest areas in the Appalachians remained with high altitude conifer forests, and the region benefited from the oceanic winds regime that prevailed during interglacial periods and the Holocene. No drought period and lower and less extensive mountain ranges permitted the survival of the TDFs in eastern North America in a homologous way as did in eastern Asia. The current composition of the North American TDFs was established probably at the beginning of the Holocene and has suffered several advances and retreats along the last 10,000 years driven by the climatic changes (Davis, 1983; Grellier, 1988).

In this large east American region, considering the structure and species composition, a high number of forests types can be recognized, depending on climate, topography and soil conditions (Barnes, 1991; Grellier, 1988). The northern variants have a number of conifers, and the southern ones bear some evergreen hardwoods. Some common species in these forests are the deciduous hardwoods: *Acer saccharinum*, *A. saccharum*, *Betula alleghaniensis*, *Carya ovata*, *C. tomentosa*, *Castanea dentata*, *Fagus grandifolia*, *Fraxinus americana*, *Liquidambar styraciflua*, *Liriodendron tulipifera*, *Quercus alba*, *Q. rubra*, *Robinia pseudoacacia*, *Tilia americana*, and some conifers such as *Tsuga canadensis*.

## 4.3 Eastern Asia

Temperate East Asian TDFs potentially cover the territories comprised between the latitudes of 30° and 50° N, where the contact with the lauroid evergreen forest and the Boreal conifer forest, respectively. Their western frontier is well inside the Asian continent, formed by the contact with the arid regions of Qinghai and Inner Mongolia and with the Hymalayo-Tibetan massif in northwestern and western China (Ching, 1991), in a line which varies between the 103° and 123° of longitude E. They also extend across Manchuria and the Russian region of the Amur, the entire Korean peninsula, except the southernmost strip, the Japanese archipelago with the exception of the southern and southeastern lowland areas, and the southern tip of Sajalin island. The climatic

limits of this biome in East Asia are concealed between Kira's index limits 45° and 85° month of warmth index (WI) and below the -10° month of the cold index (Kira, 1949; 1991). The rainfall regime is driven by the eastern trade winds and the monsoonal cycle of the Asian continent. During summer, the low pressures of the interior of the continent centered over Mongolia and Siberia, originate the maritime humid air masses from the Pacific and the Indian oceans to enter into the continent bringing abundant rainfalls. In winter, the situation reverses, and the cold and dry air masses coming from the central Asian high pressure invade the area. Precipitations vary between 500 and 1500 mm and concentrate in the warm summer, while winters are dry.

This vast area appears to be the major remnant of the great mesophytic forest that extended over the continents of the Northern Hemisphere in the Tertiary, occupying mid to high latitudes and reaching the Arctic regions. East Asia escaped from the most severe effects of the Pleistocene Ice Ages which affected the other two main regions, North America and Western Eurasia. Uninterrupted forested area covered East Asian coastal areas, from the tropical latitudes to the Boreal conifer forest, and permitted the shifting of the latitudinal belts driven by the climate change without being disturbed by any geographic obstacle, such as mountain range or a big lake or sea. Thus, this region suffered few extinctions and is richer in tree flora than its homologous, bearing a higher number of ancient vegetational and floristic elements with many relics and endemic taxa (Li, 1952).

There are numerous representatives of the genera *Acer*, *Aesculus*, *Aralia*, *Carya*, *Castanopsis*, *Cercis*, *Cladastria*, *Cornus*, *Fagus*, *Fraxinus*, *Gleditsia*, *Gymnocladus*, *Juglans*, *Liquidambar*, *Liriodendron*, *Lithocarpus*, *Ostrya*, *Populus*, *Quercus*, *Salix*, *Sassafras*, *Sophora*, *Styrax* and *Ulmus* among others.

About the variability within the TDFs of this region, there is a north-south diversification driven by the climatic gradient, which is accompanied by an increase in the tree species richness (Nakashikuza & Iida, 1995). In the southern areas and at lower elevations, with a milder climate, elements from the lauroid (lucidophyll) forest are present, as well as a number of relics (in China) of the Tertiary, such as *Ginkgo* and *Metasequoia*, together with some other trees such as *Dalbergia hupeana*, *Liquidambar formosana*, *Magnolia zenii* or *Rhus chinensis*. In this transitional fringe, the deciduous forests often occur as secondary forests of the evergreen lauroid forests (Fujiwara & Harada, 2015). In the rest of the region, thermophilic elements disappear and in the northern and northeastern sectors other tree species, related to the boreal conifer forests, occur, such as *Abies nephrolepis*, *Betula costata*, *B. ermanii*, *Larix gmelinii*, *Picea jezoensis*, *Pinus koraiensis*, or hardwoods with a northern-temperate distribution: *Kalanopanax septemlobus*, *Quercus crispula*, *Tilia amurensis*, etc. In Japan, the montane belt is occupied by beech forests (*Fagus crenata*), often accompanied by dwarf bamboos of the genera *Pleioblastus*, *Sasa* and *Sasella* (Hukushima *et al.*, 2013).

The most common species in the entire region are *Acer mono*, *Davidia involucrata*, *Diospyros kaki*, *Pawlonia tomentosa*, *Pistacia chinensis*, *Quercus*



*acutissima*, *Q. aliena*, *Q. dentata*, *Q. mongolica*, *Q. serrata*, *Q. variabilis*, *Zelkova serrata*, etc. (Fujiwara & Harada, 2015).

## 5. The differences of the TDFs between regions

Comparing the temperate broadleaved deciduous forests existing in the different large regions of the NH has appealed to the attention of geobotanists, taxonomists and ecologists since the early times of modern science as it became evident the difference in the number of tree species in both sides of the Atlantic. This was already highlighted by Alexander von Humboldt and Aimé Bonpland in their classic work of 1807. It has been generally assumed that broad-leaved deciduous tree taxa are measured in thousands in Asia, in hundreds in eastern North America and in tens in Europe (Davis, 1983; Wolfe, 1979, 1987). More or less, East Asian forests have three times more tree species than those of eastern North America and six times more than the European ones. If we include Western North America in the calculation, is generally accepted the proportion of 2:12:1:4 for Western Eurasia (WEA), East Asia (EA), Western North America (WNA) and Eastern North America (ENA), in the distribution of the 1,166 tree species forming the temperate forests of the NH (Latham & Ricklefs, 1993b). The reasons for these differences have been long attributed to historical events (Reid 1935, Huntley 1993).

Both continents, Eurasia and North America, are comparable in terms of latitude range, extent and habitat diversity and show remarkable similarities between their eastern parts. The floristic relationships between both landmasses have been extensively studied by Li (1952), Qian & Ricklefs (1999), Qian (2002), Ricklefs *et al.* 2004 and Donoghue & Smith (2004), who established that the vascular flora in Asia is significantly more diverse than in North America: it is estimated that East Asia has 1.3 times as many genera (more than twice in the case of the temperate forests) and twofold the species as North America (considering the total floras). Both continents have a relationship that has been largely discussed (Tiffney & Manchester, 2001) and was initially documented at the genus level by Li (1952).

Former contributions supported more intense relationships of East Asia with Western North America (Li, 1952; Wolfe & Leopold, 1967; Wen, 1999), a relationship consistent with the faunistic patterns (Sanmartín *et al.*, 2001). Western North American relationships with East Asian forests were due to the land connections between North America and East Asia (Xiang *et al.*, 1998) via the Beringian Land Bridge during the Tertiary. This allowed migrations between the two continents resulting in these close relationships of the current temperate flora of both sides. Today the western flora is more related to East Asia than to eastern North American (Barnes, 1991).

Furthermore, more recent authors (Donoghue & Smith, 2004) highlight an intense connection of East Asia with Eastern North America due to the high number of disjunctions between these two regions, which have also

retained a greater diversity. This could also be explained by the importance of the Beringia connection facilitating floristic interchange between Asia and North America, combined with a lower extinction rate in the East. The more intense extinctions in the Pacific side of America were likely due to an adverse climatic evolution and to huge orogenic phenomena in the late Tertiary and Quaternary.

Additionally, concerning the influences of other surrounding land areas, tropical affinity in temperate flora is stronger in East Asia than in the other two regions, indicating longer or more open access of Eastern Asian flora to tropical climatic areas as likely did happen in southern China. The southwards migration of temperate taxa supports this into tropical latitudes in Asia during the coldest episodes of the Pleistocene (Qian & Ricklefs, 2004). It is also hypothesized that the collision of the Indian subcontinent during Eocene increased substantially Asian diversity by the subsequent uplift of the Himalayas, enhancing rapid speciation due to the wide array of new niches available and also to the addition of a number of Gondwanan taxa provided by the Indian plate (Qian, 2002). This substantial increase in biodiversity in the Asian continent likely benefited the diversity of the temperate regions of East Asia. This advantage can also be combined with the high physiographical diversity in East Asia compared to North America. In addition, allopatric speciation in Asia could be promoted by the isolation of land patches during sea-level rise episodes. On the other hand, the extinction of species due to the late Pliocene and Pleistocene climatic cooling could have been more severe in North America than in Asia, where more refugee possibilities existed in lower latitudes. More simple geography and a more uniform climate have not fostered diversification in Eastern North America with the same intensity as in Eastern Asia (Qian & Ricklefs, 2000).

## 6. The case of North America: three vs four regions

In connection with the discussion about the events that happened in North America, there is the possibility of considering four instead of three regions for the temperate deciduous forests, two in each of the two continents: East and west Eurasia and, consistently, east and west North America. This would entail recognizing two regions in North America, similarly as it is done for Eurasia. In the case of the Boreal forests, the sharing of the North Americans with the Eurasians is significant, involving a large proportion of the tree species and genera. In the case of the forests of the temperate latitudes, there is much less in common: <7.5 % of the gymnosperms and < 6.5 of the angiosperm species (Huntley, 1993). This means that while the Boreal conifer forest is common to both continents, having narrow connections between the two continents even today, that is not the case for the Temperate Forests. Within North America, two main areas can be clearly distinguished: East and west, with a few trees and large shrubs species in common. This



would support the acceptance of two regions for North America, similarly as for Eurasia.

But the case is that in Western North America, there is much less surface proportion covered by TDFs than in the east. Opposite to it, a majoritarian proportion of the current forests of the temperate and Mediterranean climatic areas are formed by conifers: “*All the glory of the pacific forests is in its coniferous trees*” (Gray, 1878), being the TDFs restricted to mesic sites and riparian habitats, where sufficient groundwater is available in the growing season. There are remarkable deciduous species such as *Quercus douglasii*, *Q. gambelii*, *Q. kelloggii*, *Q. lobata*, and representatives of the genera *Acer*, *Aesculus*, *Carpinus*, *Castanea*, *Corylus*, *Fagus*, *Fraxinus*, *Juglans*, *Populus*, *Tilia*, etc. They indicate that there is a floristic endowment to supply a substantial set of deciduous forests communities, but they do not cover large extensions in the temperate latitudes of Western North America.

This small and fragmented current area is probably due to the events that did happen in the area during the late Tertiary and Pleistocene (Donoghue & Smith, 2004). The original deciduous forest on this side of the continent suffered the uplift of the Rocky Mountains, started in the Oligocene and continued in the Miocene, splitting the area into two segments, an eastern and a western one. Later started the uplift of the Sierra-Cascade range creating aridity in its leeward and originating large-scale rain shadow areas (Thompson, 1988). Additionally, the establishment of the subtropical high pressures in the western side of the continents since the late Miocene created the conditions for the Mediterranean climate and the deserts of the western side of the continents. This originated vast areas of aridity (Millar, 1996), which were occupied by drought-adapted vegetation to arid and semi-arid conditions, combined with important areas of high elevation where better cold-adapted conifers outcompeted deciduous broadleaved species (Donoghue & Smith, 2004). As a result, TDFs suffered huge reductions and likely extinctions (Leopold, 1967). In Western Eurasia, the tectonic unfolding had less severe consequences as mountain ranges lifted in an east-west direction, most of them away from the coastal areas, and there was sufficient room for the TDFs to develop and occupy vast areas during interglacial periods.

As a result, currently, Western North America is deeply affected by summer drought in comparison to the eastern part of the continent, similarly, as it happens in Eurasia, but the existence of the huge mountain ranges crossing the area in a north-south direction parallel to the coast, causes rain shadow and fragmentation to small patches to the areas suited for TDFs. Then, while Europe is also affected by the Mediterranean climate in the south and a Boreal in the north, there is a broad space occupied by a huge belt of TDFs in between.

## 7. Why is Western Eurasia special?

The comparison of Western Eurasia with Western North America is consistent from a historical and climatic

perspective, but as we have seen, both areas diverge deeply in geography and orography. Europe is a huge and prominent peninsula of Eurasia with large areas of lowlands; such a circumstance does not occur in western North America, where the coast is nearly rectilinear from north to south. This determines the influence of the warm sea currents that bathe the coasts in each case: that of the Gulf Stream in Europe -strongly influencing in the regional climate of European coastal areas- and that of Alaska in North America -having a limited influence on the coastal strip-. Furthermore, mountain ranges emerged based on radically different patterns in both areas, a huge and complex north-south mountain system close to the coast in WNA and scattered ranges running east to west in the southern regions of WEA. These conditions allow a great penetration of the low pressures of the Atlantic entering deep in the Eurasian continent, in contrast to the formidable barrier that opposes the low of the Pacific to enter inside North America. Hence the differences in continentality and aridity in both territories. For that reason, there is a vast area in WEA to be occupied by TDFs, while in WNA there are hardly any pockets of modest size with this vegetation.

Fossil evidence indicates that the late Tertiary tree flora was much richer than at present in Europe; thus, more severe extinctions should have happened in this continent during Quaternary glaciations than in the other two. This hypothesis is the more generally accepted and constitute the “historical hypothesis” for the European relative poverty of the tree flora. The information gathered about the analysis of pollen data confirms this explanation (Magri *et al.*, 2017). A more detailed examination (Huntley, 1993) finds that the differences of WEA and ENA are not so high at the species level and are focused mainly at the genus level. The poverty in European genera, likely due to the high rate of extinction of genera and families during Quaternary, is very notorious, being proportionally higher than that of the species. There is then a partial offset of richness at the species level due to a higher species/genus ratio in Europe resulting from evolutionary processes that took place also during the Pleistocene. Consistently, when compared with similar productivity level areas, European tree flora reaches comparable levels of species richness as those in East Asia and North America (Adams & Woodward, 1989).

Many of the genera now existing alive in Asia and/or North America are currently absent in Europe, but they are found in the fossil record of several late Tertiary European sites: *Actinidia*, *Ailanthus*, *Broussonetia*, *Calocedrus*, *Camellia*, *Carya*, *Castanopsis*, *Catalpa*, *Cathaya*, *Cephalotaxus*, *Cercidiphyllum*, *Chamaecyparis*, *Chionanthus*, *Cinnamomum*, *Clethra*, *Cunninghamia*, *Cyclobalanopsis*, *Diospyros*, *Engelhardia*, *Eucommia*, *Ginkgo*, *Hamamelis*, *Ilicium*, *Lindera*, *Liquidambar*, *Liriodendron*, *Lithocarpus*, *Litsea*, *Magnolia*, *Metasequoia*, *Neolitsea*, *Nyssa*, *Paulownia*, *Persea*, *Phoebe*, *Platycarya*, *Pseudolarix*, *Pseudotsuga*, *Pteroceltis*, *Robinia*, *Sabal*, *Sapindus*, *Sapium*, *Sassafras*, *Sciadophytis*, *Sequoia*, *Staphilea*, *Symplocos*, *Taxodium/Glyptostrobus*, *Thuja*, *Torreya*, *Tsuga*, *Zanthoxylum* and others, indicating they

were present in mid-Tertiary Western Eurasian forests (Jahn, 1991; Latham & Ricklefs, 1993b). Others, such as *Cedrus*, *Liquidambar*, *Parrotia*, *Pterocarya*, *Zelkova*, etc., suffered strong reductions but still are found in restricted relictual sites of environmentally favorable locations of peripheral areas of the TDFs range (Magri *et al.*, 2017), mostly in Southeastern Europe: the Caucasus and Black Sea-Caspian Sea region (Biltekin *et al.*, 2015). Those which are widespread today did survive in small southern refugial sites across the continent and recovered after the glaciations (Magri, 2010; Magri & Sardori, 1999). This story of area reductions, refugia and recoveries indicates that extinctions and area reductions in the mentioned genera were forced stepwise by the several glaciated episodes of the Pleistocene.

In central Europe, some evidence indicates the existence and dominance of some form of Tundra north to the Alps (Peterson *et al.*, 1979) during the cold phases of the Pleistocene, leaving practically no space to forests between both the northern Arctic ice-sheet and the Alps (Davis, 1983; Van der Hammen *et al.*, 1971). However, this “traditional” interpretation has to be changed as some fragmented pockets of boreal forests have been reported in that area (Kuneš *et al.*, 2007, 2008) as well as some local relictual sites for several temperate broadleaved trees (Kuneš & Abraham, 2017). These locations are more northerly found in eastern areas -up to 46°N- than in the west -up to 43°N- (Tzedakis *et al.*, 2013), so the treeless European mid-latitudes is mainly a western picture, being central-eastern Europe covered by a taiga mixed with a montane conifer woodland with some pockets of temperate deciduous trees (Willis & van Andel, 2004). Then, we can accept that TDFs had no opportunity to occupy a true vegetation zone during LGM, being relegated to pockets at mid-elevation areas in mountains of central-eastern and southern Europe, or some refuges of peripheral areas in the southern peninsulas (Balkans, Italy and Iberia) and islands in the Mediterranean (Postigo-Mijarra *et al.*, 2010, Willis *et al.*, 2011). There, the temperatures and precipitations remained suitable for the TDFs survival, but, in any case, they provided only modest areas for them. The role of the refugia in the southern European peninsulas has been considered fundamental in the survival of many vascular plant species during the hard times of the Pleistocene (Willis & Whittaker, 2000) and this should be valid also for the deciduous trees. Conversely, in North America there was a narrow strip of Tundra south of the ice-sheet margin as happened likely in East Asia, leaving a large belt to be occupied by forests.

Regarding the differences between the tree species number of the three continents, more severe extinction episodes should have taken place in Western Eurasia than in the other two continents as most of these genera are still alive in them. This poverty for Western Eurasia has been traditionally attributed to differential effects of the Quaternary glaciations (historical hypothesis). Early authors such as Gray (1878) and Reid (1935) launched the idea that extinction rates during the Quaternary ice ages were different in each of the three continents, resulting in the current differences in diversity. In the

case of Europe the massive extinctions of the late Tertiary tree floras, particularly severe for the conifers (Wolfe, 1987), were enhanced by the east-west orientation of the main southern mountain ranges (Pyrenees, Alps, Carpathians and Caucasus). Such topography would act as a trap for plants migrating southwards driven by the advancing inlandeis, which would find the escape ways closed by the mountain glaciers that were developing in the southern ranges (Jahn, 1991). In addition to this, the Mediterranean Sea, which already was submitted to severe summer drought since the Messinian Salinity crisis, would leave little room for refuge areas during the glacial maxima. On the other hand, mountain ranges in North America run north-south and in the eastern part (Appalachians) have lower altitudes than in Europe (where the Alps and Caucasus developed huge glacier systems). Eastern Asia has an orography with few difficulties, and the continent has continuity of low elevation lands southwards, allowing migrations reaching further southern latitudes in their escape from the cold climate of the glacial maxima.

A controversial point is assessing the real effect of the east-west oriented southern mountain ranges. Huntley (1993) is sceptic about the influence of this geographical feature because these ranges should be more permeable than initially supposed. There are flat and low altitude stretches that would offer gates for effective southward migration. Besides, the Mediterranean Sea, although being a barrier opposed to the migration towards North Africa, offered more room than today and more land bridges through island chains and land connections, established thanks to the sea level regression during the glacial stages.

Then it cannot be attributed the Quaternary extinctions of temperate forest in Europe mainly to the east-west orientation of the mountain ranges but also to a climatic determinism, i.e. to the climatic conditions dominant in the area during maximal cold periods (Davis, 1983; Svenning, 2003; Svenning & Skov, 2007). An essential point in the climatic evolution in the Pleistocenian oscillations is that some evidence indicates that the climatic drought was accentuated in Europe during the cold periods (Manthey & Box, 2007). Some lacustrine records evidence from southern Europe (Cheddadi *et al.*, 1991) revealed that the glacial climate in Europe had intense summer aridity, unsuitable for a temperate deciduous forest and favoring vegetation such as steppe or steppe-woodland. This summer aridity likely contributed to making it impossible for TDFs to occupy a true vegetation zone in the southern European ice-free territories, relegating them to small areas at mid-elevations in the mountains, where orographic precipitations could offset this drought.

Remarkably, the above mentioned highest species/genus ratio found in Europe (Huntley, 1993), is consistent with the hypothesis of small-sized isolated areas of temperate forests surviving in mid-elevation in southern European mountains during the cold periods. Later allopatric speciation from the isolated surviving populations originated a relatively high number of new species of trees and tall-shrubs, compensating somehow the genera loss (Magri *et al.*, 2017; Tzedakis

*et al.*, 2002). This process is consistent with the higher phylogenetic clustering found by Eiserhardt *et al.* (2015) for the European and Western North American temperate forests compared to the East Asian and East North American ones, a difference attributed to more severe extinctions happened in the former regions.

The overarching summer aridity during Pleistocenic cold periods contributed to extinctions and probably induced certain adaptations in some of the surviving deciduous tree lineages. This could be nowadays observed in Europe, in the form of semi-deciduous (marcescent) oaks, present in submediterranean areas (García-Mijangos *et al.*, 2015; Gavilán *et al.*, 2018), where they currently form forests occupying vast areas, in comparison with eastern North America (Manthey & Box, 2007), where they are underrepresented. Marcescency can be a result of such summer-drought in a few *Quercus* lineages of both continents, and this can be related to the fact that there are also some deciduous-marcescent oaks in the area of California, such as *Quercus kelloggii*, *Q. garryana* and *Q. douglasii*, which have been compared with the Iberian marcescent *Q. pyrenaica* (Barbour *et al.*, 2007). Maybe the marcescent type has to do with a history of drought accompanying low temperatures during glaciations.

The difficulties for temperate forests to survive in Europe were not comparable to those in East Asia or East North America as there the mountain ranges are north-south oriented, the climatic shifts were not so constraining, and there is more land continuity in the south, which enables the southward migration during the extreme cold periods. This is more certain for East Asia than for eastern North America, where the Gulf of Mexico could similarly hinder southward migration as did the Mediterranean.

This interpretation focuses on the different migratory and survival difficulties had the vascular plants of the TDFs of the three continents during Quaternary, when they had to adapt and escape from the advancing ice sheets and the climatic cooling (and drying) during the Pleistocenic glaciations, but it highlights the importance of the extent of the climatically suited area occupied by the refugee populations during the adverse times. As a result of having had more marked environmental fluctuations and adverse situations during Quaternary, the extent of these forests during glacial stages was likely much lower in Western Eurasia (and even lower in Western North America) than in the other two regions: East North America and East Asia (Huntley, 1993). In consequence, the low diversity (particularly at the generic level) of the current European forests can be attributed to the limited areas available (refugia) for them during the glacial stages as a result of the difficult climatic conditions - lowering of the temperatures and ice formation, combined with progressive desiccation of the climate - happened since mid-Tertiary (Tallis, 1991; Svenning, 2003).

In contrast to this historic-biogeographical hypothesis, other authors have considered that these differences in tree species can be simply explained by

current climatic conditions (Wolfe, 1979; Adams & Woodward, 1989) without any historical explanation.

## 8. Land use

The TDFs represent a biome that thrives under relatively favorable conditions for farming and ranching: a temperate climate with a rainy, warm-season and soils with medium to high fertility. In consequence, the mature forests have been removed in many areas to free space for agriculture or grasslands, and in the cases, they have remained, have been severely transformed by humans to get many products in use for the traditional rural economy: logs for house and shipbuilding, wood for fire and for charcoal, litter to fertilize fields, seeds and fruits, mushrooms, medicinal plants and many others, as it has been documented for Italy and other countries (Guarino *et al.*, 2015).

## 9. Fields for future research in TDFNH

In the previous paragraphs, we tried to summarize the basic information existing about the TDFs of the NH. One of the promising fields has opened in recent times and is related to the availability of large datasets of vegetation plots in which all the species existing in each record are registered as well as their abundance (EVA, Chytrý *et al.*, 2016; sPlot, Bruelheide *et al.*, 2019). That opens the possibility of studying these forests type by examining the trees, as it has been done so far, and by examining the complete vascular plant community.

One of the directions of the research could be to separately study the patterns of the different components of the forest. That means that it is needed to deconstruct the forest into its several components, either life-forms or forest layers. It could happen they show a different ecologic and/or biogeographic behaviour among them, and an interpretation of that should be found. That could help knowing better how the events along late Tertiary and Quaternary affected the three zones differently. What are the similarities and differences between Western Eurasia, East Asia and North America, what do they keep in common and what do they have different and why. The SH TDFs could also be considered despite their much lower extent; in that case, the analyses should include the south Chilean and Tasmanian deciduous *Nothofagus* forests.

There are issues to be addressed that could be grouped into these four groups:

1. Are the patterns observed for the trees, in terms of richness distribution, similar to that of the understory components in the three regions? For instance, the low richness in WEA in comparison to that of ENA and EA tree flora is attributed to certain events considered responsible for that; this could drag the understory flora in a parallel way or, opposite to that, the other components of the forest could show a different pattern, i.e. have the herb or the shrub layer the same patterns?



2. The existence of a common area for the TDFs of the NH in the Tertiary is revealed by the floristic affinities in the tree flora (genera and families) shown currently among the three main regions. How are the similarities or differences between the understory flora of the three regions in terms of taxonomy if compared with those of the trees? If they were high, we could figure out that there has been a common history along the Tertiary for both groups of plants (trees and understory species) having experienced a common succession of events and having similarly affected to them. Can we expect similarities in a comparable scale in the understory flora, which could reinforce the Tertiary continuous area hypothesis? Are the three zones equally distant, or are two of them more similar being the third more distant, indicating that the separation between regions happened in a different moment?
3. Can a signal of an ecological link between the trees (shade casters) and the understory plants (shade tolerant) be detected, indicating that they have been living together for a long time? If their ecologic patterns are different, we can suppose that the current understory plants had no historical links with the tree flora and could be simply an independent adaptation to the shade of some species from the surrounding light-demanding flora. Some of the areas have a long shepherding tradition, such as Western Eurasia, and a set of herb species are linked to this land use, being also some of them found in the forests. There is also the possibility that a part of the understory plants is not shade-adapted but plants that propagules are constantly imported from outside (e.g. seed rain from birds) and are surviving under the canopy in a metapopulation dynamic as sink population. Are such phenomena happening in the three regions?
4. Are the patterns observed in the traits composition of the different forest components similar in the three regions? The question is to see if the traits composition spectra are different for the understory flora and the life-form groups of the three regions. For instance, are herbs or geophytes more abundant in WEA than in ENA or EA, while woody plants are more abundant in EA than in the other two? Is the participation of conifers, evergreens, lianas, epiphytes shrubs, perennial herbs and geophytes similar or different in the three regions?.- Do this somehow reflect different historical events succession for the three regions or could it be explained by the current environmental differences? Concerning the semideciduous (marcescent) broadleaved tree species which are dominant in the southern submediterranean sectors of the Western Eurasian region (García Mijangos *et al.* 2015), are there equivalents in the other two regions representing a submediterranean transition?

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