Biogeography of European Bees

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Abstract

Bees are a crucial group of insects for terrestrial ecosystem functioning, but numerous threats from human activities challenge their conservation. Knowledge of the spatial distribution of bees is key to proposing efficient strategies for their conservation. In this chapter, we propose a synthesis of the biogeography of the European bee fauna. We describe how species diversity is distributed across the continent, with a strong positive north–south gradient. We provide maps of a set of species to exemplify the most common types of distribution for bees in Europe. We continue this chapter by moving from Northern Europe to Southern Europe and present the main characteristics of bee communities in the different major European biomes in relation to their flora. Finally, we give some perspectives to further improve our knowledge of European bee biogeography.

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Keywords

Diversity · Evolution · Distribution pattern · Biomes

4.1 Distribution of Species Diversity

Bees constitute a taxonomically and ecologically diverse group of insects worldwide, and the European bee fauna is not an exception to this tremendous diversity. The species checklist of European bees (Europe sensu IUCN, see Nieto et al. 2014) was recently revised by Ghisbain et al. (2023b) to reach a total of 2138 species. As approximately >20,000 species are described globally, Europe hosts about 10% of worldwide bee diversity, although the continent represents only 7% of the global terrestrial habitats. The most prominent and diverse bee family is the Apidae (with more than 600 species), which includes the honey bee (*Apis mellifera*) and the bumblebees (*Bombus* spp.), whereas the least diverse family is the Melittidae, with approximately 40 described species.

The distribution of European bees shows very particular biogeographical trends (Fig. 4.1). A strongly marked north–south gradient appears in species diversity—with the maximum diversity being found in Southern Europe (Leclercq et al. 2023). Bees also show a higher abundance and richness in open environments with low tree cover (Michez et al. 2019). Combining those two factors, Southern Europe, with its Mediterranean climate and largely open vegetation, constitutes the area with the highest diversity of bees in Europe (including a significant proportion of endemics) (Reverté et al. 2023). Moreover, the richest areas in bee diversity in Europe are situated close to the two centres of diversity of the Western Palaearctic region: Morocco in the west and Turkey and Iran in the east (Lhomme et al. 2020). The areas closer to those hotspots are the places with the highest bee diversity in Europe, mostly Greece and Spain (Reverté et al. 2023). Out of these centres of richness, the abundance and the diversity of bees decrease.

4.2 Origins of Bee Diversity in Europe

Europe's geological history has exerted considerable biogeographical constraints, which have played only a minor role in the world's other Mediterranean-type regions. At the end of the tertiary period and the full quaternary period, Europe was an extensive sea scattered with islands, complex coastlines and abundant peninsulas (Graham 2014). The intricate pattern of seas and mountain chains created obstacles to dispersal but also numerous situations offering microclimatic protection. This generated conditions of isolation between geographical elements, highly favourable for the appearance of endemic taxa (e.g. Valente et al. 2010).

Upheavals generated by an intense series of geological events, starting with the Messinian crisis (5.5 My BP, end of the Miocene) and ending with the Quaternary glaciation (the last glacial event, encompassing the period c. 11,5000–c. 11,700 years

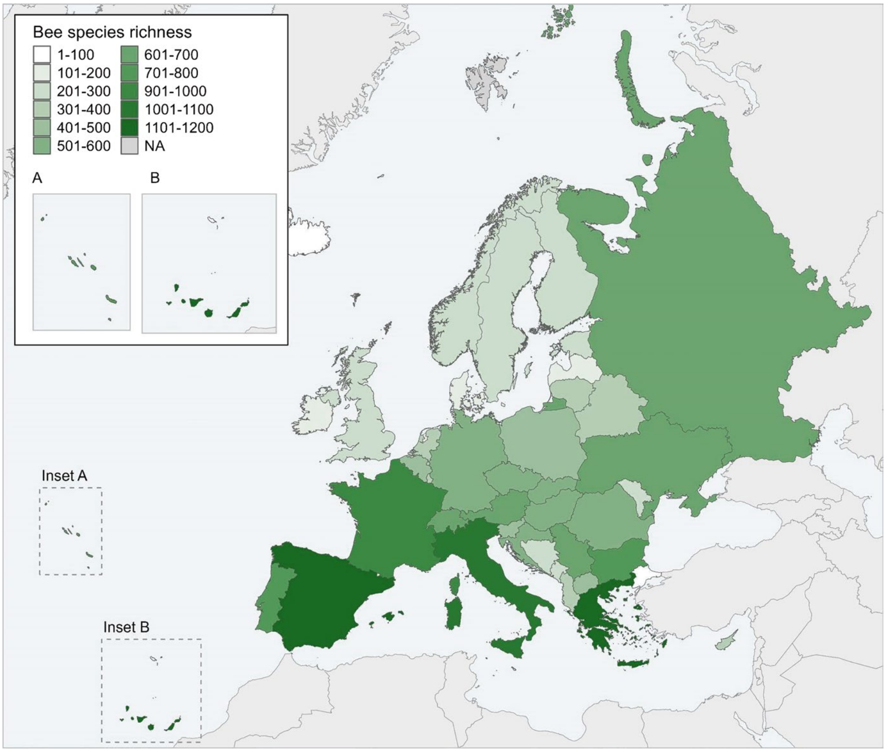

Fig. 4.1 Map of Europe, representing the richness of bee species recorded in each country (or subcountry unit) or its European part (cf. Reverté et al. 2023), where countries in grey were not included in this study (© 2024 by Denis Michez is licensed under CC BY 4.0)

ago), triggered notable changes in the faunal distribution on the continent. During the Messinian crisis, the Mediterranean dried up several times by losing its connection with the Atlantic Ocean. This event exposed a large abyssal plain of evaporates, well below the current sea level. All the Mediterranean islands became interconnected with the continent but with hot, arid and saline areas, acting as "climatic filters". This phenomenon offers insights into the current distribution patterns of species inhabiting the low-altitude regions surrounding the Mediterranean basin. During the glaciations, repeated falls in sea level (down to −150 m below extant values) again enabled the fauna to move between several islands and the continent. Most of the continent was covered in ice, and most European biomes persisted only in the southern peninsulas in those times, but they rapidly recovered, reaching their current distribution, soon after the glaciations had ended (13,000 to 10,000 years BP). As for other taxa, part of the current composition of the European bee fauna has been defined by the species' postglacial paths to recolonisation, as much as, if not more, by their ecoclimatic preferences (Hewitt 2004). However, for cold-adapted species, the mountain ranges around the Mediterranean Rim appear biogeographically as a series of islands, i.e. areas with weak to null interconnections. This implies that faunal differences between one range and another can be critical, with many instances of endemism. A maximum number of endemics and relictual taxa occur in the mountains of Corsica, Sardinia, Sicily and Cyprus. The same applies to isolated southern mountain ranges, including the Spanish Sierra Nevada or Mount Olympus in Greece (Minachilis et al. 2021).

4.3 Current Distribution Patterns and Extent of Occurrence of European Bees

Some bee species are widespread, from Southern European to Northern European countries (i.e. the Pan-European species *Halictus rubicundus*, Fig. 4.2a). Species like *Bombus cryptarum* or *B. jonellus* even extend their distribution to North America (Martinet et al. 2021b; Williams 2021). Many species are limited to southern areas, with a strong association with Mediterranean ecosystems (e.g. *Amegilla ochroleuca*, Fig. 4.2b), sometimes limited to the west (e.g. *Dasypoda crassicornis*, Fig. 4.2c), or to the east (e.g. *Hoplitis manicata*, Fig. 4.2d) (Kuhlmann et al. 2012; Rasmont 2014; Radchenko et al. 2022). A few species have a distribution centred on the most continental areas of Europe, dominated by the steppic biome (e.g. *Nomiapis femoralis*, Fig. 4.2e); (Pauly 2015).

Although the general rule is that the bee communities of Europe in southern regions are much richer in species than those in northern regions, most species of bumblebees (genus *Bombus*) stand out as important exceptions (Ghisbain 2021). Their diversity is strongest in the higher latitudes, and their abundance increases with increasing distance from the shores of the Mediterranean (Rasmont et al. 2021). They remain practically the only species of bees still common north of the 60th parallel (e.g. *Bombus alpinus*, Fig. 4.2f). The same gradient is found going from sea level towards the high mountains of the Mediterranean area, and bumblebees thus remain almost the only bees that fly at altitudes of over 2000 m in the Alps, the Pyrenees, the Balkans, the Atlas and the Caucasus (e.g. *Bombus alpinus*, Fig. 4.2f). This trend is likely linked to their highly developed endothermy and to their eusocial behaviour, which has enabled them to control the temperature at the colony level. However, bumblebees are not the only group featuring species showing distributions centred in the northern part of Europe and/or in the southern montane. Some non-bumblebee species, like *Dufourea alpina* or *Panurginus herzi*, also show distributions associated with Arctic and/or montane climates, varying in their extent across temperate regions (Patiny 2012; Patiny et al. 2014).

Notably, more than 400 species of wild bees are endemic to Europe, Melittidae being the family with the highest percentage of endemism and Megachilidae the family with the lowest proportion of endemics (Nieto et al. 2014). European endemic species are found mostly in restricted montane habitats (Alps, Cantabrian Mountains and Pyrenees: *Bombus mendax*; Sierra Nevada: *Andrena contracta*), on Atlantic islands such as the Canary Islands (e.g. *Pseudoanthidium canariense*) and on the Mediterranean islands of the Balearics, Corsica and/or Sardinia (e.g. *Anthophora sichelii*, *Panurgus corsicus*), Crete (e.g. *Ceratina teunisseni*) and Cyprus

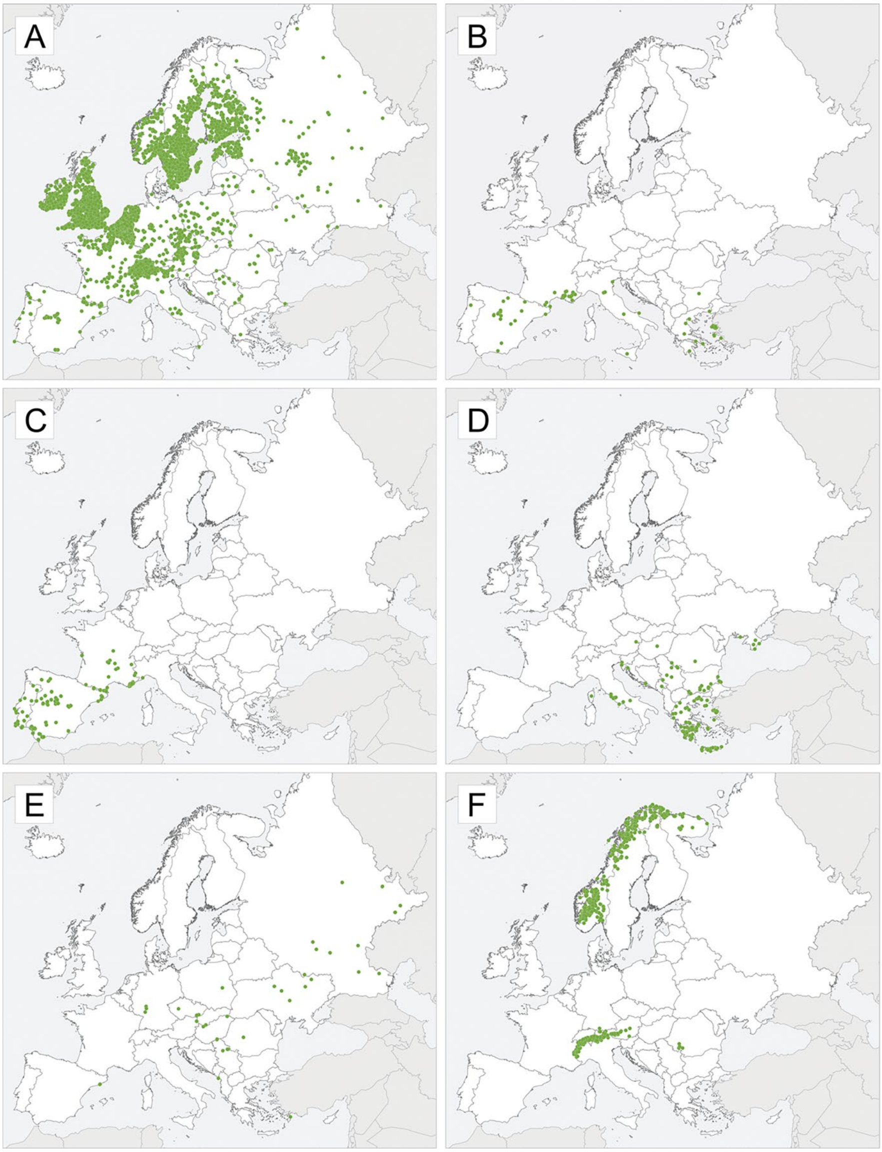

Fig. 4.2 Distribution of a selection of European bees, data for which were compiled in the framework of European projects Safeguard, Pulse and Orbit: (**a**) *Halictus rubicundus* (31,482 records); (**b**) *Amegilla ochroleuca* (444 records); (**c**) *Dasypoda crassicornis* (1589 records); (**d**) *Hoplitis manicata* (352 records); (**e**) *Nomiapis femoralis* (101 records); and (**f**) *Bombus alpinus* (2748 records) (© 2024 by Denis Michez is licensed under CC BY 4.0)

(e.g. *Megachile cypricola*) (Mavromoustakis 1938; Terzo 1997; Rasmont et al. 2021; Wood 2022; Vereecken et al. 2023). The Mediterranean peninsulas of Spain, Italy and Greece also show a higher percentage of endemic species (e.g. Ghisbain et al. 2023b; Reverté et al. 2023; Wood et al. 2020, Wood 2023).

Although the distribution of a large proportion of bee species can be explained by climate and land-cover variables (Ghisbain et al. 2020, 2023c; Casanelles-Abella et al. 2023), many species are recorded only locally, where complex combinations of landscape structure, soil texture, soil chemistry and/or floral communities are found in a given place. Microhabitats, and possibly microclimates, might act as pivotal filters explaining why superficially similar habitats under similar climates sometimes host distinct communities of bees (Fiordaliso et al. 2022). These habitats might host plant species on which bees are specialised (monolectic, oligolectic, mesolectic or heterolectic; see Michez et al. 2019; Wood 2023), in sufficient quantities (Müller et al. 2006), or soil types with the right granulometry and drainage in which they can found their nest and raise their offspring (El Abdouni et al. 2021). Species-specific ecological requirements in European bees are known for some well-studied species, but data explaining the realised niche of species are lacking for most Southern European taxa.

The current global changes in land use and climate can offer insights into what *was* necessary for some species to thrive given that the disappearance of certain landscape elements can directly affect the survival of populations (Le Buhn and Vargas Luna 2021). A good example includes the impact that agriculture-derived eutrophication has had on historical bumblebee communities, primarily attributed to an overabundance of nitrates in the soil resulting from industrial fertilisers (Rasmont et al. 2021). Such changes in soil chemistry have led to profound impoverishment in plant communities in various regions of Europe, with the cover of many plants from the Fabaceae family strongly decreasing from European landscapes. Other changes in agricultural practices, such as the abandonment of clovers (*Trifolium* spp.) for crop rotation have, in parallel, diminished the availability of these resources in landscapes. In response, bumblebee communities have largely followed this negative trend on the continent, and pollen-load analyses on these pollinators have indeed confirmed that Fabaceae constituted compulsory resources for the long-term survival of a large number of *Bombus* species (Wood et al. 2021). Although extirpations in bumblebees are also associated with many other changes in the environment and climate (Cameron and Sadd 2020; Martinet et al. 2021a; Rasmont et al. 2021; Raine and Rundölf 2024), this decline exemplifies how fine-scale landscape elements also substantially contribute to shaping bee communities on the continent.

Finally, the presence or absence of bees of a higher trophic level, namely brood parasites (sometimes referred to as kleptoparasites), can be indirectly explained by the same variables if the latter explain the presence of their hosts (Sheffield et al. 2013). Although the variables explaining why hosts and parasites do not always perfectly geographically overlap have not been thoroughly explored, differential physiological variables likely constrain parasites in regions where hosts can survive.

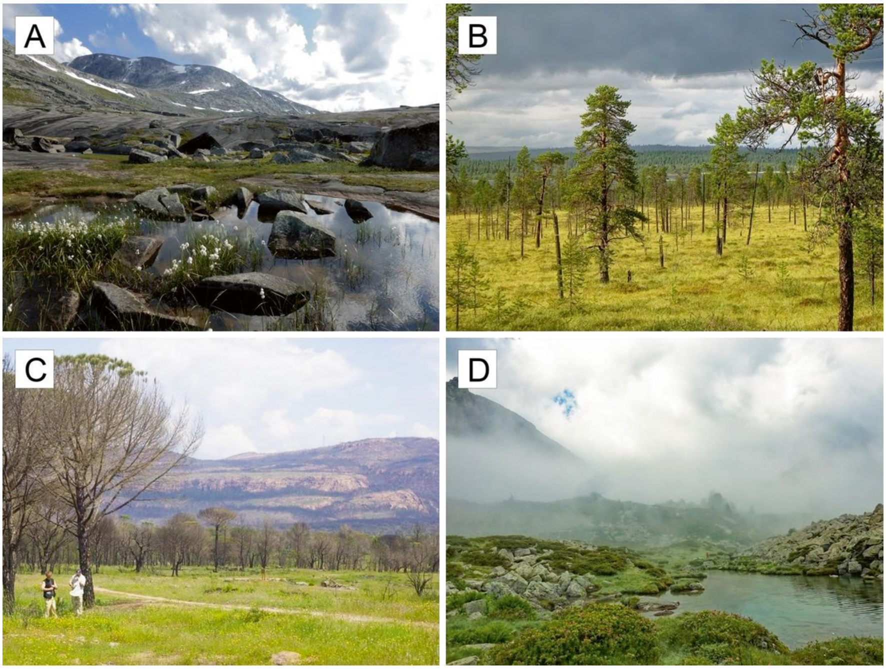

Fig. 4.3 Subset of different habitat types for European bees: (**a**) Alpine tundra in Norway. Most bee species occurring in such an environment are bumblebees (genus *Bombus*). (**b**) Boreal taiga in Sweden. This biome is especially rich in bumblebees and hosts more-modest communities of other bees, including *Andrena*, *Colletes*, *Lasioglossum* and *Osmia*. (**c**) Mediterranean habitat in southern France, 6 months after a fire. Mediterranean areas show high levels of endemism and remarkably high diversity in the tribe Anthophorini and subfamilies Xylocopinae, Nomadinae and Megachilinae. (**d**) Subalpine landscape in the French Pyrenees. A large diversity of bees are found in mountain biomes, including endemics, with bumblebees predominating at higher altitudes. Pictures by Pierre Rasmont. (© 2024 by Denis Michez is licensed under CC BY 4.0)

4.4 A Macroecological Perspective on European Biomes and Their Bee Faunas

Arctic deserts (Fig. 4.3a) have an extremely cold climate, the polar night lasting for several consecutive months. Their landscape is almost devoid of vascular plants, the ground is permanently frozen, and no bees are thriving. The tundra occurs further south, reaching the other side of the Arctic Circle. The climate is frigid with 8 to 10 months of continuous frost and temperatures frequently descending below −35 °C. Summer lasts 1–2 months, but frost and snow can still occur in the summer months. Most of the ground stays permanently frozen (as permafrost), and only the shallowest surface layers melt during summer. The tundra vegetation is rich in lichens and low-growing Ericaceae, with dwarf bushes like *Betula nana* (the dwarf birch) and *Salix lapponum* (the downy willow) or prostrate species like *Rubus arcticus* (the Arctic bramble) and *Salix reticulata* (the snow willow). The tundra supports numerous species of bumblebees, sometimes highly abundant (Kolosova and Potapov 2011; Kolosova et al. 2019; Rasmont et al. 2021). The biome is inhospitable to other bee species, with the exception of *Apis mellifera*, which has been locally recorded as an accidental migrant (Coulson et al. 2014).

The forest biomes of Europe consist of four major zones: the Nordic Forest zone of conifers, or taiga; the broadleaf forests; the Mediterranean sclerophyllous forest zone and the forest steppe. These biomes are not necessarily composed of continuous forest covers. Clearings and variously sized areas of heathland or scrubland occur where trees are sparsely scattered or absent.

The boreal taiga (Fig. 4.3b) stretches mostly from the 60th parallel to as far as the Arctic Circle. It bears woodland with conifers such as Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), larch (*Larix decidua*), common juniper (*Juniperus communis*) and deciduous trees such as birches (*Betula nana*, *B. pendula* and *B. pubescens*) and willows (*Salix* spp.). The understory is especially rich in Ericaceae (*Vaccinium* spp. and *Erica* spp.) and fireweed (*Epilobium angustifolium*). The most open communities of the taiga are Ericaceae heathlands and moorlands. These heath communities are intermingled with those among their counterparts that are associated with the broadleaf forest. Along the Atlantic coastline, these heath environments reach from Scotland and northern Norway to as far south as northwest Spain. The boreal taiga, with its woodland edges and clearings and its Ericaceae heathlands, is rich in bumblebees (Bolotov and Kolosova 2006). Solitary bees from the family Andrenidae (e.g. *Andrena lapponica*) and Halictidae (e.g. *Lasioglossum boreale*) can also be found in these biomes, along with a few Colletidae (e.g. *Colletes impunctatus*) and very few Megachilidae (e.g. *Osmia maritima*), and kleptoparasitic Apidae (e.g. *Nomada panzeri*) are even more rare (e.g. Söderman 1999; Paukkunen and Kozlov 2020).

The deciduous forest covers a vast expanse of terrain in the Western Palaearctic region. It extends mostly from the 40th parallel to the 60th parallel. In terms of climate, this largely broadleaf temperate forest grows under highly heterogeneous climatic conditions but with two constant features: a cold winter period of plant dormancy, without permafrost, and precipitation present almost throughout the year. A common feature in this extensive biome is the presence of deciduous oaks (*Quercus* spp.) or beeches (*Fagus sylvatica* or *F. orientalis*). However, such dense woodland can be interspersed with variously sized clearings. These open environments can be heaths composed of Ericaceae, damp grasslands if the humidity level is suitable or dry steppe-like grassland under more-arid conditions. This biome is very rich in bees, especially in the more open areas. All the bee families and practically all the genera are found there; however, Panurgini, Anthophorini, Eucerini, Melectini and several other tribes of Nomadinae are rather poorly represented, and some genera, like *Ancyla*, *Tarsalia* and *Ensliniana*, are totally absent and restricted to Southern Europe. Humans have been inhabiting and clearing deciduous forests for 1000 years. First, the landscape was considerably reshaped as people favoured the more open areas (heaths and dry steppe-like grasslands) because such areas are highly suitable for pastoralism. Woodland clearance made fields for cereal crops, which were devoted mainly to forage plants highly favourable for a great many species of bees (e.g. clover and sainfoin). The high fertility of most of the soils of this biome enabled the human population to grow substantially. Subsequently, this increase in demography and settlement demanded an intensification of agriculture. The result was the abandonment of forage crops and the replacement of pastoralism by intensive animal husbandry. The marginal lands long ago opened up by pastoralism have now been in a steady process of reforestation for almost a century. This phase of agricultural development has accelerated recently (since the mid-twentieth century). This phenomenon is particularly detrimental to the fauna and flora of open areas, with bees associated with open environments receding particularly strongly from this ongoing reshaping of the landscape (Goulson et al. 2015; Rasmont et al. 2021). However, some operations of habitat restoration have been proven to be successful, improving both the taxonomic diversity and the functional diversity of plant–pollinator communities as well as their interactions (Winsa et al. 2017; Öckinger et al. 2018; Rotchés-Ribalta et al. 2018). For example, the restoration of previously abandoned pastures not only reshaped the plant community composition but also profoundly increased both pollinator richness and abundance. Restored pastures were proven to provide new nesting sites, extremely helpful for ground-nesting bees, and potentially attract a distinct set of species that did not occur previously or in other habitat categories (Noreika et al. 2019).

The Mediterranean Forest zone (Fig. 4.3c) is largely delimited by climate characteristics: temperatures are high in summer, freezing spells are short or absent in winter, summers are dry, and rainfall is more or less abundant but concentrated between October and March. This biome is highly diverse in terms of floral communities (Cowling et al. 1996). It includes formations that can be strongly xeric with dry steppe-like grassland or woody shrubland, where the vegetation follows the rainfall patterns. A few species of mass-blooming shrubs flower during winter or early spring (*Rosmarinus officinalis*, *Thymus* spp. and *Erica* spp.) and numerous bulbous species flower during spring and autumn. A highly species-rich but scattered plant community is found during the summer drought, when most of the bee community is less active (Flo et al. 2018). Conversely, the Mediterranean also includes some humid formations with dense forests, particularly in the valleys. The vegetation characteristically comprises evergreen oaks (species such as *Quercus ilex*, *Q. suber* and *Q. coccifera*), pines (such as *Pinus pinea*, *P. pinaster* and *P. halepensis*) and numerous bushy ligneous plants, often evergreen (*Erica* spp., *Cistus* spp., *Pistacia* spp., *Rhamnus* spp. and *Olea europaea* var. *oleaster*, among others). Another fundamental characteristic of Mediterranean vegetation, which is visible only part of the year, is the abundant covering of annual plants with a high proportion of annual leguminous forms (*Trifolium* spp. and *Medicago* spp., among others) and Asteraceae (e.g. *Calendula* sp.). These annuals fade and disappear completely in summer, leaving large patches of bare ground, available for wild bee nesting.

The geographic boundary of the Mediterranean region traditionally coincides with that of the olive-growing area (*Olea europaea*). Its traditional northern limit corresponds to the town of Valence in southern France, on the 45th parallel. The southern boundary is more difficult to define but lies largely around the 30th parallel in North Africa. The Mediterranean biome is by far the richest in bee species in all parts of the world (Michener 1979), showing high levels of endemism that apparently reflect ecological resilience to multiple environmental stressors (Kantsa et al. 2023). The tribe Anthophorini and subfamilies Xylocopinae, Nomadinae and Megachilinae show remarkable diversity. Conversely, bumblebees are fewer in number and eventually absent in the hottest areas. Further up towards mountainous elevations, however, bumblebees again become more frequent and diverse (including European endemics such as *Bombus inexspectatus*, *B. konradini*, *B. mendax* and *B. pyrenaeus*), whereas most of the other Apoidea rarify. Human settlements can reach very high densities in the Mediterranean region, and their development has considerably modified the habitats once available for bees. In spite of these profound changes, the bee fauna in the Mediterranean area appears to have receded less in recent decades than that in mid-European areas (Patiny et al. 2009).

The forest steppe contains the most arid formations of the forest zone. In Western and Central Europe, these areas are designated as dry grasslands. In Eastern Europe, this formation occupies large expanses and is considered a distinct biome. In the forest steppe, the actual forest appears only as islands of vegetation amid vast herbaceous or scrub communities, and tree density can therefore be very low. The forest steppe seems to bear a strong resemblance to the true steppe, but its hydrological system, soil structure and vegetation differ significantly. The forest steppe hence appears as a transitional biome, with its northern and southern limits not clearly defined.

The general appearance of a steppe is an area of dry open terrain with sparse vegetation, resulting in a large proportion of bare ground with greyish leaves amid sparse plant cover. Paradoxically, a plant survey will often reveal a diversity of plant species surpassed only in the Mediterranean environments. Similarly, entomological expeditions will confound first impressions of barren ground: steppes are highly diversified and very rich in insects (Přidal and Veselý 2014; Bogusch et al. 2020). The climatic parameters associated with steppes include low rainfall, generally less than 300 mm per year. A steppe is therefore a plant community functioning under a chronic water deficit. Starkly contrasting winter and summer temperatures (continentality) are the usual climatic patterns associated with this biome. Steppic landscapes are devoid of trees, except for isolated thickets. They support communities comprising a great number of grass species and lignified leguminous plants. These plants have a characteristic growth form in cushion-like tufts, and they yield proportionally less plant cover than bare ground. The result is a scene of a regular scattering of cushion-like tufts separated by extensive patches of bare soil. Steppes occurring within European areas are distributed over its eastern reaches, limited to the north by a line running roughly from Kiev to Saratov to Urals, between 50° and 51° N. This biome covers a large expanse of territory in Ukraine, also from Moldavia and the south of Russia. Out of these main areas, steppes are found here and there in atypical forms in Romania (Transylvania), Hungary and the east of Austria (Lower Austria and Burgenland) (Zimmermann et al. 2023). In Spain, the steppe occupies a large proportion of the province of Almeria in the south and, further north, the plateau of Old Castile and the Upper Basin of the Ebro. The steppes are very rich in rare and/or threatened Anthophorini (e.g. *Anthophora fulvipes*), Eucerini (e.g. *Eucera hungarica*), Megachilidae and Halictidae (Heneberg et al. 2019). The most arid steppe areas are the poorest in terms of species diversity, especially in bumblebees.

Mountain biomes (Fig. 4.3d) differ from those of the adjacent plains in that they have a temperature that decreases with altitude (by −6° to −9 °C per 1000 m) and more-abundant precipitation. Mountainous environments also offer innumerable microclimatic situations due to slope effects and variations in relief forms. Moreover, even the most southerly located mountains of the region experience an icy spell above a certain altitude. Altitude acts clearly as an environmental filter on phylogenetic composition, traits and diversity in European bee communities (Hoiss et al. 2012).

In the northern parts of Europe (the Scandinavian Peninsula, Finland and the north of Russia), the mountains harbour fauna and flora almost identical to those living on the plain at a higher latitude. The Anthophila found at the upper mountain stages of the Scandinavian Peninsula and the Urals, exclusively bumblebees, are species characteristic of the tundra.

The mountains of Central Europe are clearly differentiated into mountain, subalpine and alpine stages. The characteristic plant communities are not duplicates of the biomes on the plains situated at higher latitudes. Many of the climate characteristics of these mountains are remarkably different, including sunlight pattern and duration, inclination and the spectral composition of the light, seasonal variations and precipitation. For example, the mountains of Southern Europe are all strongly influenced by the Mediterranean type of climate, with rainfall at a minimum level in summer. Such climate characteristics pose a dual challenge to the local flora and fauna: a cold winter followed by a summer drought. The following habitat types can be distinguished:

- *Hill or mountain stage on north-facing slope in the shade for part of the day* (“*ubac*”). The mountain beech (*Fagus* spp.) woodland, particularly on ubac sites, is frequently mixed with silver fir (*Abies alba*) and even Norway spruce (*Picea abies*). These environments are poor in bee diversity.
- *Hill or mountain stage on the side of a valley that is less exposed to the sun (“adret”)*. The mountain pine woods with Scots pine (*Pinus sylvestris*) and black pine (*Pinus nigra*) are established on adret slopes. They are drier and better lit than ubac forests. The Anthophila of these dry light adret forests can be highly diversified and abundant. Species of European deciduous forests are found there, with some subalpine species appearing.
- *Subalpine stage on ubac slopes*. The vegetation is, in general, a conifer forest made up of Norway spruce (*Picea abies*), European larch (*Larix decidua*) and various pines like Swiss pine (*Pinus cembro*) or mountain pine (*Pinus uncinata*). These subalpine forests often have an underwood very rich in Ericaceae. They are highly favourable for bumblebees, which show enormous diversity and abundance, but few other bees are present (Baumann et al. 2021; Minachilis et al. 2020).

- *Subalpine stage on adret slopes*. The subalpine forest type of ubac slopes is often replaced by more- or less-arid subalpine meadows. Altogether, these landscape features form a mosaic according to the degree of aridity in the natural conditions. This subalpine mosaic is the most favourable environment for bumblebees but also for other bees, such as Halictidae, Andrenidae or Osmiini (Maihoff et al. 2023).
- *Alpine stage*. This is characterised by locally persistent névé. No trees appear here. It begins at 2000 m (6000 ft) in the northern Alps and at around 2300 m (6900 ft) in the inner Alps and Pyrenees. The vegetation may consist of rhododendrons (*Rhododendron ferrugineum* or *R. hirsutum*) in alpine meadows rich in *Gentiana* spp., corridor and scree vegetation and snowbed plants. The bee fauna (particularly some bumblebees and Panurginae) form a large proportion of the species of the subalpine adret stage but with a steadily decreasing number of species at increasing altitudes (Peters et al. 2016; Sponsler et al. 2022).

4.5 Gaps and Future Research on European Bee Distribution

Nature conservation in Europe is at a turning point with the recent vote on the Nature Restoration Regulation by the European parliament. Many challenges associated with the growing pressures of land use and climate change are ahead. Conservation actions must be taken according to a robust and accurate knowledge of the spatial distribution of wild organisms to tackle the Wallacean shortfall (Garnett and Christidis 2017; Mace 2004; Orr et al. 2021). Precisely identifying hotspots of diversity (i.e. species, functional and phylogenetic diversity) is key to implementing efficient action plans for safeguarding wildlife, both locally and at a continental level. This is especially true for bees, for which taxonomic revisions are still currently undertaken across most clades (e.g. Bossert et al. 2022; Dorchin and Michez 2024; Wood 2023). Although the current knowledge on the European bee fauna is substantial (Michez et al. 2019), new species are still frequently described (e.g. Ghisbain et al. 2023a; Praz et al. 2019; Radchenko 2017; Wood et al. 2020). Such updates, fundamental to refining the knowledge of the bee fauna of the continent, also demonstrate that many uncertainties persist in the taxonomy and distribution of European wild bees (Ghisbain et al. 2023b; Reverté et al. 2023). These uncertainties not only hinder our ability to accurately identify both museum specimens and freshly collected material but also impede our understanding of their temporal and spatial distributions, limiting the efficiency of action plans. This issue was exemplified in the first Red List of European Bees, in which ~55% of all bees reported on the continent had to be classified as "data deficient" (DD) (Nieto et al. 2014). In this work, although ~9% of bees were considered threatened, the real percentage of threatened taxa would have been between 4% (if none of the DD species were threatened) and ~60% (if all of the DD species were threatened). This knowledge gap is substantial given that data from other animal groups suggest that both unassessed and DD species are more likely to be threatened with extinction than their fully assessed counterparts (Caetano et al. 2022; Howard and Bickford 2014).

Regarding bee data, Marshall et al. (2024) recently identified key areas in Europe where knowledge gaps should be filled. They advocate "the long-term goal to mobilize and aggregate European wild bee data into a multi-scale, easy access, shareable, and updatable database which can inform research, practice, and policy actions for the conservation of wild bees." This goal is being partly filled by current European projects, namely SAFEGUARD (https://www.safeguard.biozentrum.uni-wuerzburg.de/), ORBIT (https://orbitproject.wordpress.com/) and the IUCN European Red List reassessment (https://www.iucnredlist.org/). In this context, a new aggregated and validated dataset of more than five million records of European bees will be soon published. However, more work on the taxonomy, biogeography and ecology of European wild bee species is clearly still urgently required. Most of the available data were collected opportunistically in time and space, with poor information on the level of spatial precision. We hope that an ambitious programme of European pollinator monitoring (EU-PoMS) will be soon implemented to develop adequate conservation strategies for the European bee fauna (Potts et al. 2020).

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