SAFEGUARD

Identifying the relationship between habitats, diversity and conservation of European pollinators

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Summary

Habitat loss and alteration are widely recognized as primary drivers of the current decline in pollinator diversity. However, there is still limited understanding of habitat preferences and specialization among major pollinator groups. Specifically, a comprehensive European synthesis of habitat preferences across various biogeographical regions is lacking. In this context, large-scale databases of occurrence records collected at the continental level offer valuable insights into the significance of different habitats for pollinator diversity and species-specific habitat preferences. Understanding these preferences is crucial for devising effective conservation measures for endangered species, including those listed on red lists.

In this study, we aim to empirically rank and evaluate the importance of different habitats for bee and hoverfly pollinators, determine their habitat preferences and avoidance, and quantify the diversity of pollinators within and among habitats. Utilizing the first pan-European dataset of wild bees and hoverflies generated within the Safeguard project, we characterized the species pools associated with specific habitats. By focusing on beta-diversity patterns, we elucidated the requirements for habitat complementarity at both regional biogeographic and continental scales. Additionally, we assessed the effectiveness of the Natura 2000 network of protected areas for pollinators. Due to the spatial resolution of the data, we were unable to evaluate the importance of urban habitats for pollinator conservation.

Our analyses revealed significant compositional differences in pollinator species pools across various European biogeographical regions and between habitats within the same region. For wild bees, Mediterranean areas were particularly important, exhibiting high species diversity and unique species compositions. Complex Mediterranean landscapes with woody vegetation supported the highest number of specialist species. In contrast, hoverflies displayed a more balanced distribution of species diversity across different regions, with the Alpine region being notably diverse.

For both wild bees and hoverflies, beta-diversity between habitats was significantly higher within Mediterranean areas compared to other biogeographical regions, underscoring the conservation priority of all Mediterranean habitats, even where species diversity may not be the highest. Agricultural-dominated landscapes showed low diversity and a low occurrence of specialists, thus receiving a lower conservation priority across Europe. Deciduous forests, particularly for hoverflies, exhibited high ecological uniqueness due to their significant dissimilarity from other habitats. For wild bees, complex landscapes comprising multiple habitats demonstrated the highest diversity.

The current network of protected areas appears insufficient for protecting bees at European scale, particularly in colder regions where protected areas are predominantly located at high elevations where climate is often too cold for bees. For hoverflies, the

effectiveness of existing protected areas varied across biogeographical regions, indicating a need for region-specific conservation strategies. Maintaining a high diversity of habitats listed in the Habitat Directive seems an appropriate strategy for protecting bees across Europe, with the exception of the Mediterranean region, where a general increase in land protection measures may be more effective. In contrast, habitat diversity was less important for hoverflies. The contrasting patterns observed between bees and hoverflies and between biogeographical regions highlight the challenge in formulating effective policies for pollinator conservation across whole Europe. In particular, the stark contrast between south and north in terms of species uniqueness and sampling completeness requires urgent research initiatives to fill these important knowledge gaps in species distribution and species-habitat preferences.

1. Introduction

Despite habitat loss and alteration being widely considered among one of the main drivers of current pollinator diversity loss (Senapathi et al., 2015), little is known about habitat preferences and specialization for major groups of pollinators. Trends of pollinator abundance and/or species richness across habitat types still under debate: while some authors reported lower diversity in forests compared to more open habitats such as semi-natural grasslands and low-intensively managed habitats (Winfree et al., 2011), others indicated opposite trends (Ganuza et al., 2022). However, the empirical literature is dominated by studies on species richness that do not reveal changes in species composition such as replacement of specialists with common generalist species. Many studies compared moderately anthropogenic habitats such as pastures, fallows, and urban green areas with more intensive land uses, typically intensive agricultural habitats, finding that the loss of semi-natural habitats has negative effects on pollinators. This body of work provides additional support for the hypothesis that moderate human land use is compatible with the persistence of at least some pollinator species. However, we still lack a European synthesis on preferences for specific habitat types across different biogeographical regions. Against this background, large databases of occurrence records collected at the continental level can provide a better picture about the importance of different habitats for pollinator diversity and about species habitat preferences (Collado et al., 2019). The latter are crucially important to derive effective conservation measures for endangered species such as those included in red-lists (Nieto, 2014).

In Europe, insect pollinators are a complex guild of species belonging to several orders that greatly differ in their life styles, traits, resource and habitat needs. At present, there is no exhaustive evaluation of the relative importance of the different pollinating taxa for European wild flora and crops (Rader et al., 2020). However, with the exception of the coldest regions in Europe bees can be considered the predominant pollinators for most plants and are present in a wide variety of terrestrial habitats. Besides bees, hoverflies are a second very important and well-studied group. While hoverflies are recognized as important pollinators in many landscapes, much of the information is derived from temperate or Mediterranean regions and future research should aim to address this imbalance (Doyle et al., 2020). Also, non-syrphid dipterans are acknowledged as key pollinators in alpine and subarctic ecosystems where bees are less abundant (Orford et al., 2015; Tiusanen et al., 2016).

Here, we aim to empirically rank and assess the importance of different habitats for bees and syrphids, to determine their preferences and avoidance of habitat use and to quantify the diversity of pollinators within and among habitats. Based on the dataset generated in T1.1, we also aim to characterize the species pools associated with particular habitats. Here we used the landscape structure of habitats at a large spatial scale (10km), considering the overall

composition depending on the biogeographical area. Focusing on beta-diversity patterns, we will elucidate the requirements of habitat complementarity at the regional level (Marini et al. 2019) across the EU. Finally, based on the previous results and using available spatial datasets (e.g. COPERNICUS) we will also evaluate the representativeness of the Natura 2000 network of protected areas for pollinators and the relationship between habitat and pollinator diversity.

2. Materials and methods

2.1.   Pollinator data

We used data of bees and hoverflies for the whole Europe. The two datasets were delivered on the 14th of March 2024 by the WP1 team. Datasets have been compiled separately. Because of structural differences (type of data and information available) among the datasets and the different biology of the groups, we analyzed the data separately. Both databases were cleaned by removing records before 1990 to match the age of the habitat data at the European scale. Both bee and hoverfly data were provided with coordinates. However, many of those were referred to centroids or localities. Discriminating those having precise coordinates with high resolution (~c. 10 m) from those associated with broad resolution (a few km) was not possible because many of these issues were inherent to the original data sources. For that reason, we used a 10 km grid and aggregated information at this broader resolution. For this purpose, we used the official map of the European Biogeographical Regions (EBRs), which contains the official boundaries used in the Habitats and Birds Directives, originally provided by the European Environment Agency and recently updated with an European classification of biogeographical regions (Cervellini et al., 2020). Pollinator data were pruned by keeping only those records with an associated grid cell. We aggregated pollinator data per cell and calculated the number of independent observations (for each locality and sampling date) for each species.

2.2.   Habitat classification

First, we divided Europe in biogeographical regions following Cervellini et al. (2020). We selected the most important biogeographical regions at the European scale focusing on the mainland: Alpine, Atlantic, Boreal, Continental, Mediterranean, and Pannonian.
Then, we used the CLC+ Backbone product from Land Monitoring Service of Copernicus to retrieve habitat information (https://land.copernicus.eu/en/products/clc-backbone). The CLC+ Backbone is a 10 m pixel-based land cover map based on Sentinel time series from July 2017 to June 2019. For each pixel, it shows the dominant land cover among the 11 basic land cover classes: sealed, needle-leaved trees, deciduous broadleaved trees, evergreen broadleaved trees, low-growing woody plants (bushes, shrubs, and permanent woody crops), grasslands, annual agricultural fields, lichens and mosses, sparsely-vegetated lands, water, and permanent snow. Within each biogeographical region, each cell was categorized based on the habitat mosaic using the K-means clustering algorithm. We used the function fviz_nbclust() function of factoextra() package to visualize the total within sum of square plot and inform the number of clusters. We named each cluster based on the habitat composition of the centroid.

Table 1 Classification of the 10 x 10 km grid cells based on the K-means centroids. Figures are % habitat covers.

Biogeographical regions	Cluster names	Agricultural	Deciduous broadleaves	Evergreen broadleaves	Coniferous	Low-growing woody	Grassland	Sealed	Snow	Sparsely vegetated	Water	Lichens and mosses
Continental	Agricultural	65	10	0	3	1	15	4	0	0	1	0
Continental	Conifers	12	15	0	44	1	22	3	0	0	2	0
Continental	Broadleaves	8	60	0	6	2	21	2	0	0	1	0
Continental	Mosaic	37	19	0	9	2	24	6	0	1	3	0
Continental	Grasslands-broadleaves	13	25	0	9	2	42	6	0	1	2	0
Alpine	Conifers	1	13	0	49	3	26	1	0	3	3	0
Alpine	Above-treeline	0	6	0	5	1	28	0	5	45	6	5
Alpine	Grasslands	1	12	0	9	3	57	1	0	8	6	5
Alpine	Broadleaves	4	54	0	11	2	23	2	0	2	2	0
Mediterranean	Mosaic	19	7	8	5	11	28	8	0	6	8	0
Mediterranean	Grasslands	8	4	11	3	10	58	2	0	2	2	0
Mediterranean	Agricultural	59	3	5	2	5	17	2	0	5	1	0
Mediterranean	Low-woody	5	5	8	10	40	19	2	0	7	5	0
Mediterranean	Broadleaves	4	51	4	6	8	21	2	0	2	1	0
Mediterranean	Conifers	4	9	5	43	17	14	2	0	3	3	0
Mediterranean	Evergreen-broadleaves	5	5	41	5	13	20	4	0	2	3	0
Atlantic	Mosaic	7	20	2	13	5	29	7	0	4	12	1
Atlantic	Agricultural	50	14	0	3	1	25	6	0	0	2	0
Atlantic	Grasslands	6	8	0	5	3	68	3	0	2	5	0
Boreal	Agricultural	44	14	0	16	1	19	2	0	1	2	0
Boreal	Conifers-large extension	1	5	0	70	0	18	0	0	1	5	0
Boreal	Conifers-middle extension	7	12	0	49	1	18	2	0	1	11	0
Boreal	Mosaic	12	25	0	21	2	34	2	0	1	4	0
Boreal	Freshwater	2	6	0	20	0	7	1	0	2	62	0
Pannonian	Agricultural	69	9	0	0	2	16	3	0	0	1	0
Pannonian	Broadleaves	25	36	0	3	4	25	4	0	0	2	0
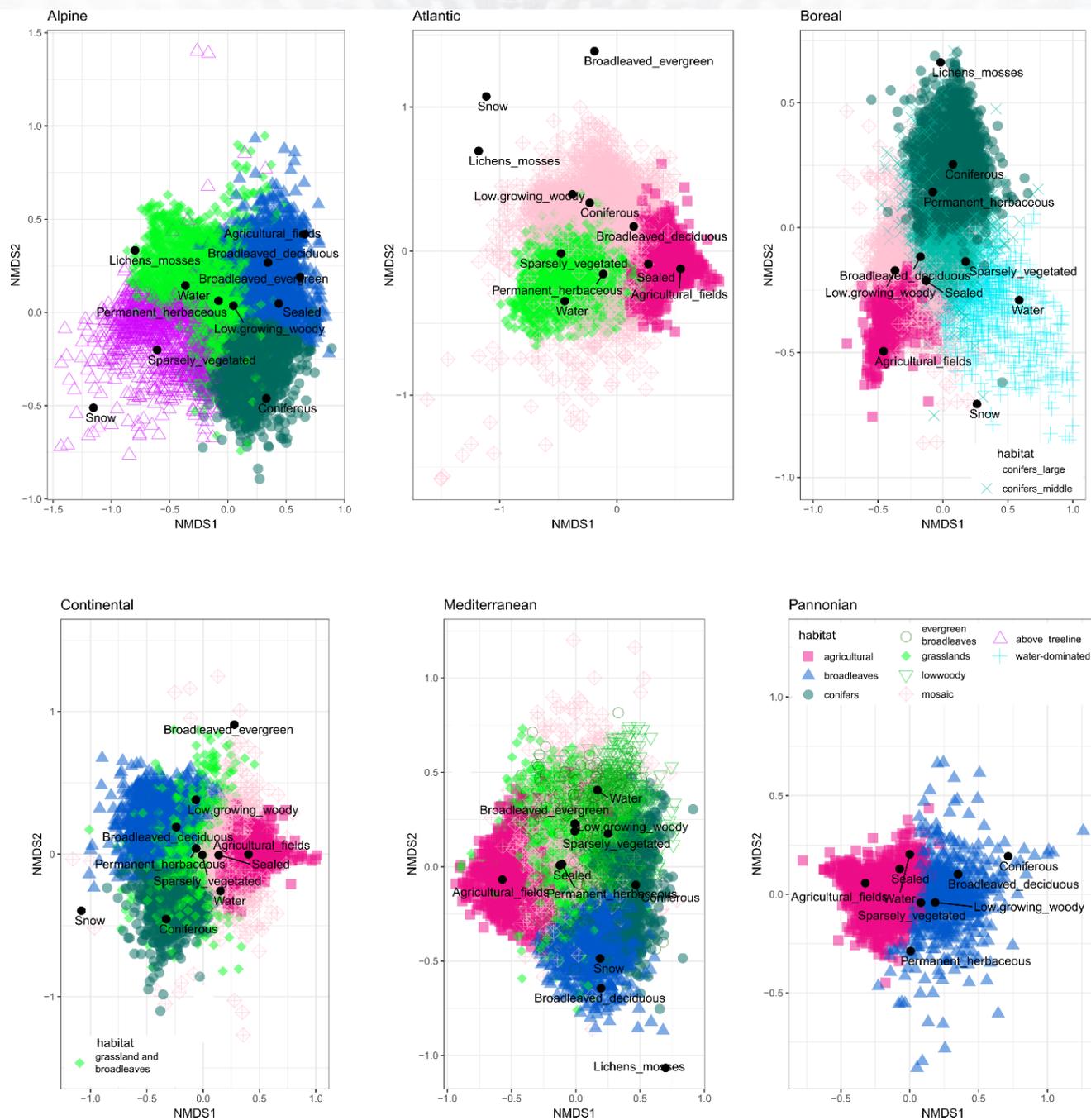
Figure 1 Visualization of the habitat clusters for each biogeographical region through non-metric multidimensional scaling (NMDS). Different habitats are shown with different colours and shapes. Centroids of landcover categories are shown.

2.3.   Data analysis

2.3.1. Meta-network at the European scale

At the European scale, pollinator data were organized in a species by cluster (a combination of biogeographic region and habitat) matrix by summing the independent observations for each cell. We removed singletons in European matrix before analyses. First, to test the sampling completeness in each habitat (i.e., cluster) we computed the sample coverage using iNEXT package in R (Hsieh et al., 2016). Second, to understand the importance of each habitat at the European scale, we computed for each biogeographical region by habitat combination the estimated richness using estimateD() function in iNEXT, and the strength using strength() function in bipartite (Dormann et al., 2008). Node strength quantifies how strongly a node is directly connected to other nodes in the network (i.e., by summing all absolute edge weights of edges connected to the given node). Finally, we computed the pairwise beta diversity using betapair() function in betapart package (Baselga and Orme, 2012). We used the Jaccard family and extracted the turnover component of beta diversity. Results were visualized using hclust() function with an average clustering algorithm with turnover component as distance.

2.3.2. Habitat importance within different biogeographical regions

Within each biogeographical region, data were organized in a species x habitat adjacency matrix by summing the independent observations for each cell. Then, we repeated the analyses described in the section above within each biogeographical region.

2.3.3. Species preferences

To test the importance of different habitats, we assessed the habitat preference of each species. First, we used the European meta-network without singletons to compare all the biogeographical regions across Europe. We generated 1000 random null models of the entire meta-network using the Patefield algorithm (Collado et al., 2019). Then, we categorized each species in "exploiters", i.e. species occurring more than 95th percentile of the null distribution in a given habitat and "avoiders", i.e. species occurring less than 5th percentile of the null distribution in a given habitat. To test whether habitat preference changed along biogeographical gradients, we repeated the habitat preference analyses within each biogeographical region, separately.

2.3.4. Habitat protection and diversity of habitat included in the Habitat Directive

First, for each 10 x 10 km cell, we estimated the rarefied species richness at 60% for both pollinator groups. Second, we computed the area covered by protected areas (including N2K sites) using the official polygon layer of Natura 2000 sites and the Emerald pan-European network of protected areas (European Environment Agency, www.eea.europa.eu). Third, we also retrieved the distribution of protected habitats under the Habitat Directive (European Council, 1992) from the European Environment Agency Datahub (www.eea.europa.eu). This dataset is based on the same 10 km grid we already used to aggregate pollinator data. For each cell, we counted the number of unique terrestrial protected habitats (i.e. included in the Habitat Directive). Then, we tested the cover of the protected area (we distinguish between all protected areas and only N2K areas), the number of unique habitat protected and biogeographical region as the explanatory variables, and the rarefied richness at the same sample coverage (60%) as the response variable. We used spatial lag models to account for spatial autocorrelation. Before the analysis, we removed the cells with less than 60% of sample coverage. As sensitivity analyses, we also rerun the analyses using 80% sample coverage as the new threshold.
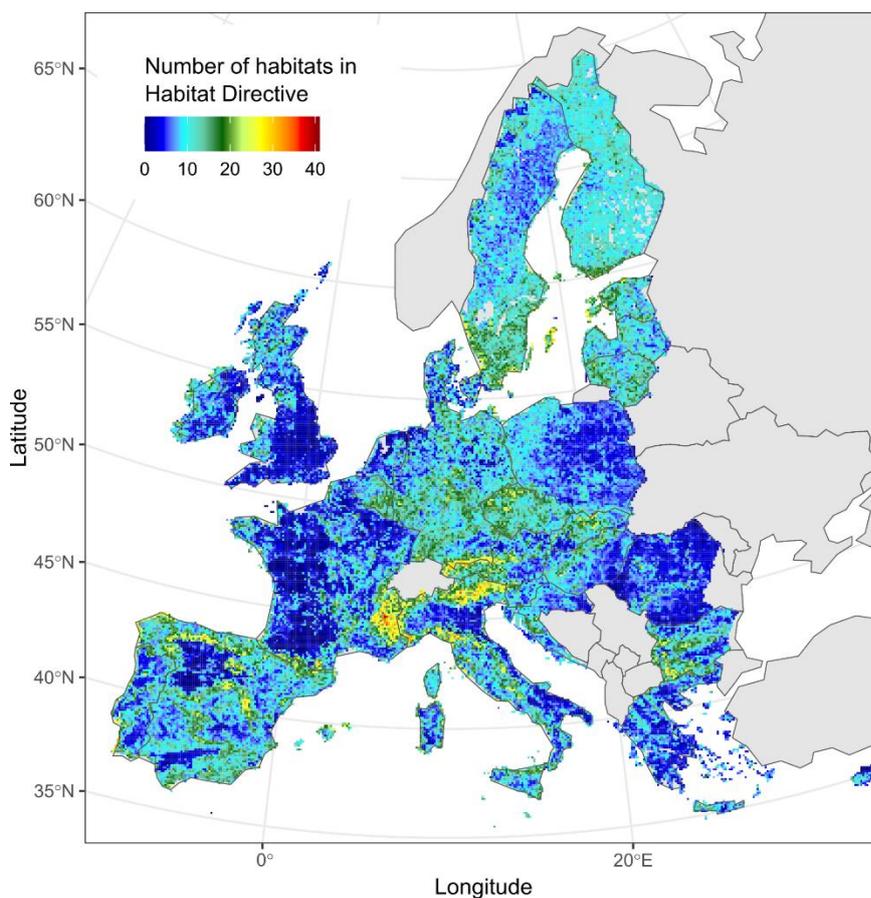
Figure 2 Distribution of terrestrial protected habitat in Europe in a 10x10 km size grid.

2.3.5. Community uniqueness

We used aggregated data at 50 km grid size to compare the sampling effort in different regions of Europe. We used a larger cell size to improve species coverage. We used presence/absence data to compute the sample coverage for each cell. For the following part, we used cells with at least 60% sample coverage to compare the communities, but as sensitivity analyses, we conducted the same analyses using 70%, 80%, and 90% thresholds for sample coverage. To highlight those areas contributing more to the overall beta diversity in Europe, for each cell we used a beta-uniqueness index (Local Contribution to Beta Diversity) (Legendre and De Cáceres, 2013) to estimate its importance. Cells with a high percentage of rare species or unique species assemblages have a higher value. A 999-permutation procedure has been used to assess the significance of uniqueness. We used a moving window to calculate the proportion of neighboring cells (8-neighbors rule) having more than 60% sample coverage. We used binomial models (the LCBD-significant as a response variable; 0 non-significant LCBD, 1 significant LCBD) to test the relationships with the observed richness in the cell and the percentage of neighbor cells with less than 60% sample coverage.

To better visualize the differences among communities at the European scale, we used a PCoA based on the turnover component of the Jaccard dissimilarity index and we assigned a rgb color scale using the first three axes.

3. Results and discussion

3.1.   General results

The six biogeographical regions presented different habitat diversity. As expected, the Mediterranean region had the highest number of unique habitats (7) followed by the continental and boreal regions. At the 10 km resolution a large proportion of European landscapes were characterized by a mosaic of different habitats. The habitats that occurred in all biogeographical regions were: agricultural fields (annual crops), grasslands, conifer forests, broadleaved forests, and complex mosaic. The alpine region presented sparse high elevation habitats while the Mediterranean presented low shrub habitats. Due to the relative large spatial resolution of our data compared to the scale of urban aggregation, urban habitats were present with low cover in almost all the habitat clusters.

Due to the large number of records included in the dataset, sampling coverage was very high for all habitat clusters with values close to 100% for both bees and hoverflies, i.e. the habitat clusters can be compared due to their sampling completeness. This was an expected result considering the relatively small number of species compared to the number of occurrence records.

3.2.   Species-habitat meta-network at the European scale

For bees, the species-habitat network at the European level clearly indicated that the Mediterranean region represents a species diversity hotspot (Figure 3). In this region, all habitat clusters presented the highest diversity. Within the Mediterranean region, the strength values for these habitats varied substantially, being lowest in agricultural-dominated clusters, intermediate in forest and grassland clusters, and highest in complex mosaic and complex low woody vegetation. This is because the strength value for a habitat cluster does not only increase with species richness but also when the species are highly dependent on that particular habitat. All other biogeographical regions presented much lower diversity. However, the complex clusters characterized by high habitat diversity also had higher strength values in non-Mediterranean regions.

For hoverflies, the pattern was very different with forest habitats (especially in the Alpine and Mediterranean regions) presenting higher diversity than the others. Overall, complex clusters tended to have higher strength indicating that many species were highly dependent on this type of landscape. Clusters dominated by agriculture were those with the lower diversity and strength. Again, strength values should be used to compare habitats with similar degree (i.e. species richness).
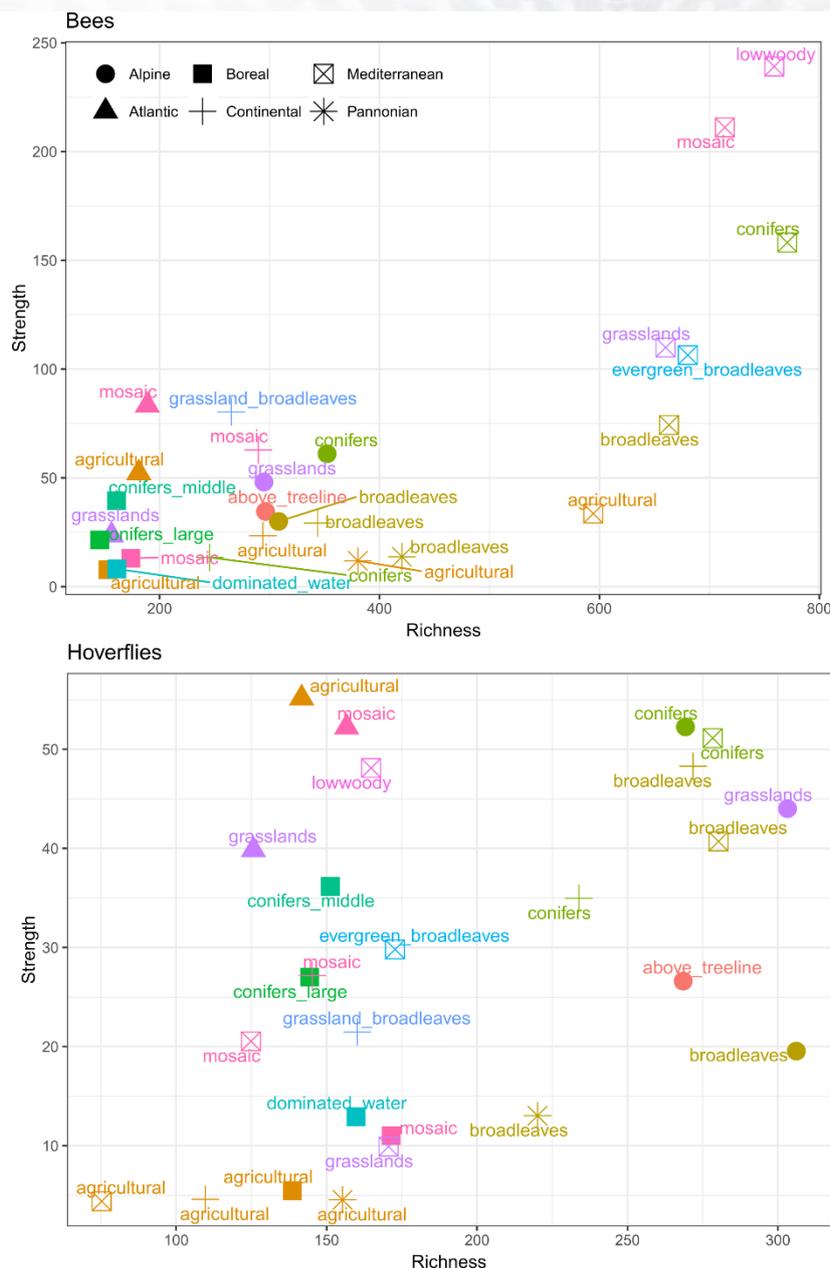
Figure 3 Scatterplot showing raw species richness and strength for each habitat by region cluster at the European level. As strength increases with both species richness and species dependency on that specific habitat, a positive relationship between richness and strength is expected.

The beta-diversity analysis of the European meta-network based on the turnover component showed strong biogeographical patterns. For bees, two main clusters emerged: Mediterranean-Pannonian and a cluster of three cold-climate regions (Boreal, Atlantic and Continental). The differences between habitats within these clusters were less pronounced indicating that many species are able to use landscapes with contrasting compositions (Fig. 4).
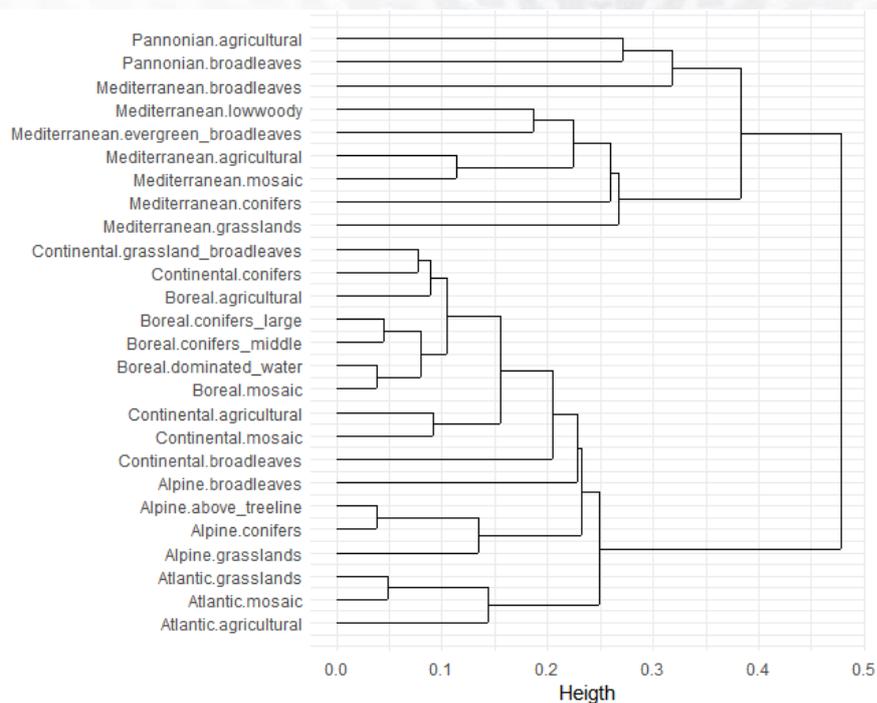
Figure 4 Cluster representing the similarity in species pool between biogeographical regions and habitat. The distance represents the turnover component of beta diversity for the bees.

For the hoverflies, we consistently found a strong biogeographic structure of the data. However, there are also a few associations based on the habitat type, such as the coniferous forests of the Continental and Alpine regions (Fig. 5). Again, we found a strong distinction between the Mediterranean cluster and the others, with the Pannonian in between.
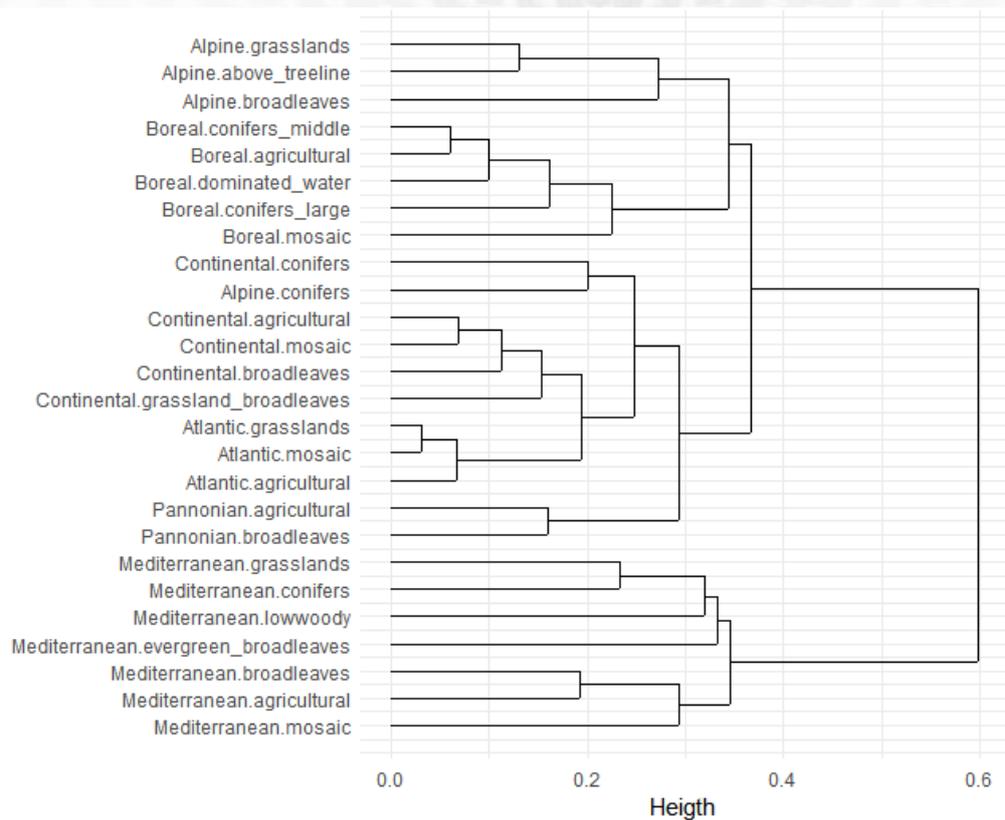
Figure 5 Cluster representing the similarity in species pool between biogeographical regions and habitat. The distance represents the turnover component of beta diversity for the hoverflies.

3.3.   Habitat importance within different biogeographical regions

In this section, we present the scatterplot of diversity and strength for each biogeographical region for bees. Since sampling coverage was very similar between regions and habitats within regions, we could use non-rarified original data sets.

Bees

In the Alpine and boreal region, the complex coniferous cluster was the habitat with more specialists (Fig. 6). This cluster includes montane and subalpine forests interspersed with grasslands hosting several high-elevation specialists (Hoiss et al., 2012). However, in the alpine region, very high-elevation areas (above the tree line) presented the lowest strength indicating that bees found there are mainly a subset of the species pool inhabiting lower elevations. In the Atlantic region, the mosaic cluster was the most important habitat for bees while grassland- or agricultural-dominated clusters were mostly composed of generalists. The dominated-agriculture habitats in Continental, Pannonian and Mediterranean regions were those with lowest strength, while the complex clusters were those with the highest strength.
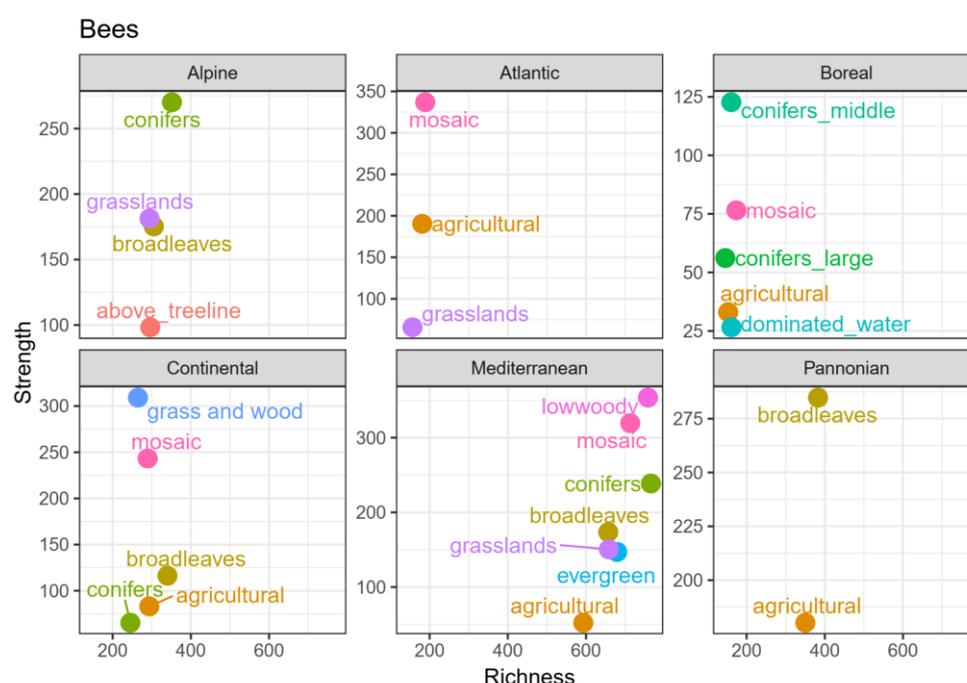
Figure 6 Scatterplot showing raw species richness and strength for each habitat within each region. As strength increases with both species richness and species dependency on that specific habitat, a positive relationship between richness and strength is expected.

The beta-diversity analysis indicated that the Mediterranean presented the highest dissimilarity in species composition between habitats (Fig. 7). The uniqueness of the habitats in this region suggests a high priority for bee conservation. In particular forest habitats were

more dissimilar in terms of species composition. The continental and Alpine regions also exhibited relatively high beta-diversity between habitats with the deciduous forests showing the highest dissimilarity from other habitats. Boreal and Atlantic regions were those with the lowest dissimilarity between habitats indicating a high degree of biotic homogenization.

Considering the whole Europe, all the Mediterranean habitats were well distinct from the others (Fig. 8). The Boreal region was characterized by a low dissimilarity compared to the other northern regions (i.e., Atlantic, Continental, and Alpine). The highest dissimilarity was between the Mediterranean agricultural area and habitats in the Boreal region.
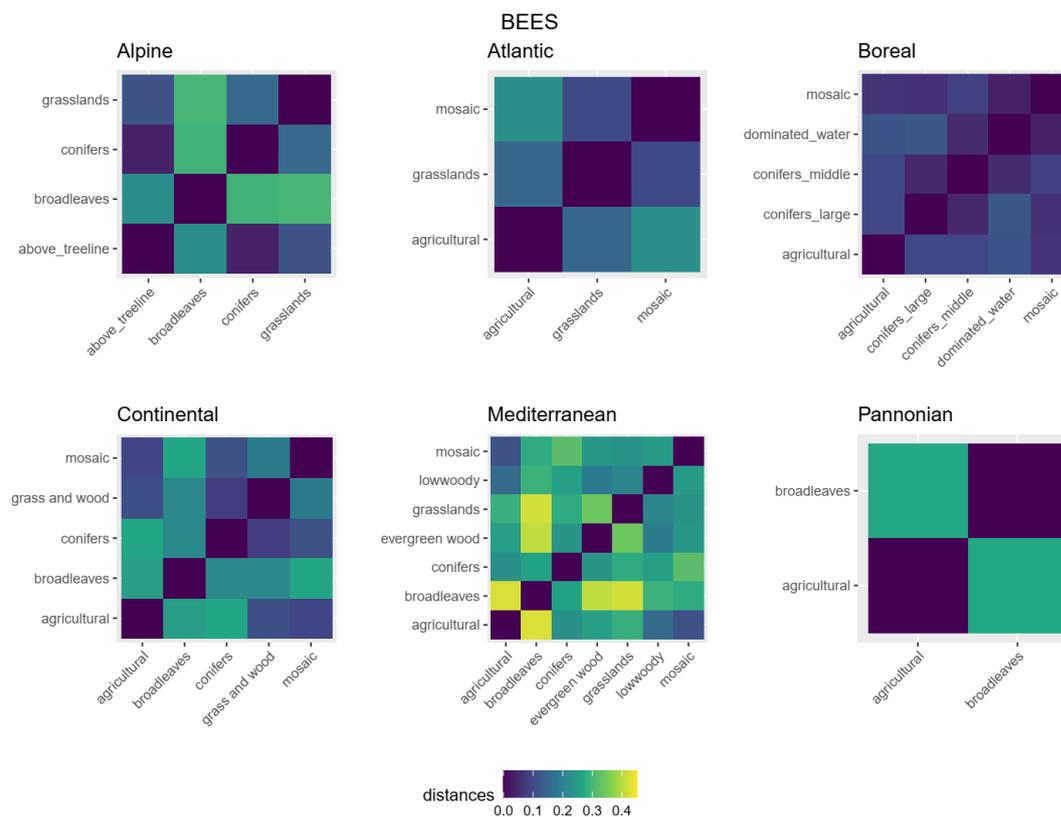
Figure 7 Beta-diversity between habitats within each biogeographical region. The distance is the turnover component of the Jaccard index.
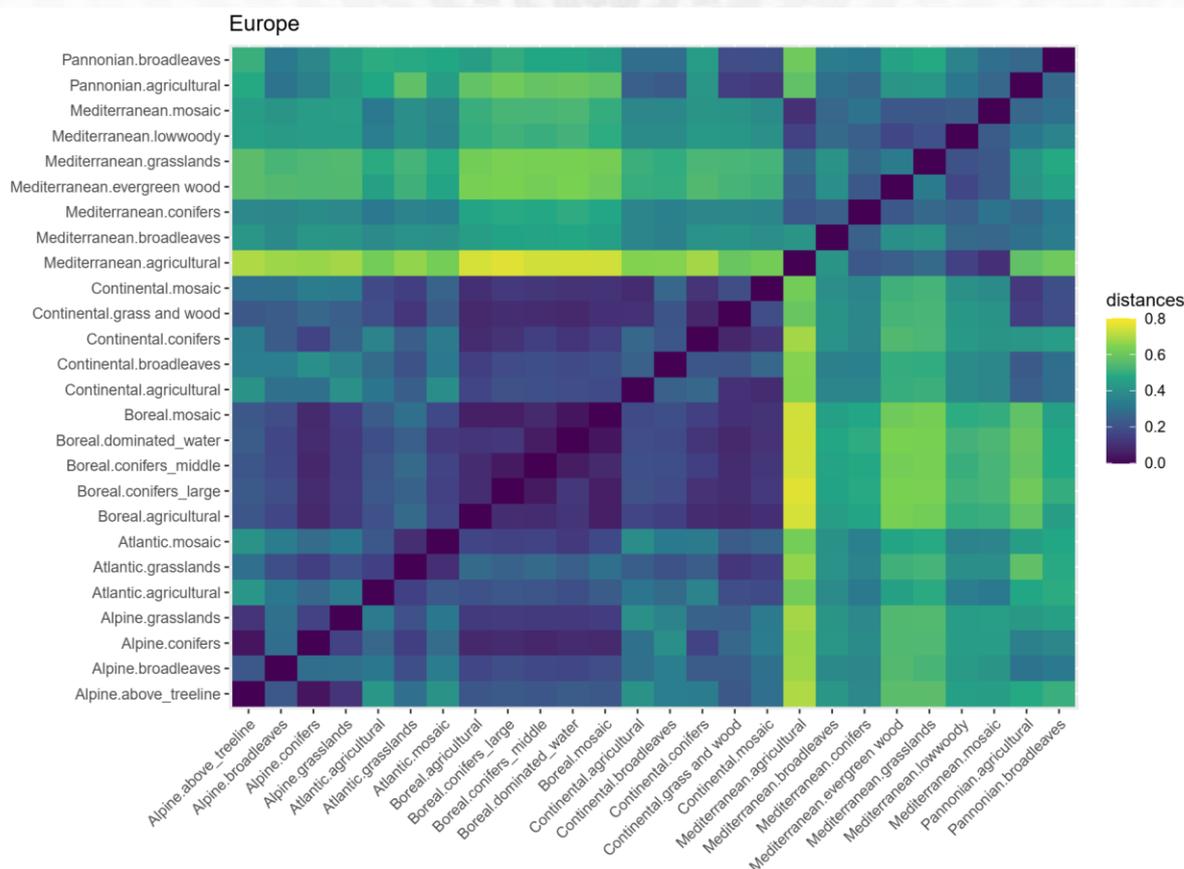
Figure 8 Beta-diversity between habitats among biogeographical regions. The distance is the turnover component of the Jaccard index.

Hoverflies

For hoverflies, the analysis showed that agricultural- and grassland-dominated clusters were those with the lowest diversity and strength across most of the biogeographical regions (Fig. 9). Contrary to bees, forest habitats emerged as the most relevant for hoverfly conservation hosting a large number of specialists. Moreover, several complex clusters composed of multiple habitats also presented high strength.
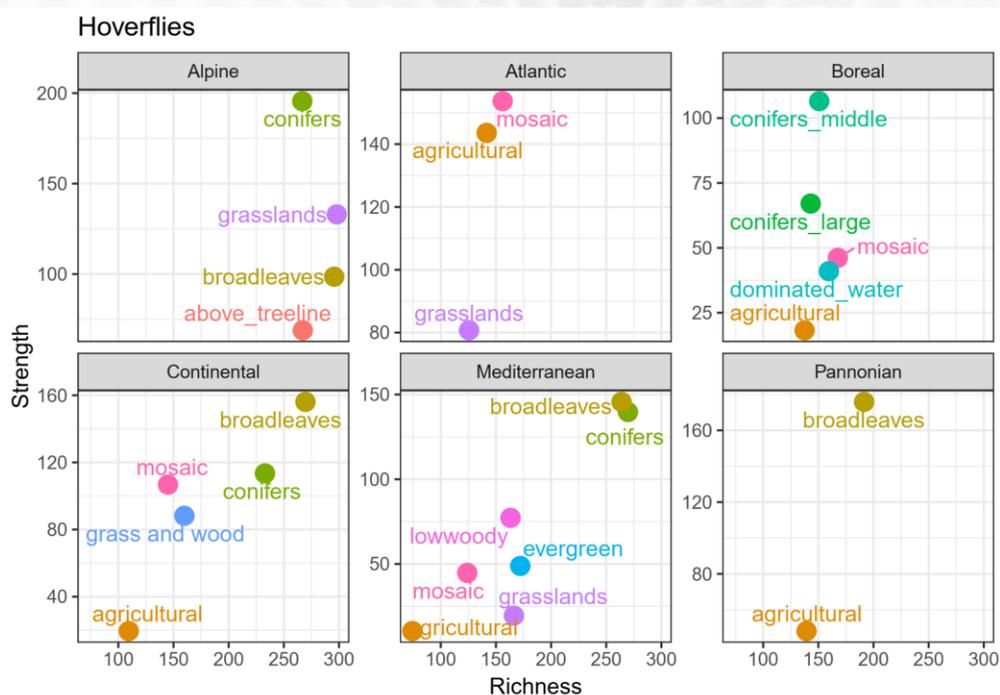
Figure 9 Scatterplot showing raw species richness and strength for each habitat within each region. As strength increases with both species richness and species dependency on that specific habitat, a positive relationship between richness and strength is expected.

The beta-diversity analysis for hoverflies yielded similar results compared to bees (Fig. 10). The Mediterranean region presented the highest dissimilarity in species composition between habitats. The uniqueness of the habitats in this region suggests a high priority for hoverfly conservation of all habitats. Cold-climate regions such as Continental, Boreal, and Atlantic regions were those with the lowest dissimilarity between habitats indicating a high degree of biotic homogenization.

Considering the entire Europe (Fig. 11), results for hoverflies were similar to those for bees. We consistently found a high dissimilarity between the Mediterranean area and the other regions. Again, the higher dissimilarity was found between Mediterranean and Boreal regions, due to their very different environmental conditions and geographic distance. Overall, the Mediterranean region offered high dissimilarity among the different habitats and high dissimilarity with the other biogeographical regions in Europe.
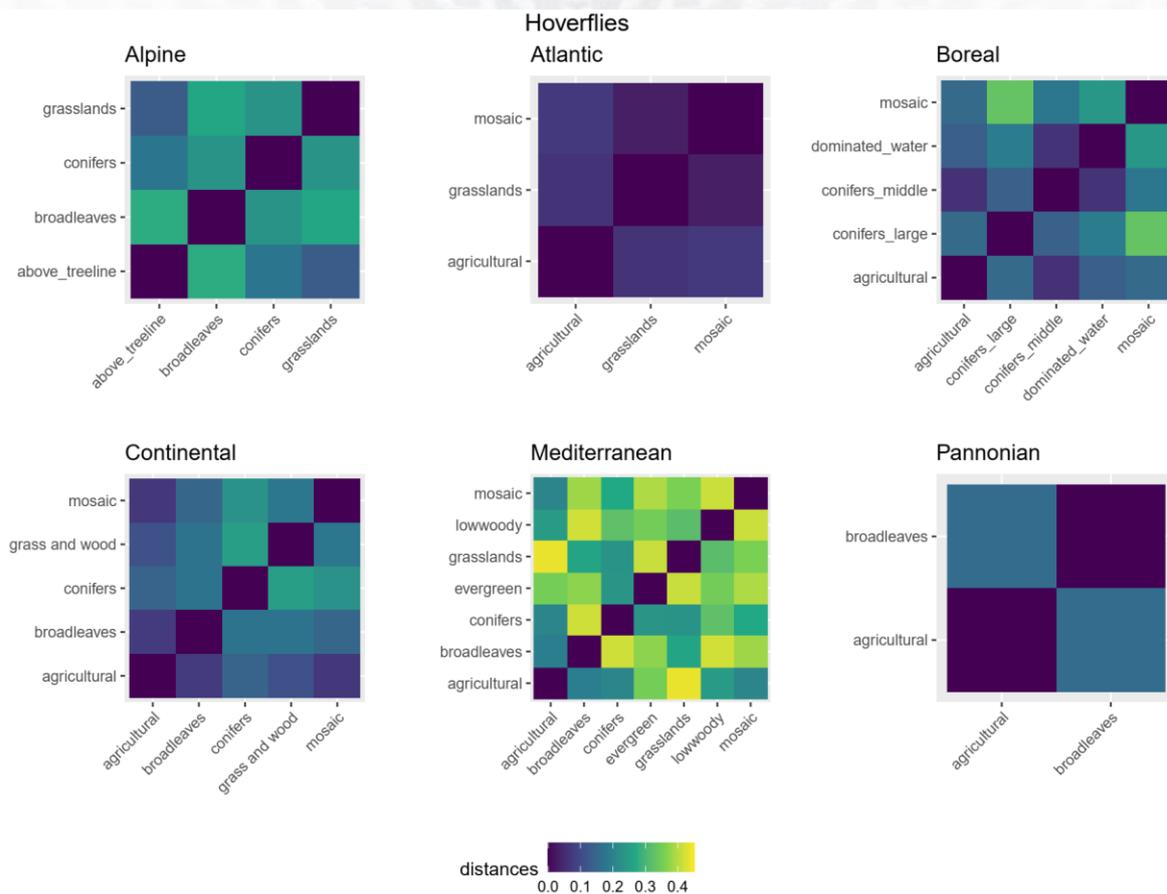
Figure 10 Beta-diversity between habitats within each biogeographical region. The distance is the turnover component of the Jaccard index.
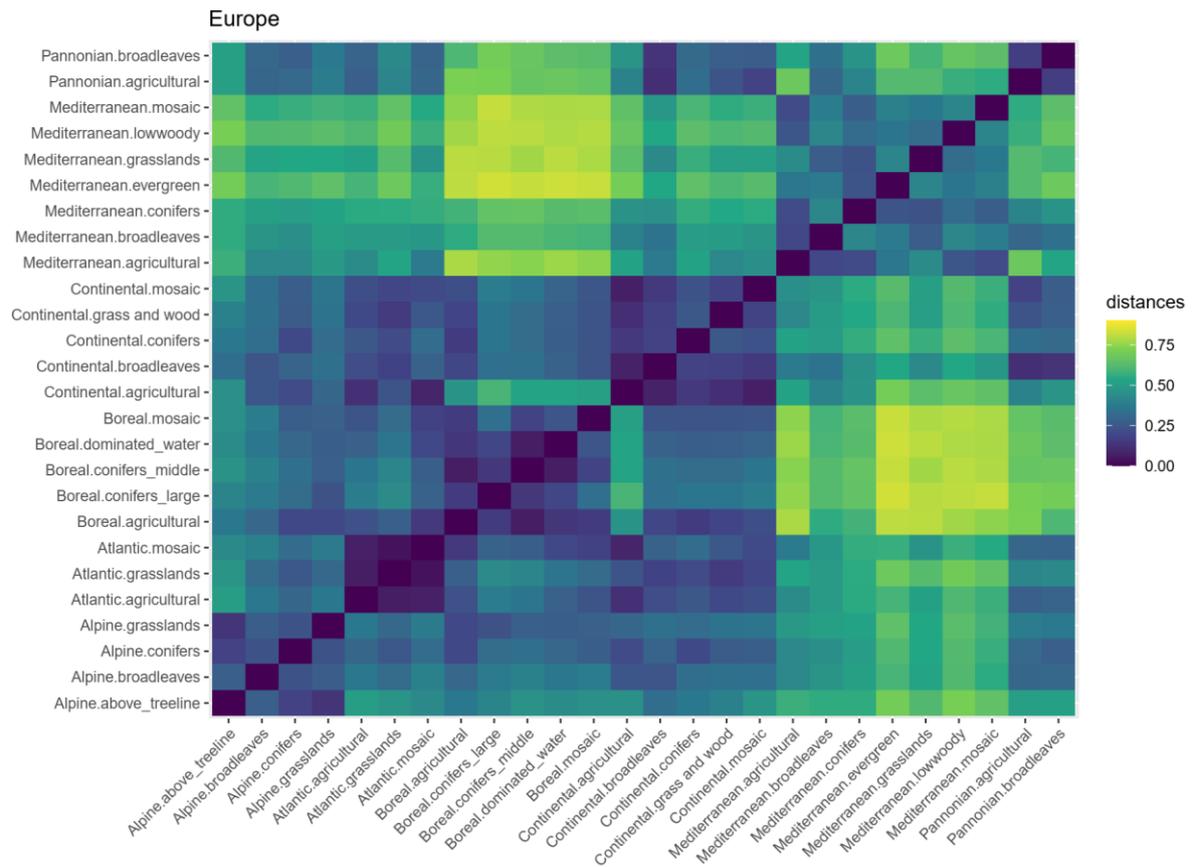
Figure 11 Beta-diversity of hoverflies between habitats within each biogeographical region. The distance is the turnover component of the Jaccard index.

3.4.   Species preferences

Bees

The analysis of species habitat preferences at the European level using deviation from null models confirmed previous findings (Fig. 12). Mediterranean habitats exhibited a very large number of habitat specialists (i.e. "exploiters") with a proportion around 50% for complex woody habitats. All other regions presented much lower proportions of specialists with Atlantic and Boreal at the lowest end.
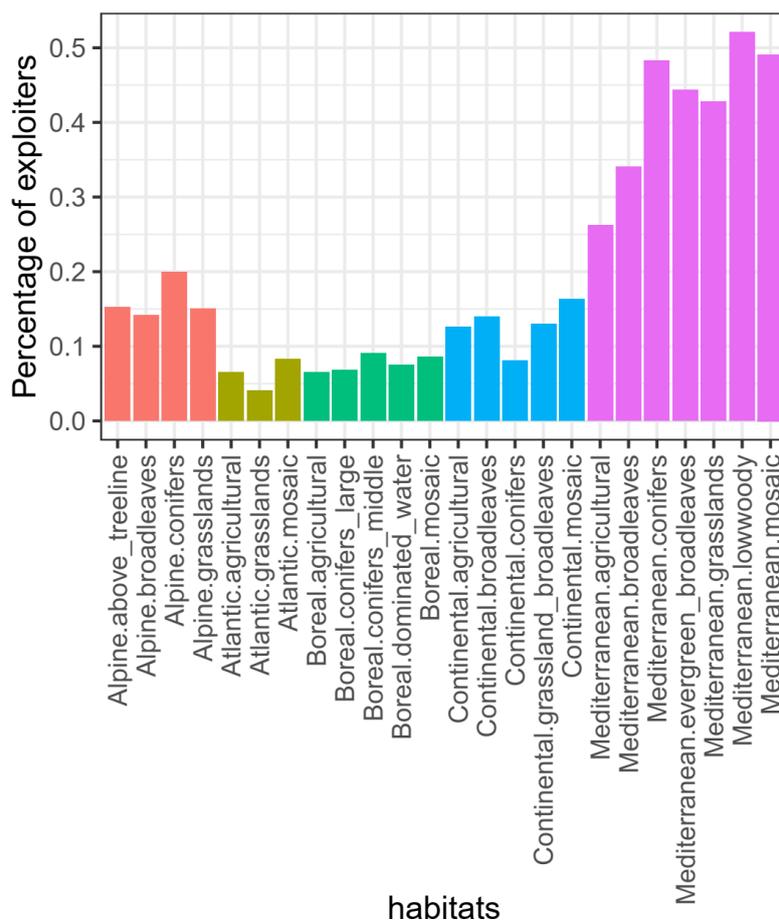
Figure 12 Proportion of habitat specialists for bees at the European level (analysis carried out using all records at the continental scale)

Hoverflies

Compared to bees, the analysis at the European level on hoverfly species habitat preferences indicated lower differences between biogeographical regions (Fig. 13). The number of specialists varied between 3% and 26%. In general forest habitats had a higher occurrence of specialists than open habitats. Deciduous forests, in particular, emerged as a key habitat hosting a large number of specialists across several biogeographical regions. Agricultural-dominated clusters were those with the lower number of specialists indicating a dominance of generalist species.
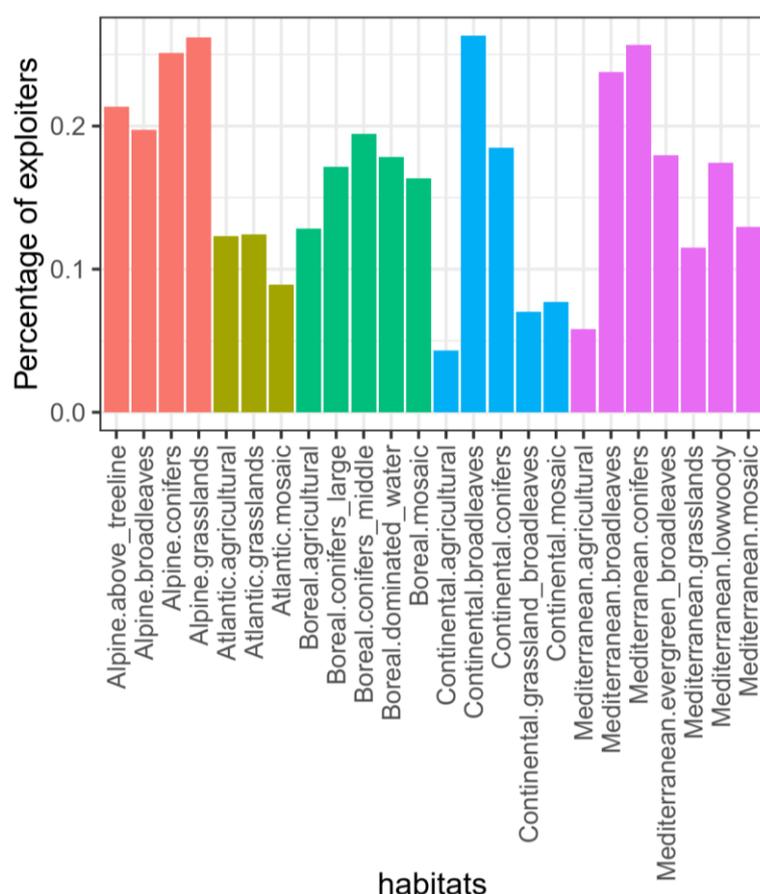
Figure 13 Proportion of habitat specialists for hoverflies at the European level (analysis carried out using all records at the continental scale)

3.5. Habitat protection and diversity of habitat included in the Habitat Directive

Bees

We compared the rarefied number of bee species (at 60% sample coverage) with the cover of the protected areas and the number of habitats within each cell (Fig. 14-15A). The model showed an interaction between biogeographical region and habitat protection (Table 2). In particular, we found a decreasing trend for the Boreal, Continental, and Alpine regions, with high-richness cells in areas with low coverage of protected areas. This effect can be explained by the frequent distribution of protected areas in high-elevation areas in the Alpine, Continental, and Boreal regions where cold temperatures are usually associated with low wild bee diversity.
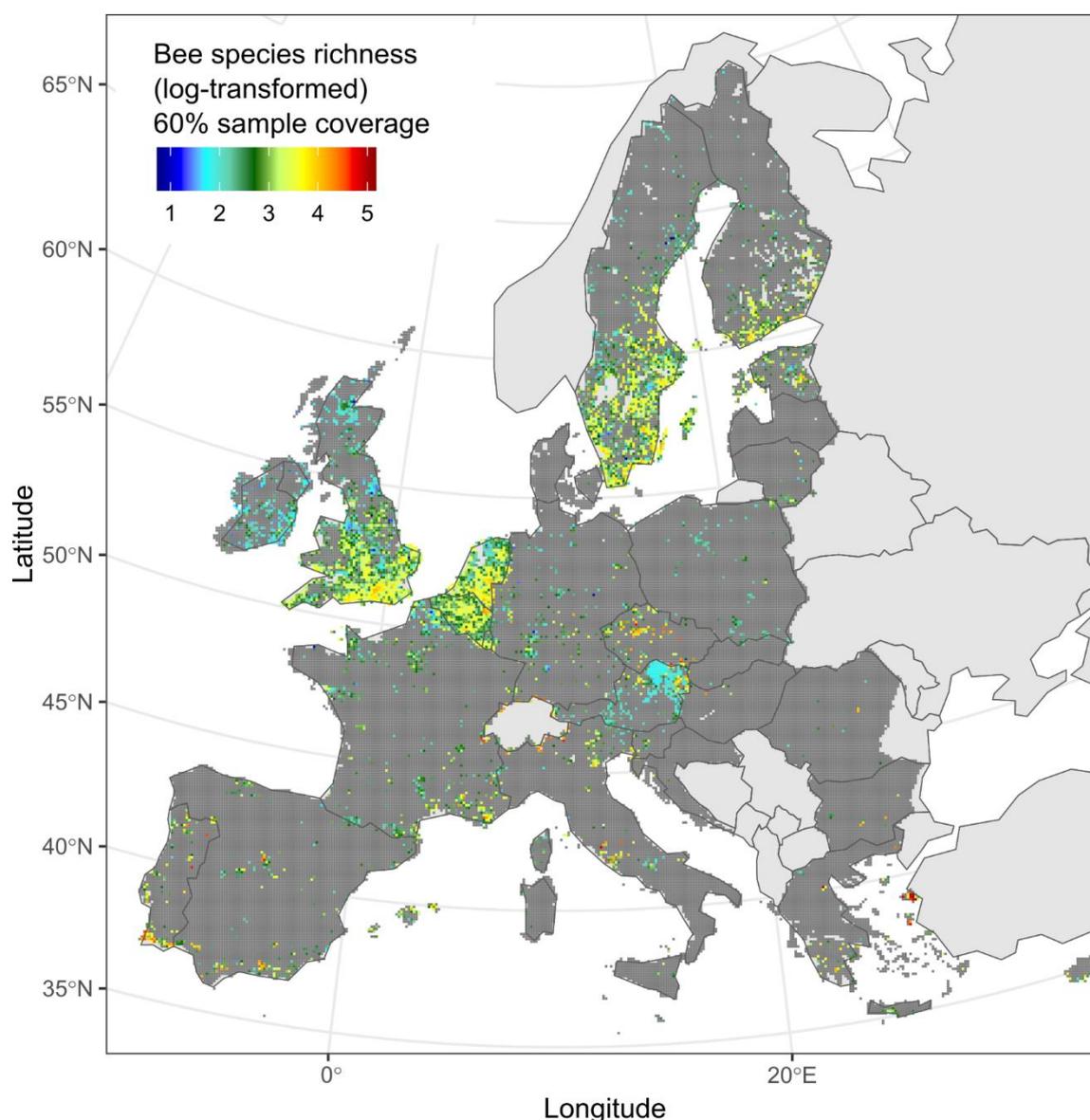
Figure 14 Distribution of the 10 x 10 km cells with at least 60% sample coverage for bees. Estimated species richness is reported on a logarithmic scale.
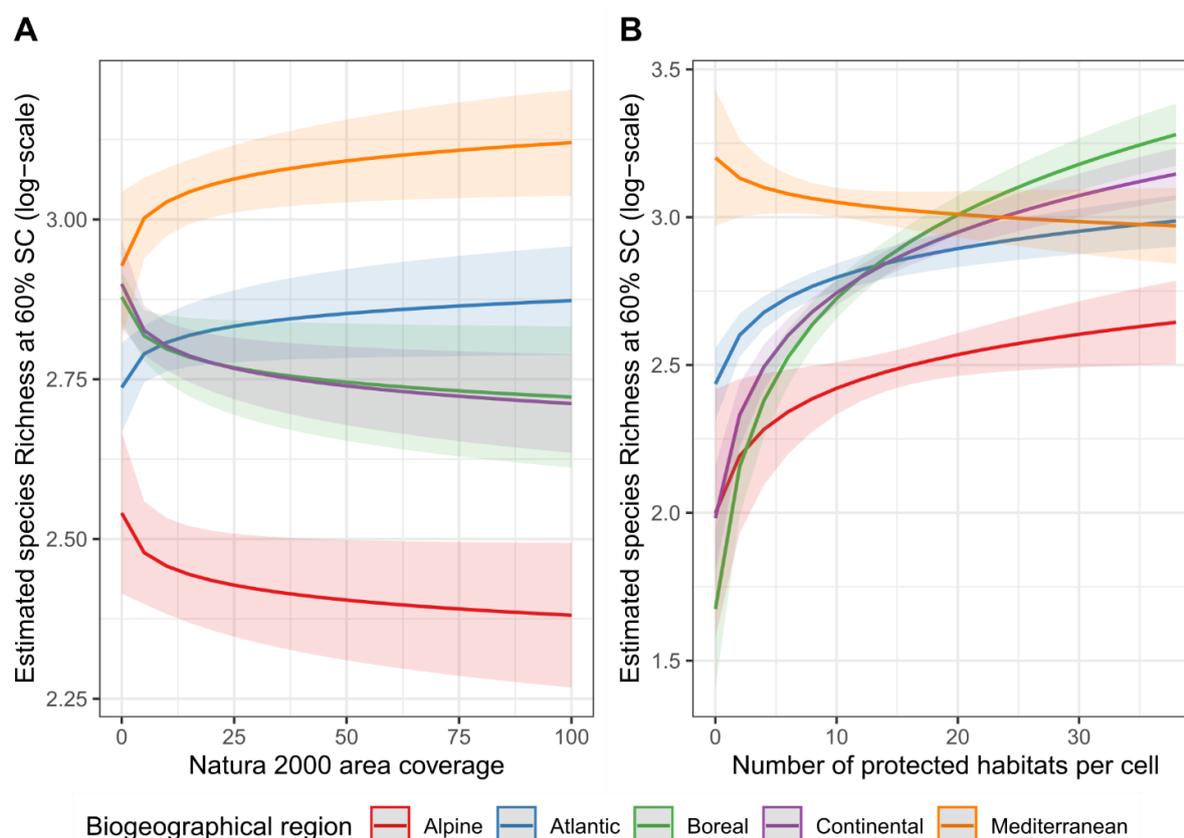
Figure 15 Effects of A) protected area coverage and B) number of habitats included in the Habitat Directive on bee species richness.

Testing the effect of the number of habitats protected by the Habitat Directive inside the cell with species richness of bees, we found a strong positive relationship for all the biogeographical regions except for the Mediterranean region (Fig. 15B), i.e. there was an interaction between habitat diversity and biogeographical region (Table 2).

Table 2 Results from the GLM testing the effect of habitat protection, habitat diversity and biogeographical region on rarefied bee richness (60% coverage).

Variable	SS	DF	F value	p-value
Intercept	37.55	1	104.41	< 0.001
Biogeographical region	31.55	4	21.93	< 0.001
Protected area (only N2K)	1.02	1	2.84	0.092
N° of protected habitats	1.98	1	5.50	0.019
Biogeo x protected area	8.78	4	6.11	< 0.001
Biogeo x no protected habitats	25.05	4	17.41	< 0.001

Hoverflies

We compared the number of hoverfly species at the 60% sample coverage with the cover of the protected area within each cell (Fig. 17-18). Contrary to bees, the model showed a slight positive relationship between the number of species (log-transformed) and the coverage of protected areas (For N2K network: estimate = 0.004, Z value = 3.72, p-value < 0.001; For overall protected areas: estimate = 0.004, Z value = 4.49, p-value < 0.001). However, the relationship changed depending on the biogeographical regions we considered. In particular, we found a decreasing trend for the Boreal and Atlantic regions, with high-richness cells in areas with low coverage of protected areas. While positive trends were found for the Alpine and Mediterranean regions.
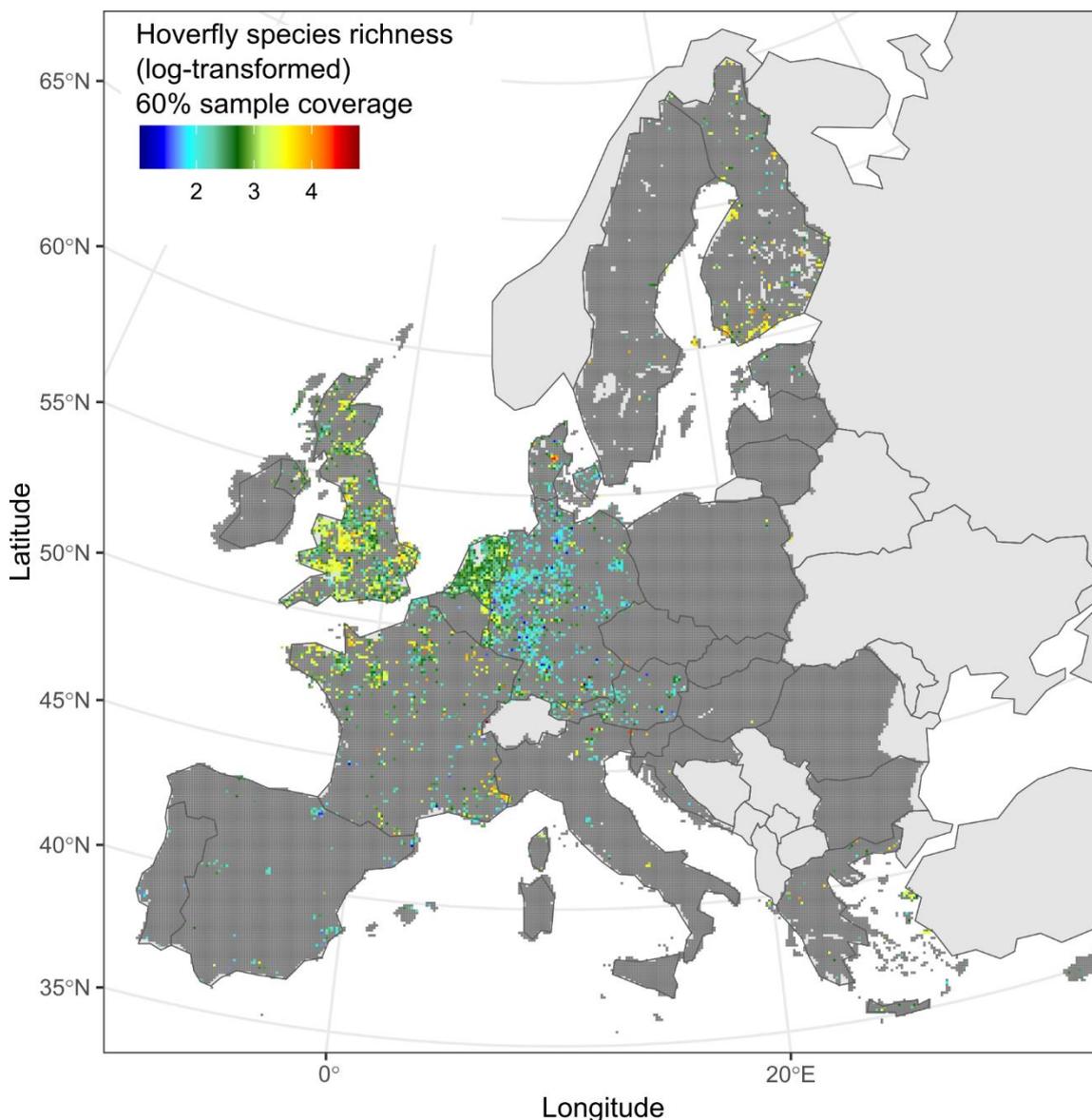
Figure 17 Distribution of the 10 x 10 km cells with at least 60% sample coverage for hoverflies. Estimated species richness is reported on a logarithmic scale.
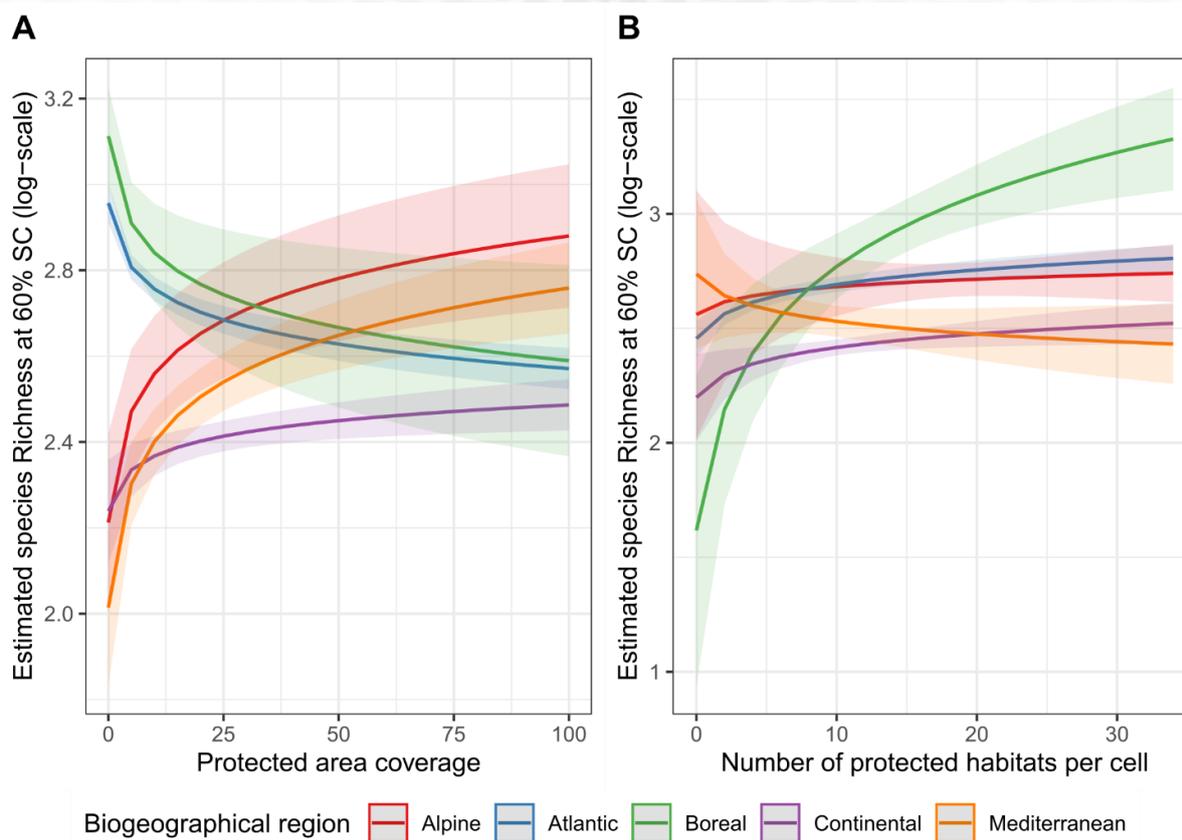
Figure 18 Effects of A) protected area coverage and B) number of habitats included in the Habitat Directive on species richness of rarefied hoverfly richness (60% coverage).

We found a significant interaction between the cover of protected areas and hoverfly species richness. In the Atlantic and boreal regions, we found a negative effect of habitat protection while in the other regions there was a positive effect of habitat protection. In contrast with bees, we found a weak effect of habitat diversity on hoverfly species richness with the only exception of the Boreal region (Fig. 18B).

Table 2 Results from the GLM testing the effect of habitat protection, habitat diversity, and biogeographical region on hoverfly richness.

Variable	SS	DF	F value	p-value
Intercept	20.70	1	75.05	< 0.001
Biogeo region	4.84	4	4.39	0.002
Protected area (only N2K)	7.72	1	28.01	< 0.001
N° of protected habitats	0.02	1	0.08	0.772
Biogeo region x protected area	12.98	4	11.76	< 0.001
Biogeo region x no protected habitats	3.81	4	3.45	0.008

3.6. Community uniqueness

Bees

The index of local contributor to beta diversity (LCBD) showed a very strong geographical pattern (Fig. 19). We found that the communities of species in Portugal, Spain, France, Italy, Greece, the Balkan Peninsula and, partially, in the northern boreal areas and Eastern Europe showed a significant contribution to the overall beta diversity at the European scale (Jaccard index based on presence/absence of species). Large portions of these regions are also under-sampled. For instance, southern Italy and most of the Balkan Peninsula have large areas with insufficient data, although these areas largely contribute to European biodiversity by hosting unique communities. On the contrary, the British Isles, Central Europe, and the southern part of Norway, Sweden, and Finland are well-known in terms of species distribution but their contribution with unique species is limited.

We used the significance of LCBD (0 not significant; 1 significant) to understand the relationship between sampling coverage and species richness (Fig. 20). We found a strong positive relationship between the probability of having a significant LCBD value and the proportion of under-sampled neighbor cells. The results showed that there is a systematic under-sampling in areas with unique communities of bees at the European scale. We also found a negative non-linear relationship with the species richness, showing that the cells significantly contributing to the overall beta diversity have fewer species.

Finally, we used a PCoA multivariate analysis based on the turnover component of the distance to visualize the difference in terms of communities (Fig. 21). The first axis explained 20% of the variance, the second 11%, and the third 8%. The map shows that Southern Europe hosts a very different community of bees, which are partially different even from the Southern France. Moreover, there is a clear distinction between Central-Eastern Europe and the Atlantic region. Axis 1 can be mostly interpreted as latitude. This analysis stresses again a strong biogeographical signal in species composition for wild bees.
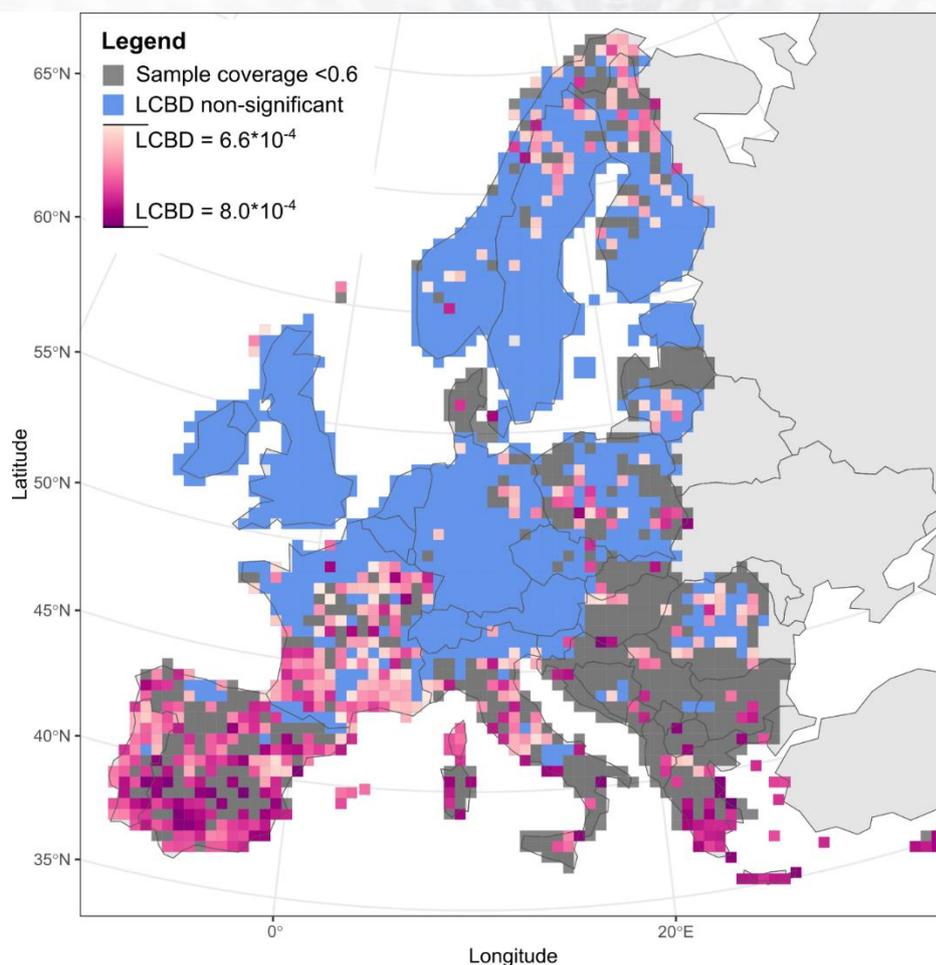
Figure 19 Uniqueness index (LCBD) for bees at 50 x 50 km resolution: cells with purple shade show significant values of uniqueness; blue cells show non-significant values; grey cells show areas with less than 60% sample coverage. Cells with pink-to-dark violet color indicate cells with unique species composition compared to the rest of Europe.
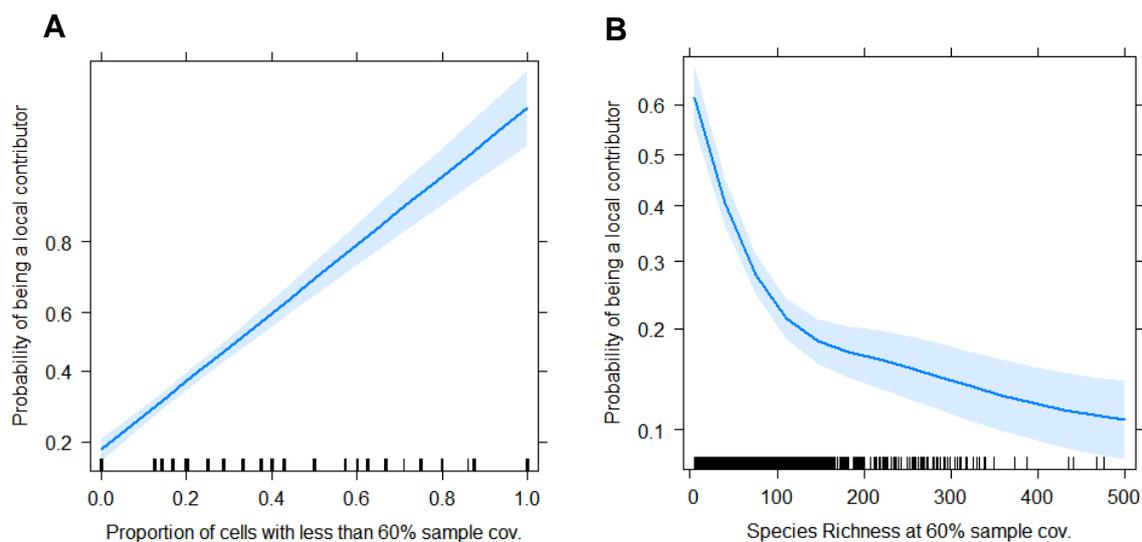
Figure 20 A) Relationships between LCBD significance and the proportion of neighbor cells with less than 60% sample coverage. B) Relationships between LCBD significance and the bee species richness.
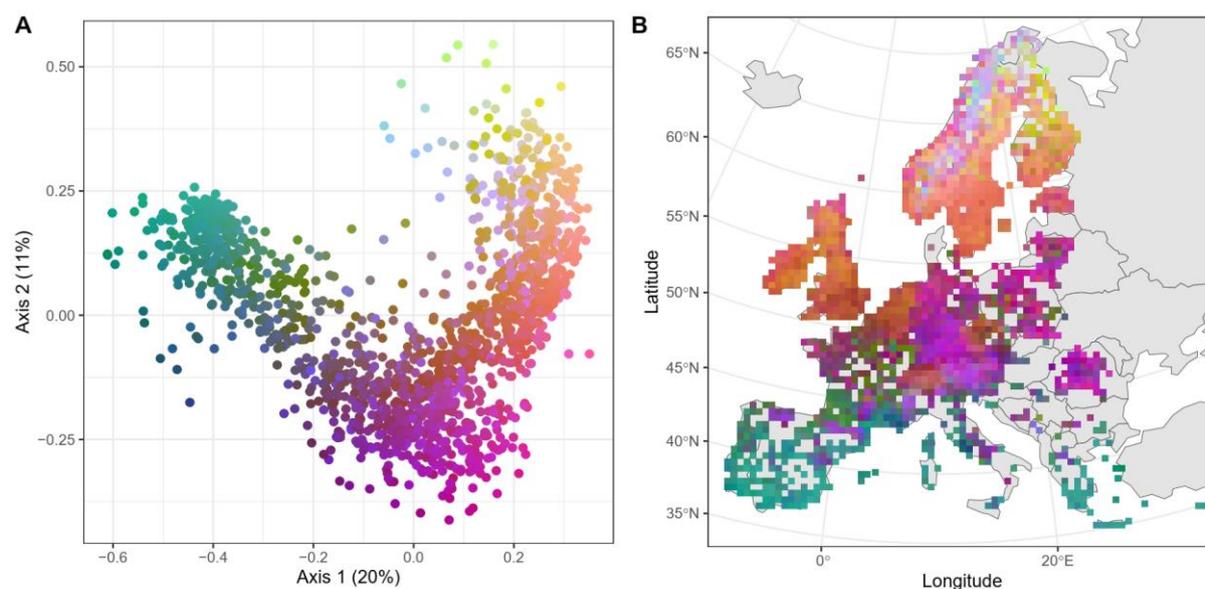
Figure 21 A) PCoA results plotted in a reduced multidimensional space. B) Map of PCoA results plotted with latitude and longitude values. Similar colors indicate similar species composition.

Hoverflies

Similar to the bees, the index of local contributors to beta diversity (LCBD) for hoverflies showed a strong geographical pattern (Fig. 22). We found that the communities of species in Italy, Greece, the Balkan Peninsula, Eastern Europe, and partially, in the Iberic Peninsula and Scandinavian countries showed a significant high contribution to the overall beta diversity at the European scale (Jaccard index based on presence/absence of species). For hoverflies, only the United Kingdom, Belgium, Netherlands, Austria, Estonia, and partially France exhibited a good sample coverage.

We used the significance of LCBD (0 not significant; 1 significant) to understand the relationship between sampling coverage and species richness (Fig. 23). We found a strong positive relationship between the probability of having a significant LCBD value and the proportion of under-sampled neighbor cells. The results showed that there is a systematic under-sampling around areas with unique communities of hoverflies at the European scale. We also found a negative non-linear relationship with the species richness, showing that the cells significantly contributing to the overall beta diversity have fewer species.

Finally, we used a PCoA multivariate analysis with the turnover component of the distance to visualize the difference in terms of communities (Fig. 24). The first axis explained 22% of the variance, the second 13%, and the third 8%. The map shows that Southern Europe hosts a distinct community of hoverflies, but a gradual gradient of dissimilarity exists from Spain to Central Europe indicating a weaker biogeographical structure compared to bees. However, there is a strong distinction between Western and Eastern Europe in terms of species composition. Another clearly distinct cluster can be found in the Scandinavian countries.
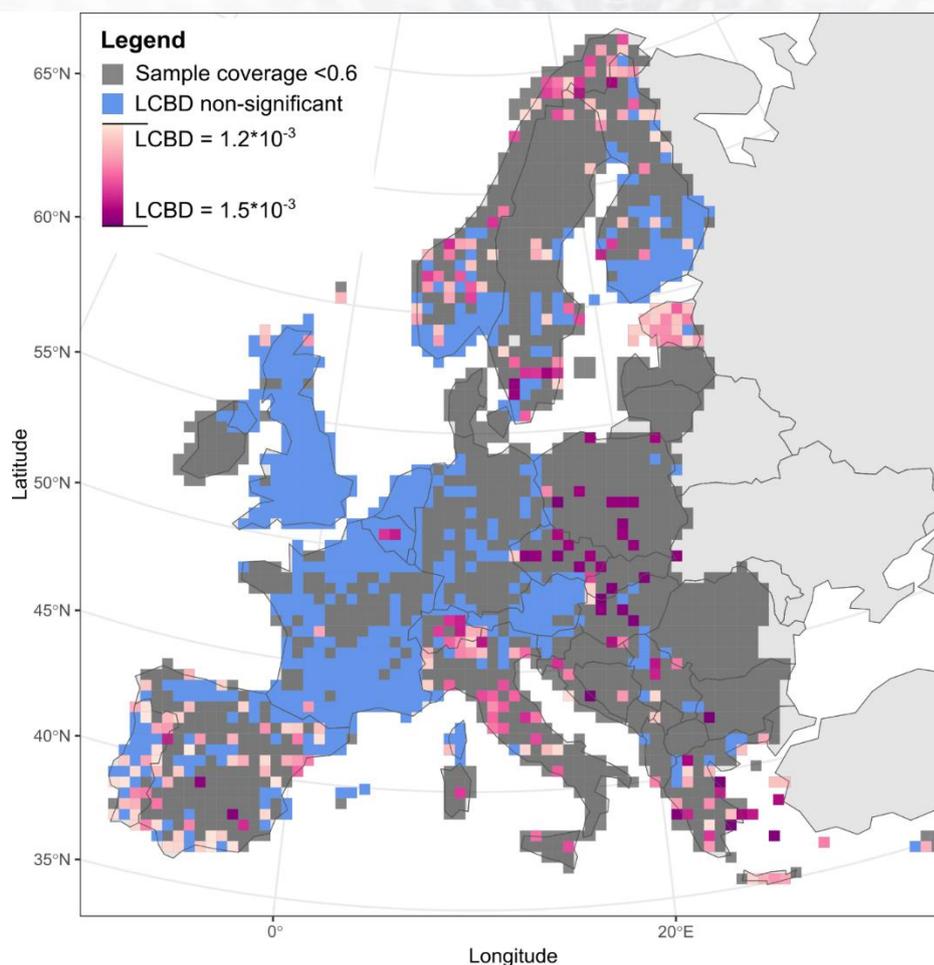
Figure 22 Uniqueness index (LCBD) for hoverflies at 50 x 50 km resolution: cells with purple shade show significant values of uniqueness; blue cells show non-significant values; grey cells show areas with less than 60% sample coverage. Cells with pink-to-dark violet indicate cells with unique species composition compared to the rest of Europe.
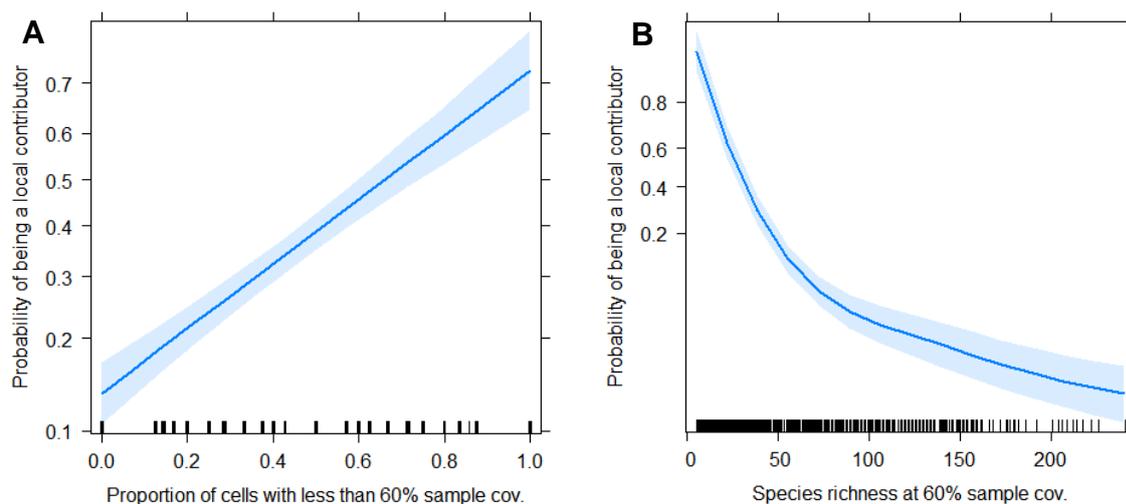
Figure 23 A) Relationships between LCBD significance and the proportion of neighbor cells with less than 60% sample coverage. B) Relationships between LCBD significance and the bee species richness.
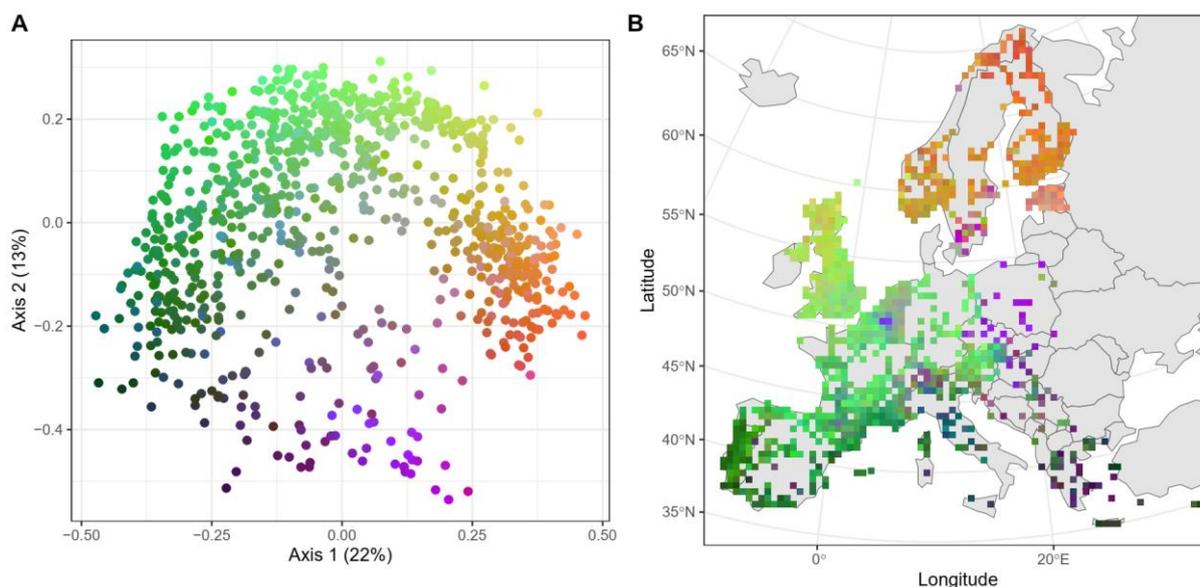
Figure 24 A) PCoA results plotted in a reduced multidimensional space. B) Map of PCoA results plotted with latitude and longitude values.

4. Conclusions

Our analyses revealed significant compositional differences in pollinator species pools across major European biogeographical regions, as well as between habitats within the same region. The Mediterranean habitats stood out as particularly important for wild bees, showcasing the highest species diversity and unique species compositions. Notably, complex landscapes with woody vegetation supported the greatest number of specialist species. In contrast, hoverflies exhibited a more evenly distributed importance across regions, with only the Alpine and Mediterranean areas emerging as particularly diverse.

For both wild bees and hoverflies, beta-diversity between habitats was markedly higher in the Mediterranean region compared to all other biogeographical zones. This indicates a high priority for the conservation of Mediterranean habitats, even when species diversity is not the highest. Conversely, agricultural-dominated landscapes exhibited low diversity and a paucity of specialist species, thus receiving low conservation priority for both wild bees and hoverflies. Among habitats, deciduous forests were notable for their high ecological uniqueness, particularly for hoverflies, as indicated by the greatest dissimilarity from other habitats.

The sampling effort within Natura 2000 areas varied significantly between European countries and between wild bees and hoverflies. Overall, we found a relatively low number of species strongly associated with protected areas, suggesting that habitat conditions inside and outside these protected zones are not substantially different at a European scale. The spatial resolution of our data did not allow for an evaluation of the importance of urban habitats for pollinator conservation.

Policy implications

The current network of protected areas appears inadequate to protect wild bees at a European scale, especially in colder regions such as the Alpine and the Boreal where protected areas are predominantly located on high mountains that are climatically not suitable for many bee species. Similarly, for hoverflies, we observed variable effectiveness of protected areas across different biogeographical regions, highlighting the need for tailored conservation strategies at the regional level. Since both groups exhibit strong biogeographical patterns that go beyond administrative boundaries, conservation policies at the country level might be inadequate to maximize the effectiveness of current and future conservation initiatives, in particular concerning the designation of new protected areas and/or habitats. Lastly, maintaining a high diversity of habitats listed in the Habitat Directive appears to be a suitable strategy for protecting bees across Europe, except for the Mediterranean region, where general land protection measures may prove more effective. In contrast, habitat diversity was less important for hoverflies. The contrasting patterns observed between bees and hoverflies and between

different biogeographical regions underscore a key challenge in formulating effective policies to protect pollinators across whole Europe. The current broad spatial resolution of the available pollinator distribution data does not allow to identify species preferences for single habitats. To fill this important knowledge gap, we suggest for the future to support ad-hoc sampling campaigns at least across the habitats listed in the Habitat Directive.

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