EuPPollNet: A European database of plant-pollinator networks

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Abstract

Motivation: Pollinators play a crucial role in maintaining Earth's terrestrial biodiversity and human food production by mediating sexual reproduction for most flowering plants. Indeed, the intricate network of interactions formed by plants and pollinators constitutes the backbone of plant-pollinator community stability and functioning. However, rapid human-induced environmental changes are compromising its long-term persistence. One of the major challenges for pollinator conservation is the lack of robust generalisable data capturing how plant-pollinator communities are structured across space and time. Here, we present the EuPPollNet database, a fully open and reproducible European-level database containing harmonized taxonomic data on plant-pollinator interactions referenced in both space and time. This database offers an open workflow that allows researchers to track data-curation decisions and edit them according to their preferences, while also providing other ecological variables of interest. Furthermore, this work provides an in-depth assessment of the taxonomic and sampling coverage of the database at the European level, complemented by analyses of key structural properties in plant-pollinator networks. We hope this database can help researchers to: 1) identify taxonomic, ecological, and geographical gaps of knowledge on plant-pollinator interactions; and 2) explore the impacts of global change on plant-pollinator networks to guide future conservation planning for both plant and pollinator species.

Main Types of Variables Included: EuPPollNet contains 1,144,369 interactions between plants and pollinators from 1,147 distinct locations (i.e., plant-pollinator networks), which belong to 51 different studies distributed across 17 European countries. In addition, information about sampling methodology, habitat type, bio-climatic region, and further taxonomic rank information for both plant and pollinator species are also provided.

Spatial location and grain: The database contains 1,147 different sampling locations from natural and anthropogenic habitats that fall in 5 different bio-climatic regions. All records are geo-referenced and presented in the World Geodetic System 1984 (WGS84).

Time period and grain: Species interaction data was recorded between 2004 and 2021. All records are time-referenced and most of the studies documented interactions in a single flowering season (68.63%).

Major taxa and level of measurement: The database contains interaction data at the species level for 94.72% of the records, including a total of 1,353 plant and 2,065 pollinator species. The database covers 5.34% of the European species of flowering plants, 33.82% of bees, 26.21% of butterflies, and 33.08% of syrphids species at the European level.

Software format: The database was built with R software and is stored as ".rds" and ".csv" formats. The construction of the database is fully reproducible and can be accessed at the following PERMANENT LINKS.

KEYWORDS

plant-pollinator networks, plant-pollinator interactions, flowering plants, Angiosperms, pollinators, nestedness, connectance

1 | INTRODUCTION

The interaction between plants and pollinators is one of the most well-documented mutualisms on Earth. Plant-pollinator interactions involve a great diversity of species, largely attributed to their coevolutionary history (Ollerton 2017), and are critically important for terrestrial biodiversity and the human economy. The synergistic effects of climate change with other global change pressures are threatening worldwide biodiversity (Sala et al. 2000; Bellard et al. 2014), including plant and pollinator species as well as their interactions (Goulson et al. 2015; Settele, Bishop, and Potts 2016; Eichenberg et al. 2021). Under this scenario, the increasing availability of biodiversity data plays a major role in our ecological understanding of species and guiding conservation planning (Heberling et al. 2021). However, our knowledge of plant and pollinator species and their network of interactions still exhibits major temporal, spatial and taxonomic biases (Archer et al. 2014; Troia and McManamay 2016; Poisot et al. 2021; Marshall et al. 2024), limiting our ability to effectively protect their biodiversity.

Europe is one of the continents with a larger amount of available biodiversity data (Proença et al. 2017), yet still exhibits major gaps (Wetzel et al. 2018; Bennett et al. 2018). While species checklists need to be treated carefully, especially at a macro-ecological scale (Grenié et al. 2023), the growing number of European plant and pollinator checklists along with occurrence data, is setting a foundation for the conservation of its flora and their pollinators. However, species richness is just one component of biodiversity and documenting the interaction between plants and pollinators is essential for understanding the fate of the species within an ecosystem (Jordano 2016). Numerous works have studied plant-pollinator interactions in the last decades, originating thousands of plant-pollinator interaction networks worldwide. Several initiatives have tried to integrate plant-pollinator interaction data into databases such as *Mangal* (Poisot et al. 2016) or *GloBI* (Poelen, Simons, and Mungall 2014), resulting in numerous large scale comparative analyses that have enhanced our understanding of the ecology of plants and pollinators (e.g., European wild bee data trends; Marshall et al. 2024). Despite all these resources, Europe lacks accessible harmonized plant-pollinator interaction data that allow researchers to evaluate the state of the art of plant-pollinator interactions at European level, which will guide research efforts, conservation planning and will set a foundation for future global change research.

The interactions between different plant and pollinator species within a community form complex networks. Macro-ecological analyses of the topology of these networks have revealed common properties across them, such as truncated power-law degree distributions (Jordano 1987) or nestedness (Bascompte et al. 2003). In addition, this type of large scale analyses can help understanding landscape level processes that cannot be explored at the community level, such as ecological patterns across geographic regions (Olesen and Jordano 2002; Traveset et al. 2016) or environmental gradients (Ramos-Jiliberto et al. 2010; Rech et al. 2016; Saunders et al. 2023). Although macro-ecological approaches make significant contributions to knowledge, they tend to be rare, and are strongly influenced by the spatio-temporal availability and nature of the data (Burkle and Alarcón 2011; Trøjelsgaard and Olesen 2013). For instance, plant-pollinator studies tend to differ in sampling effort and methodology which can impact the structure of the resulting plant-pollinator networks (Gibson et al. 2011; Jordano 2016). Further, despite little sampling effort could capture most of the relevant functional species (Hegland et al. 2010), most plant-pollinator networks have unobserved interactions because undersampling (Olesen et al. 2011; Chacoff et al. 2012). Thus, the lack of strong spatio-temporal coverage, along with the current intrinsic limitations of sampling plant-pollinator networks, highlight the need of keep gathering and integrating informative species interaction data to properly unravel the different ecological processes that shape plant-pollinator interactions at large scales.

Here, we present the EuPPollNet database, an acronym derived from European plant-pollinator networks, which contains harmonized information on interaction data of plants and pollinators at European level. The primary focus of the pollinator taxonomic groups is on the main orders of entomofauna that visit and pollinate flowering plants in Europe. These include insect species from the orders Hymenoptera, Diptera, Lepidoptera, and Coleoptera (Potts et al. 2015), which comprise almost the totality of recorded interactions in the EuPPollNet database (99.88%). To understand the scope of the database, we examine the taxonomic and sampling coverage of the different plant and pollinator species at European level with the help of the most up-to-date species checklists and rarefaction analyses. In addition, we investigate how two key structural metrics of plant-pollinator networks, such as connectance and nestedness, change across the latitudinal range of studies and bioclimatic regions. Finally, we also examine whether plant-pollinator networks fulfill the expectation of being more nested than null expectations. EuPPollNet aims to cover a wide range of taxonomic groups and habitats, while also providing other variables of interest that allow better control for the ecological context and sampling methods. In addition, EuPPollNet offers a transparent and accessible workflow of its data management and species harmonization that allows it to be reused and keep building on it over time. This database provides a large number of community-level networks with curated and harmonized data, distinguishing it from other currently available resources that contain plant-pollinator interactions. We expect that this database will help to evaluate macro-ecological processes and current gaps of plant-pollinator interactions at European level.

2 | METHODS

Data acquisition

This database is the result of one of the working packages of the European project Safeguard. The EuPPollNet database includes published and unpublished studies compiled initially by a wide number of researchers and institutions within the European continent. Data acquisition followed a non-systematic approach. First, data was directly asked to members of the Safeguard project and then, the request was extended to data owners outside of the project. These other studies were identified by direct communication with other colleagues and by directly searching studies on Google Scholar of under-represented regions within the database. To keep high quality standards that will allow robust future ecological research, we only included studies meeting the following criteria: 1) studies that contained time- and geo-referenced records of plant-pollinator interactions; and 2) studies with phyto-centric plant-pollinator networks with quantitative visitation data.

Dataset description

The database contains 51 independent published and unpublished studies conducted during the time period 2004 - 2021 on 17 different countries (**Figure 1a** and **Figure 1b**). The different studies differ in sampling effort and methodology, although most studies took place within a single flowering season (68.63%), sampled a given location an average of 7.22 days, and documented interactions mostly by using transects as sampling method (62.75%). The database includes a total of 1,144,369 distinct interactions, considering interaction as the contact of a given pollinator to the reproductive structure of a particular plant. Most of the pollinator species in the database belong to the orders Hymenoptera and Diptera, each comprising approximately 1,000 species. However, the majority of plant-pollinator interactions are from Hymenoptera species (91.04%; **Figure 1c**). Notably, *Apis mellifera* represents 70.68% of the total interaction records from the database and an average of 31.00% of the total interactions per network.

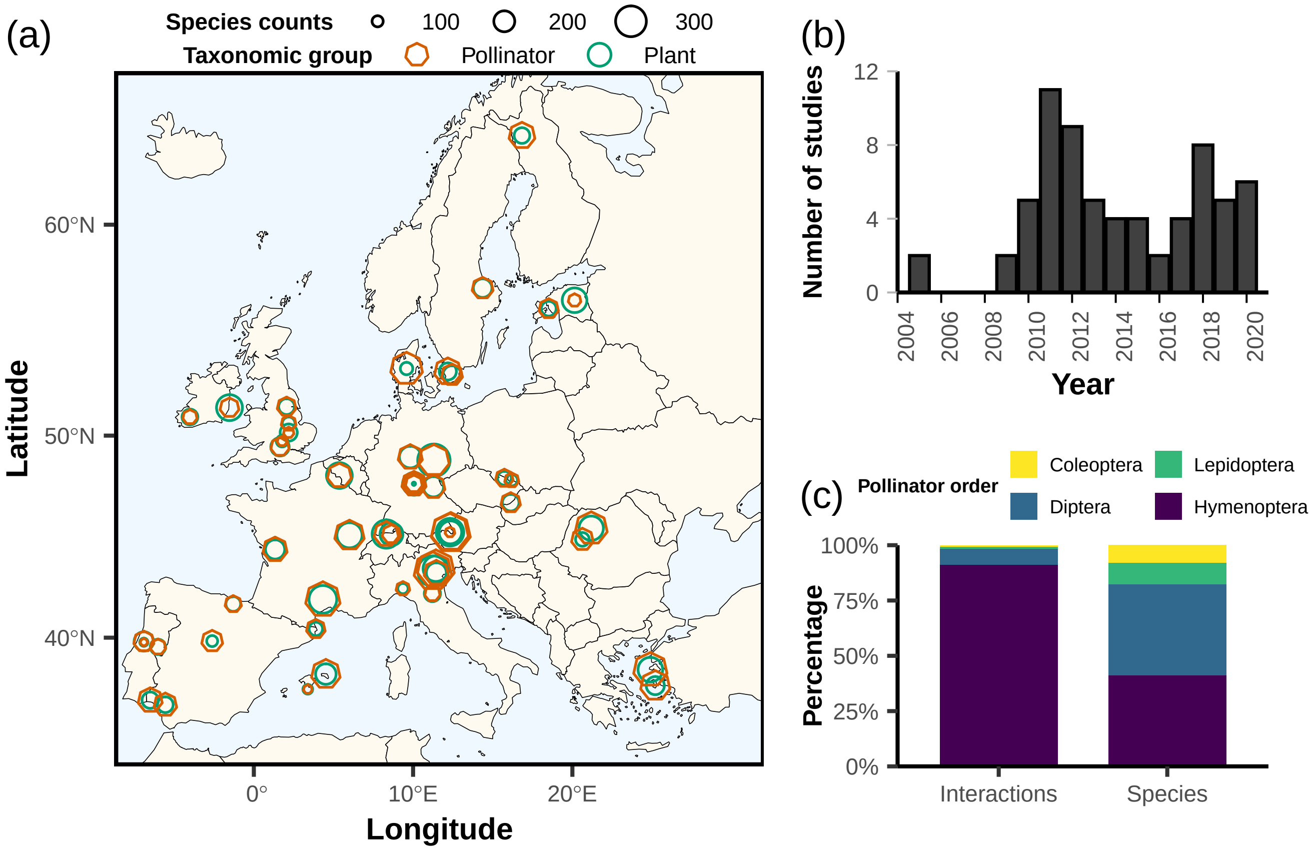

Figure 1. (**a**) Approximate locations of the studies of the EuPPollNet database showing the total number of pollinator (i.e., orange heptagon) and plant (i.e., green circles) species per study. The sizes of these shapes are proportional to the respective species counts. For visualization purposes, we have focused only on the European region with studies and selected a single location per study. (**b**) Number of studies by year within the database. (**c**) Number of species and interactions across the 4 main pollinator orders at European level.

Data structure

The EuPPollNet database is available in both .csv and .rds formats. The .csv file contains data in long format, while the .rds file stores the data in a list structure, with networks organized within each study. The file contains a total of 30 columns that depict where and when the plant-pollinator interaction was observed (**Table 1**). To provide a standard unit of plant-pollinator interaction across studies, each row depicts a single interaction between a plant and a pollinator species. To build a plant-pollinator network matrix at a site level, authors only need to group interactions by plant and pollinator species, site and study. Information about habitat type and bioclimatic region are also provided in this file. In addition, the interaction dataset includes a column that describes the presence or absence of floral counts for each study. The flower count data is provided in a separate file given that one third of studies lack floral measurements and that the units differ greatly across studies. Finally, metadata at the study level is provided, including information about the authors, digital object identifier if available, sampling time and taxonomic coverage of the main pollinator groups for each study.

Sampling coverage

The completeness of the EuPPollNet database was evaluated by exploring the rarefied accumulation curves of plant and pollinator species and their interactions across the different sampling sites. In addition, an outstanding question in ecology is how many pollinators are required to pollinate flowering plants (Kleijn et al. 2015). To that end, we also calculated the accumulation curve of pollinator species with increasing number plant species. The rarefied and extrapolated sampling curves were obtained with the help of the **iNEXT** package (Hsieh and Chao 2016). This was complemented with 100 random accumulation curves obtained programmatically to guide the visualization of the different rarefied curves.

Taxonomic harmonization

All plant and pollinator species names were checked and standardized according to large scale taxonomic databases. To ensure reproducibility of the workflow, we have conducted this harmonization in R with **rgbif** (Chamberlain, Oldoni, and Waller 2022) as pivotal package to check for species names and retrieve further taxonomic information (i.e., phylum, order, family and genus) from the Global Biodiversity Information Facility (GBIF). The protocol for plants and pollinators is similar but slightly different given the availability of the different taxonomic resources. For transparency, we have included in the database the old species name, the new assigned name, and, if the name of the species is uncertain (e.g., species complex or species alike).

For plants: (i) we initially verified the exact matches against the GBIF species checklist; (ii) selected unmatched cases and fix orthographic errors; (iii) retrieved again taxonomic information for those unmatched cases, evaluated accuracy of fuzzing matching and programmatically fixed

Table 1. Column names and their descriptions within the EuPPollNet database.

Variable	**Description**
Study_id	Identifier of the study
Network_id	Identifier of a site sampled within a study
Sampling_method	Type of plant-pollinator sampling
Authors_habitat	Type of habitat as described by the authors
EuPPollNet_habitat	Type of habitat homogenized across studies
Bioregion	European biogiographical regions
Country	Country where the plant-pollinator interaction was observed
Locality	Locality where the plant-pollinator interaction was observed
Latitude-Longitude	Coordinates of the observed interaction in decimal degrees
Date	Year, month and day when the observation took place
Interaction	Number of interactions. By default is 1 as interactions are provided ungrouped
Plant_old_name	Plant species name given by the authors
Plant_accepted_name	Harmonized plant species name in the database
Plant_rank	Taxonomic rank of the observation
Plant_order	Order taxonomic rank of the observed plant species
Plant_family	Family taxonomic rank of the observed plant species
Plant_genus	Genus taxonomic rank of the observed plant species
Plant_unsure_id	Category to indicate if the plant species name is unsure (Yes) or not (No)
Plant_uncertainty_type	If the name is unsure, type of species uncertainty is provided
Pollinator_old_name	Pollinator species name given by the authors
Pollinator_accepted_name	Harmonized pollinator species name in the database
Pollinator_rank	Taxonomic rank of the observation
Pollinator_order	Order taxonomic rank of the observed pollinator species
Pollinator_family	Family taxonomic rank of the observed pollinator species
Pollinator_genus	Genus taxonomic rank of the observed pollinator species
Pollinator_unsure_id	Category to indicate if the pollinator species name is unsure (Yes) or not (No)
Pollinator_uncertainty_type	If the name is unsure, type of species uncertainty is provided
Flower_data	Floral data availability (Yes) or (No)
Flower_data_merger	Column to merge floral data with the interaction dataset

records that are still not found; (iv) finally, we used the World Flora Taxonomic Backbone (Govaerts et al. 2021; WFO, July 7, 2022) as the ultimate filter for taxonomic information as we used it to calculate the plant taxonomic coverage of our database.

For pollinators: (i) we first created a checklist of species names for the most representative pollinator groups at European level by combining the recently published checklists of bees (Ghisbain et al. 2023), syrphids (Kočić et al. 2023) and butterflies (Wiemers et al. 2018); (ii) then, we compared pollinator species names against the checklist and recovered some unmatched cases with restrictive fuzzy matching by using **stringdist** package (Van der Loo et al. 2014); (iii) we programmatically fixed unmatched records when necessary and retrieved the taxonomic information for all species from GBIF; (iv) we fixed the non-found cases in the GBIF checklist and made sure that all species names from bees, syrphids and butterflies were named according to their respective species checklists.

Taxonomic coverage

To assess the completeness of plant and pollinator species in the EuPPollNet database at European level, we used the aforementioned checklists for plants and pollinators. Specifically for plants, we refined the checklist to include only European flowering plants and excluded taxonomic groups not associated with biotic pollination. We did this by first excluding the families considered to have exclusively a wind pollination mode (see Culley, Weller, and Sakai 2002), and then by filtering out the genera with wind or non-biotic pollination from families that exhibit both biotic and non-biotic pollination modes. Additionally, we manually included some exotic species and added unresolved species names that were not present in the accepted names of the checklist at the current version of usage. For pollinators, we compared only the taxonomic coverage of bees, syrphids and butterflies by using their species checklists at European level. The potential number of pollinator species at European level was estimated by adding the total number of species of bees, syrphids, and flies from the checklists, along with the extrapolated number of species from other insect pollinators. This extrapolated number was estimated by assuming that the sampling coverage of these other insect pollinators is equal to the average coverage across bees, syrphids, and butterflies (mean coverage = 31.03; sd = 4.19).

Finally, to evaluate if the presence-absence of interaction records for bees and flowering plants follows a phylogenetic pattern within the database, we calculated its phylogenetic signal at genus and family level, respectively. The phylogenetic signal was calculated by using the *phylosig* function from the **phytools** package (Revell 2012). We extracted the phylogenetic information for bees from a genus level phylogeny (Hedtke, Patiny, and Danforth 2013) and processed it with the help of the packages **ape** (Paradis et al. 2019), **MCMCglmm** (Hadfield 2010) and **phytools**; and for plants the phylogenetic tree was obtained from a species level plant phylogeny (Smith and Brown 2018) with the help of **rtree** package (Li 2023).

Habitat type and bioclimatic region

The different sites per study were described with a habitat type by the authors. As these habitats are not standardized across studies, they were standardized with the additional help of land cover information and visual checks on current satellite imagery. For each georeferenced site, the land cover information was extracted from Corine Land Cover (CLC, version 2018) with the help of the Terra package (Hijmans et al. 2022). Based on the habitat classification from the authors and the CLC classification, we created habitat categories that intend to summarize the diversity of habitats in the EuPPollNet database (see habitat type definition in supplementary material). These categories allow a quick comparison and understanding of the habitat types from the database. However, we advise authors to revise this classification if they intend to rely on this field for their analyses as this is a non-fully objective process. Moreover, Europe is characterized by a great variety of environmental conditions that harbor different biota. Thus, to allow authors to explore set of studies that share similar environmental conditions and species, we assigned to each site a biogeographical region. The biogeographical regions were downloaded from the European Environment Agency (version 2016) and were matched to the different sites with the help of a spatial joint from the **sf** package (Pebesma et al. 2018).

Network analyses

To provide a general overview of the main aspects of this set of plant-pollinator networks, we evaluated network patterns of connectance and nestedness across the latitudinal range of studies and bioclimatic regions. We selected these two network metrics as they are commonly evaluated in plant-pollinator network studies and capture structural properties with a straightforward interpretation. However, these network metrics are not independent of sampling effort (e.g., number of species) and to allow comparisons across them, we implemented "standardised" versions of connectance and nestedness. As connectance is negatively associated with network size (Jordano 1987), we evaluated how network connectance was associated with the number of species (i.e., log of geometric mean of plants and pollinators) and extracted the residuals from this association (i.e., residual connectance) as a measurement of corrected connectance. This was done with the help of a Beta regression implemented with the package **betareg** (Cribari-Neto and Zeileis 2010). Second, we implemented a metric of nedstedness (i.e., NODFc) that allows the comparison across networks as it corrects by connectance and the number of species (Song, Rohr, and Saavedra 2017). This metric was calculated with the help of the **maxnodf** package (Hoeppke and Simmons 2021), which employs a computational efficient approach to calculate it. Both residual connectance and NODFc were used as dependent variables to evaluate their association with latitude. In addition, we explored the association between connectance and nestedness with the number of species per network by conducting Kendall rank correlation coefficient in order to be able to compare the strength of this association across both network metrics.

Finally, to compare if networks are more or less nested than expected by chance, we employed the traditional z-score approach with the widely used nestedness metric (NODF) from Almeida-Neto et al. (2008), as this approach allow us to compare our results with previous published nestedness analyses in plant-pollinator networks and only compares each unique network against their randomized versions. We calculated 100 null models for each network with the help of the vaznull function from the package **bipartite** (Dormann, Gruber, and Fründ 2008) that implements the null model from Vázquez et al. (2005). These null networks have the same connectance and number of plant and pollinator species as the empirical ones, but different marginal totals. Both connectance and nestedness (NODF) were estimated for each network by using the function *networklevel* from **bipartite**.

3 | RESULTS

Sampling coverage

The estimated sampling coverage of plant and pollinator species within the database across the different sampling sites is approximately 97% for both taxonomic groups. This suggests that the rarefied accumulation curves of both plant and pollinator species exhibit already a "quasi-asymptotic" growth of species richness by considering the current number of sampling sites or networks (**Figure 2a-2b**). The predicted observed species richness by doubling the sampling effort on the already sampled habitat types within the database will only increase pollinator richness by 24.13% and plant richness by 21.14%. However, the sampling coverage of interactions is 74.17%, and by doubling the sampling effort the predicted number of unique interactions recorded will have approximately a twofold increase (54.83%; **Figure 2c**). Similarly, to the plant and pollinator species accumulation curves across sampling sites, when we consider the accumulated pollinator richness across sampled plant species, this curve also shows a "quasi-asymptotic" growth with a sampling coverage value of 96.66%. The predicted recorded pollinator species by doubling the number of plants sampled is expected to increase by 21.90% (**Figure 2d**). In addition, when we explore how common or rare are plant and pollinator species across all sampling sites, we find that the majority of plant and pollinator species tend to be regionally specific, and only a minor portion of them is being shared across a broad range of sampling sites (**Figures 2e-2f**). For instance, most plants (84.70%) and pollinators (87.07%) are exclusively found in less than 1% of sampling sites; and the most common plant (*Trifolium pratense*) and pollinator (*Bombus pascuorum*) species are only found in 37.32% and 64.80% of sampling sites, respectively.

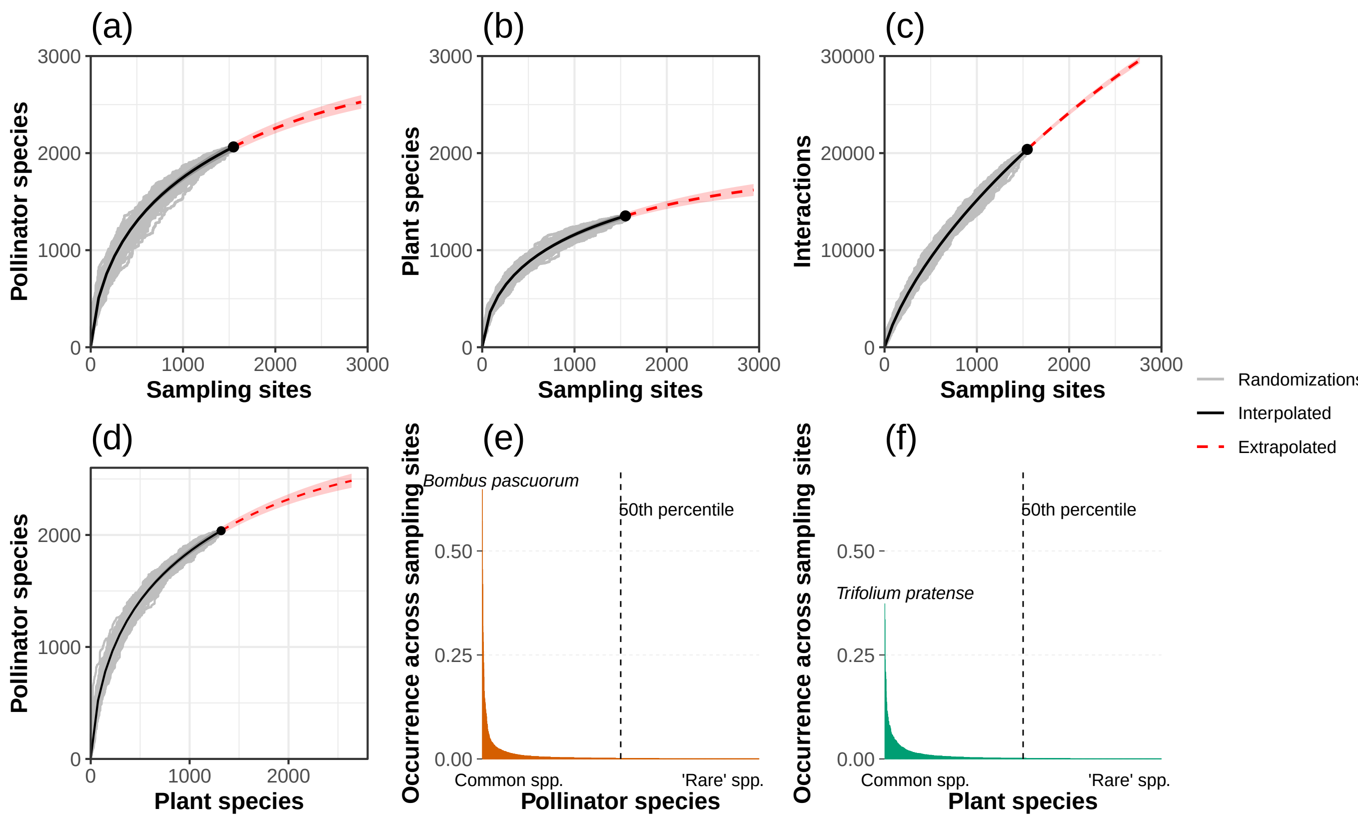

Figure 2. Graphs (a-b-c) indicate the accumulation curves for pollinators, plants, and their interactions across sampling sites. Grey solid lines represent 100 randomized accumulation curves, the black solid lines represent the interpolated curve (i.e., the mean across curves), and the red dashed lines illustrate the extrapolated curve for approximately 3000 sampling sites. The solid black points indicate the number of species and interactions contained in the database. Graph (d) shows the accumulation curve of pollinator species across an increasing number of plant species. This last graph uses the same color and shape structure as the ones in the top panel. Graphs (e-f) indicate the percentage of occurrence (i.e., incidence) of plant and pollinator species across sampling sites. Species on the left (i.e., common) are found in many sampling sites, while species on the right (i.e., rare) are found in few or only a single sampling site. Note that indeed *Apis mellifera* is the most common pollinator but was excluded from this visualization.

Taxonomic coverage

The database contains a total of 2,065 pollinator and 1,353 plant species. The coverage of the main pollinators groups occurring in Europe is 33.82% for bees, 33.08% for syrphids and 26.21% for butterflies (see **Figure S1** for coverage at the family level for bees and butterflies, and at the subfamily level for syrphids). Bees constitute 90.58% of the interactions of the database, and 78.03% of the interactions when excluding honey bees. Within the database, 83.82% of bee genera have at least one species with interaction records, and the average coverage at the bee genus level is 36.99% (**Figure 3**). In addition, the presence or absence of interactions records for bees seems not to follow any sort of phylogenetic pattern ($\lambda = 0.07$; $P = 0.65$). The database coverage of all flowering plant species occurring in Europe is 5.34% (**Figure 4**), with an average coverage of 9.04% at the plant family level. Approximately, half of the plant families have at least one species with interaction records (52.56%), and the presence or absence of interaction data for the different plant species also seems not to follow a statistically relevant phylogenetic pattern ($\lambda = 0.26$; $P = 0.07$).

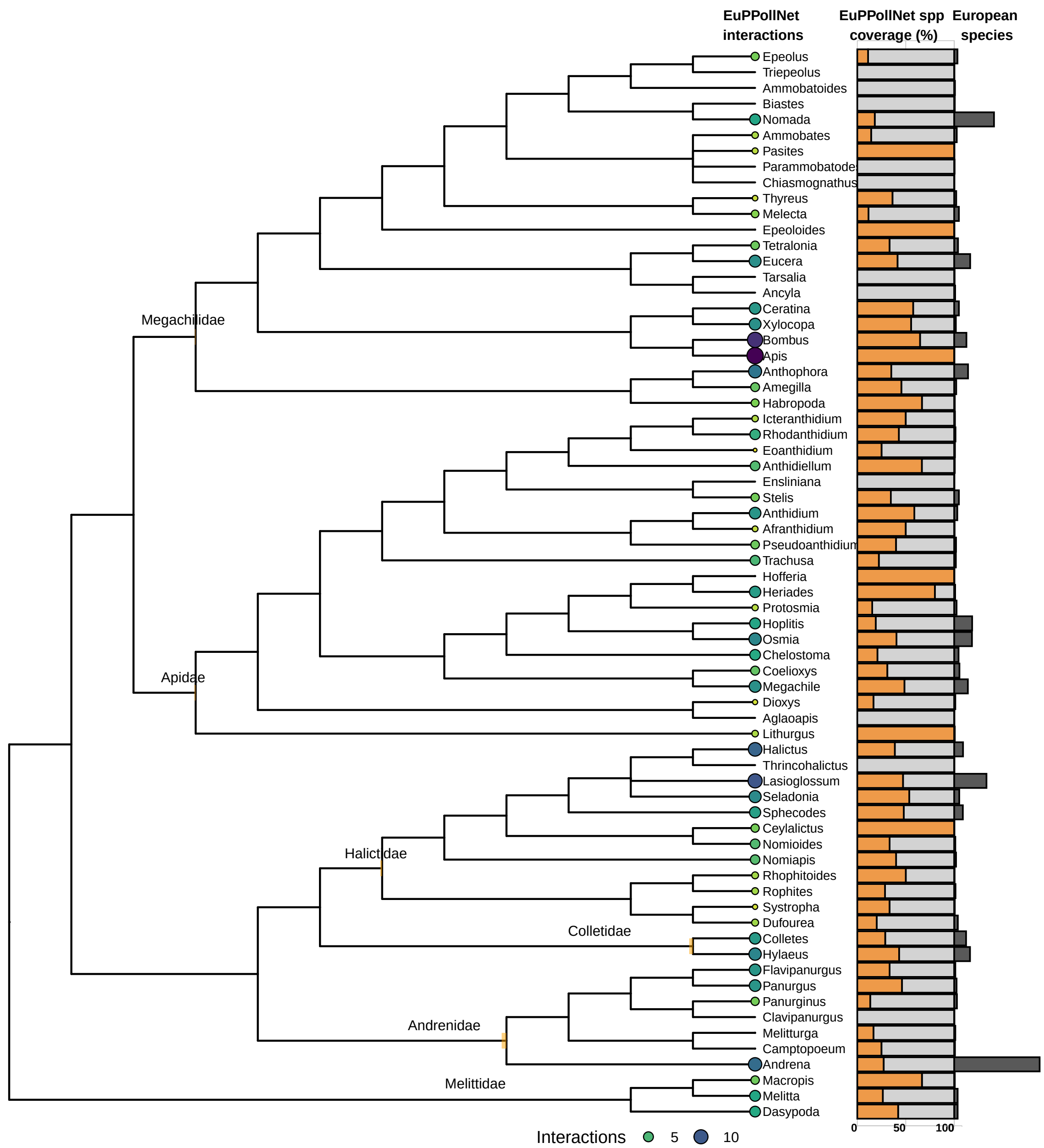

Figure 3. Phylogenetic representation of bee genera in the EuPPollNet database within the context of all European bee genera. The number of interactions recorded per genus in the database is illustrated using circles, with their sizes proportional to the number of interactions on a logarithmic scale. Additionally, a gradient of colors ranging from yellow to dark purple aids in this visualization. The coverage of species recorded in EuPPollNet per genus at the European level is depicted with orange and light grey bars, representing the percentage of species included and not included in the database, respectively, out of the total number of bee species per genus at the European level. Grey bars indicate the total number of species per genus at the European level.

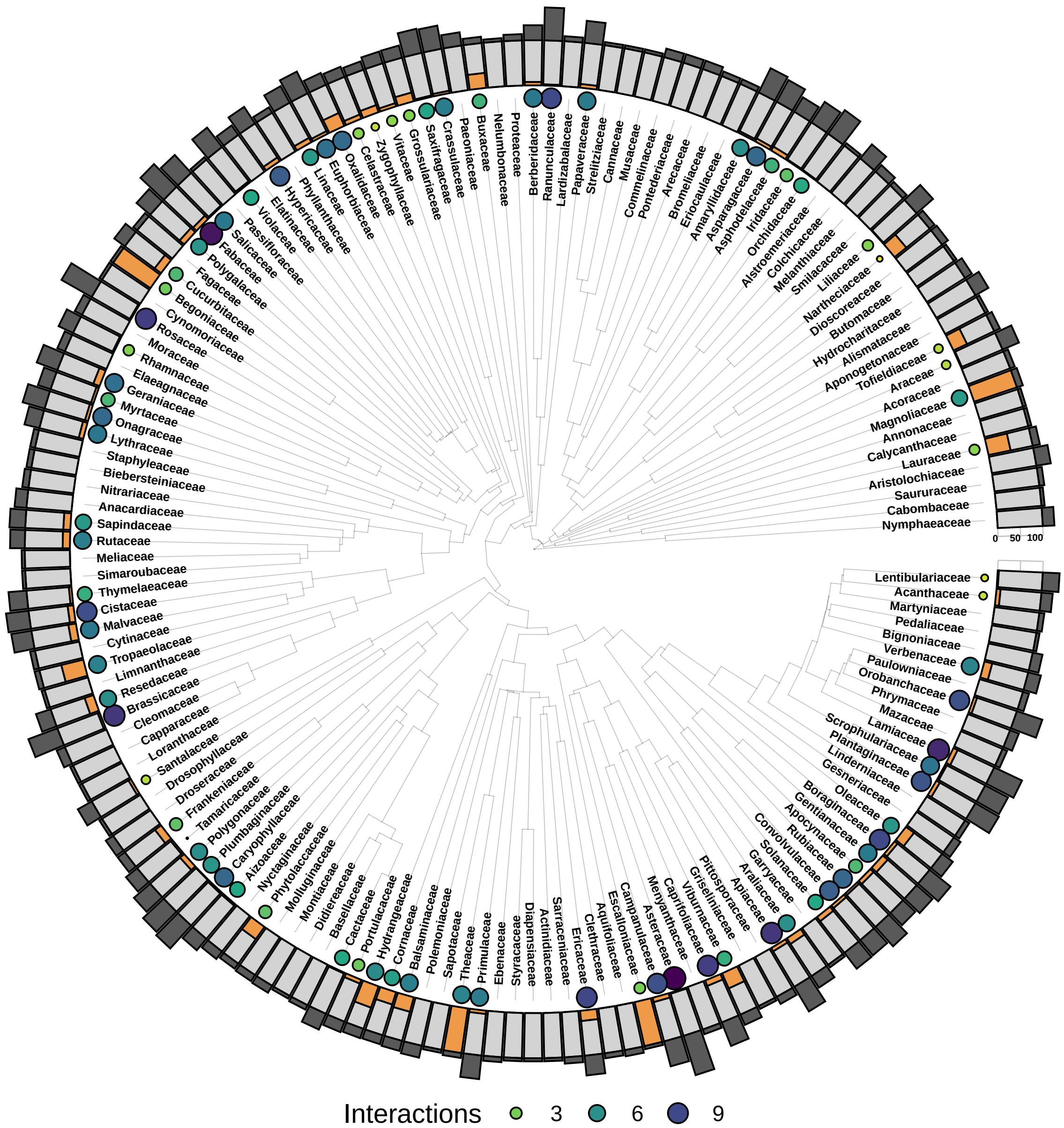

Figure 4. Phylogenetic representation of the plant families in the EuPPollNet database within the context of all flowering plant families occurring in Europe. The number of interactions recorded per genus in the database is illustrated using circles, with their sizes proportional to the number of interactions on a logarithmic scale. Additionally, a gradient of colors ranging from yellow to dark purple aids in this visualization. The coverage of species recorded in EuPPollNet per genus at the European level is depicted with orange and light grey bars, representing the percentage of species included and not included in the database, respectively, out of the total number of flowering plant species per family at the European level. Grey bars indicate the total number of species per family at the European level on logarithmic scale.

Habitat type and bioclimatic region

The proportion of the major pollinator orders within the database differed across habitats and bioclimatic regions (**Figure 5**). As expected, Hymenoptera was the main taxonomic order on the majority of habitats, exceeded only by Diptera on the habitat categories of riparian vegetation, moors and heathland, and alpine grasslands. Overall, the proportion of Lepidoptera and Coleoptera was low across all habitats but Coleoptera showed a notably increase in sclerophyllous vegetation and beaches, dunes and sands habitat categories. Similar patterns were observed when exploring the pollinator proportions by bioclimatic region. In this particular case, Hymenoptera was the predominant order in all bioclimatic regions with Diptera taking more importance in Alpine and Atlantic regions. Again, Lepidoptera shows low proportions across all bioclimatic regions and Coleoptera seems to be only relevant in Mediterranean regions at European level. Notably, the number of studies (**Figure 5**) and sampling sites (**Figure S2**) also differs across habitats and bioclimatic regions. The habitats sampled by a higher number of studies in the database are pastures (27), semi-natural grassland (11) and sclerophyllous vegetation (9). However, the habitats that contain a higher number of sampling sites are pastures (589), agricultural margins (432) and agricultural land (141). The bioclimatic regions with a higher number of studies are continental (22), atlantic (13) and mediterranean (12); and the ones that contain a higher number of sampling sites are atlantic (459), continental (454) and boreal (439).

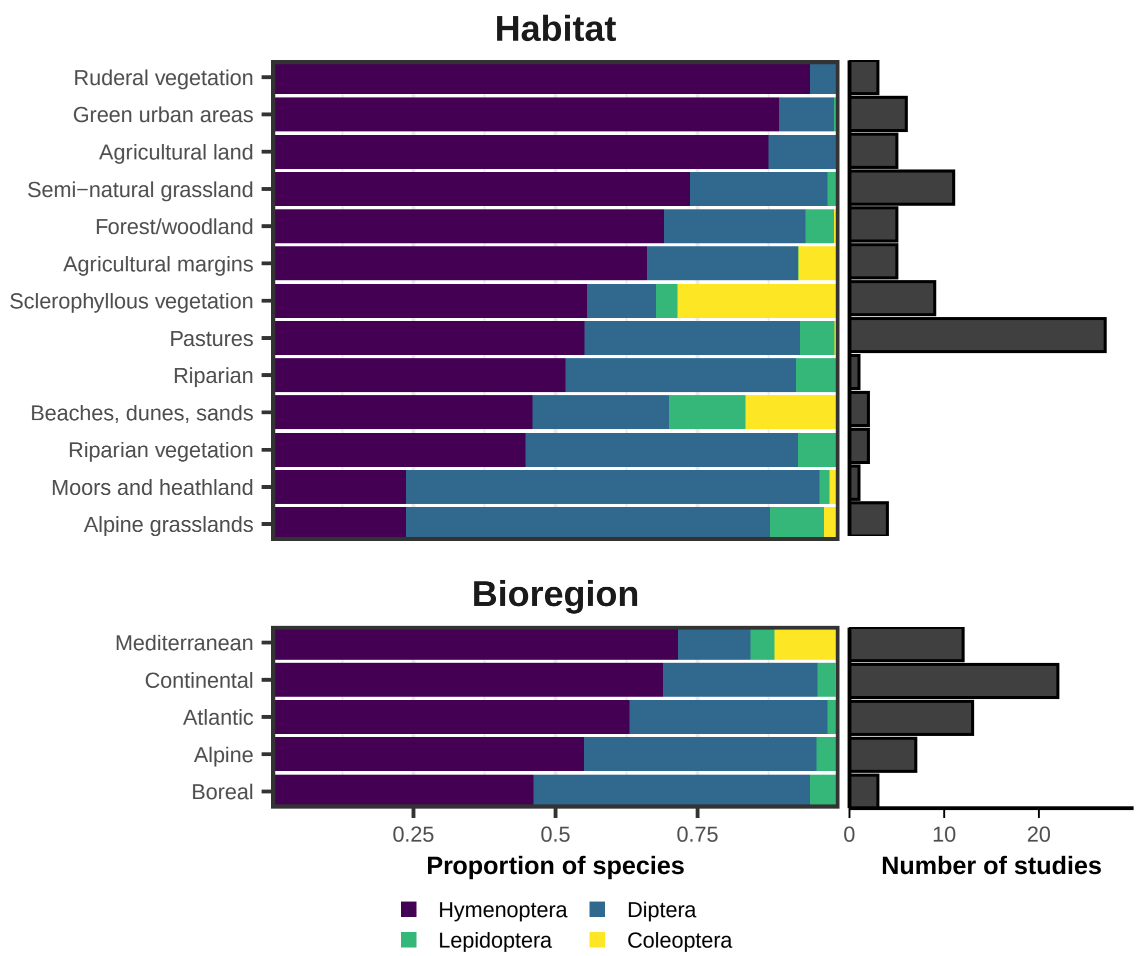

Figure 5. Proportion of the major pollinator orders by habitat types and bioclimatic regions in the EuPPollNet database. The orders, from left to right, include Hymenoptera, Diptera, Lepidoptera and Coleoptera. The horizontal barplot on the right indicates the number of studies that were conducted on each habitat type or bioclimatic region. Note that a single study can contribute to more than one habitat or bioclimatic region. Areas with a greater number of studies are more likely to depict accurate proportions of the different pollinator orders in those systems.

Network properties

Connectance values ranged between 0.03 to 0.4 ($\bar{x} = 0.14$) and as expected, followed an negative exponential relationship with the number of species per network (Kendall τ = -0.75, $P < 0.01$; **Figure 6a**). Nestedness values (NODFc) ranged between 1.34 to 7.94 ($\bar{x}$ = 2.81), and as expected for this metric, were independent of the mean number of species (Kendall τ = -0.06, P = 0.03; **Figure S3**). We found that only 31.62% of networks were statistically more nested than expected by chance, with 68.38% showing no statistical difference, and none being less nested than null expectations (**Figure 6b**). Latitude explained little of the observed variability of residual connectance and nestedness across networks (connectance: $R^2 = 0.02$, P = 0, **Figure 6a**; NODFc: $R^2 = 0.01$, $P = 0.02$, **Figure 6b**). Overall, networks towards higher latitudes showed lower residual connectance and higher nestedness that networks located in lower latitudes. Note that residual connectance and normalised nestedness have a moderate negative correlation (Kendall τ = -0.06, $P = 0.03$).

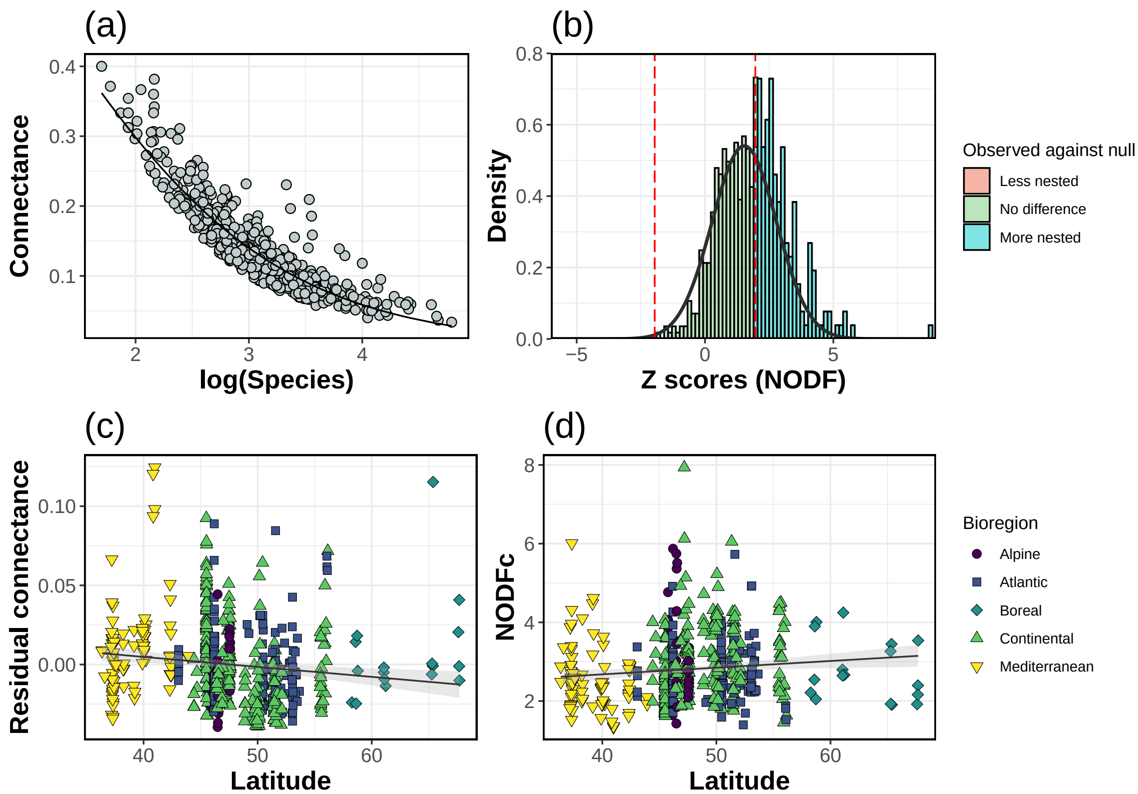

Figure 6. Graph (a) shows the association between network connectance and the geometric mean of plant and pollinator species per network on a log-scale with the respective fitted line from a Beta regression. Graph (b) shows the distribution of z-scores when comparing the nestedness from the empirical networks with their randomised counterparts (100 null models for each network). The vertical red dashed lines represent the z critical value for a two tailed test with alpha = 0.05. Z-scores to the left of the first vertical red dashed line indicate that networks are less nested than expected by chance (red), those between the two dashed lines indicate no statistical difference from random expectations (green), and those to the right indicate that networks are more nested than expected by chance (blue). Graphs (c-d) show the fitted regression of residual connectance and nestedness across the latitudinal range of the studies from the database. In addition, the bioclimatic region of each network is indicated with points of different shapes and colours.

3 | DISCUSSION

EuPPollNet offers the largest set of plant-pollinator networks and plant-pollinator studies compiled to date at European level. The database contains 1,353 plant and 2,065 pollinator species with over a million of interaction records. While the overall sampling coverage of species and interactions is relatively high across the sampled sites, the taxonomic coverage of plants and the main pollinator groups at the European level is still relatively low (e.g., 5.3% for flowering plants and 33.8% for bee species). Given that most of the plant-pollinator networks from the database are sampled on pastures, and habitat heterogeneity is a crucial factor in understanding pollinator diversity at European level (Kleijn et al. 2015; Hass et al. 2018; Martínez-Núñez et al. 2022), adding studies on other habitat types is likely to result in a rapid increase of the coverage of plant and pollinator species and their interactions. Plant and pollinator species were rarely shared across multiple sites, indicating that there are few "common" species and many "rare" ones at the metaweb or continental level. This high number of "rare" species results in an upward slope of the species or interaction accumulation curves (Thompson and Withers 2003). In other words, minimal sampling efforts are capturing a substantial number of species and interactions, but achieving a comprehensive inventory will require of numerous sampling events within and across habitats, particularly for plant-pollinator interactions.

Bees conducted the majority of the interactions at the metaweb level, but their relative relevance changed across habitats and bioclimatic regions. For instance, plant-pollinator communities in the Mediterranean were dominated by bees, while communities in Alpine or Boreal regions were especially fly species rich or fly-dominated. These patterns are consistent with our current understanding of bee diversity, which peaks in dry or temperate areas (Orr et al. 2021; Leclercq et al. 2023); and with the fact that colder environments (i.e., altitude and latitude wise) harbor a larger fraction of fly pollinators compared to other taxa (Elberling and Olesen 1999; Lefebvre et al. 2018). In addition, beetles were only species rich in the Mediterranean region. Although the networks from the database are visitation networks and do not capture pollinator efficiency (Ballantyne, Baldock, and Willmer 2015), the high proportion of beetles as floral visitors in the Mediterranean provides further support for their role as pollinators in this region (Herrera 2019; León-Osper and Narbona 2022). The number of butterfly species and interactions were relatively low compared to the other taxa. While Europe contains fewer butterfly species than other regions of the world (Ollerton 2017), their relevance as pollinators is likely underestimated within this database. This is because a large fraction (~40%) of studies did not sample butterflies, and conventional sampling methods for monitoring other insect pollinators (e.g., bees or flies) may be inadequate for sampling plant-butterfly interactions (Isaac et al. 2011). Honey bees were present in 86.3% of networks and conducted in average a third of the total interactions per network. This proportion is higher that the one found when considering only natural communities at a global scale (~13%; Hung et al. 2018), which highlights the need of further work evaluating how honey bees and their management impact natural pollinator communities.

Although Europe contains a much larger number of flowering plants than pollinator species (~4 to 1 ratio), the observed number of pollinator species almost doubled the one of plants in the database. This could be explained by the fact that all networks are phytocentric, resulting in sampling bias towards pollinator species (Jordano 2016; Vizentin-Bugoni et al. 2018). While animal-centred sampling is likely to increase the plant:pollinator species ratio (e.g., Encinas-Viso et al. 2023), the spatial scale and environmental context of the sampled communities will also influence their observed diversity, especially given the ability to move of pollinators and the sessile nature of plants. As expected (Jordano 1987), we found that network connectance decreased exponentially with the number of species. Overall, latitude did not explain major changes in residual connectance or normalised nestedness of the plant-pollinator networks. Consistent with Olesen and Jordano (2002), residual connectance was lower at higher latitudes, while nestedness, which is negatively correlated with residual connectance, increased towards higher latitudes. Given their correlation, the potential ecological explanations that can help understanding these structural patterns can be similar. For instance, networks at lower latitudes in Europe are exposed to higher temperatures and are bee-dominated, which can result in higher visitation rates (Arroyo, Armesto, and Primack 1985; Classen et al. 2015; Herrera 2019); and, the level of pollinator generalization seems to be higher at lower latitudes (Schleuning et al. 2012). Therefore, these different factors can increase the possible number of connections that can be established between plants and pollinators for a given network size, resulting in more connected networks but less nested ones in comparison to networks at higher latitudes. In addition, while one third of networks were more nested than expected by chance, two thirds of them did not show statistical difference with null expectations. This goes against the common view that all plant-pollinator networks are nested (Bascompte et al. 2003), and supports the idea that despite a tendency towards it, being nested is not the rule in this type of mutualism.

Nestedness

Finally, these networks have different sampling effort and employ different metodologies which can impact the resulting structure of interactions [REF].

Finish this paragraph with an idea of how sampling can bias our view and that is important to be aware of that when understanding plant-pollinator patterns

Discuss that other type of informative networks could be useful a increase connectance?

visitation networks

Link with interactions –>

More species less connectance, which increases the number of missing links.

Nestedness Pattern across latitude

Missing links?

networks condense information but this workflow allo possibility to explore species phenology… and more

Interactions: Sampling area, spp accumulation vs interactions: https://doi.org/10.1890/12-0367.1 Sampling completeness (e.g., Chacoff et al. 2012)

Networks, ref: https://www.biorxiv.org/content/10.1101/2020.04.02.021691v1.abstract

Conclusion paragraph

foundation for future work

Geographic and taxonomic biases! Supporting reference: https://doi.org/10.1111/ecog.05926

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Author contributions

Supplementary material

Supplementary text 1

Habitat definitions:

1) **Ruderal vegetation**: Plants growing on highly disturbed sites such as road sides or mineral extraction sites.
2) **Agricultural margings**: Sides of crops that can include any type of vegetation from low growing plants to trees.
3) **Green urban areas**: Parks, private gardens or small pastures within an urban setting. Botanical gardens are included in this category.
4) **Agricultural land**: Includes any type of crop and any type of vegetation growing within them.
5) **Forest/woodland understory**: Any plant community sampled under a wooded group of plants. The forest could be embedded in an agricultural setting or in a fully natural scenario. We have included here agro-forestry areas and open to dense forest. Note that we have excluded from this category forest that contains sclerophyllous vegetation.
6) **Semi-natural grassland**: Low growing plant community with relatively low disturbances but under low pressure such as seasonal mowing or extensive grazing.
7) **Pastures**: Any type of low growing plant community that is highly influenced by human disturbance. For instance, agriculture, mowing, moderate to high grazing or urban environments. Note that this category also includes old pastures with regrowth of woody vegetation.

8) **Sclerophyllous vegetation**: Any type of system with a dominant shrub community adapted to drought. Typical of the Mediterranean region. Note, that we have include in this category also woodlands (open coniferous forest) where the shrub community was the main focus of the study.

9) **Beaches, dunes, sands**: Plant communities growing on sandy soil.

10) **Riparian vegetation**: Plant communities growing on river margins.

11) **Natural grassslands**: Low growing plant communities with little or none human disturbance. Often located in high elevation areas within Europe.

12) **Moors and heathland**: Low growing woody vegetation characteristic from low fertile soils near the coast or in alpine areas.

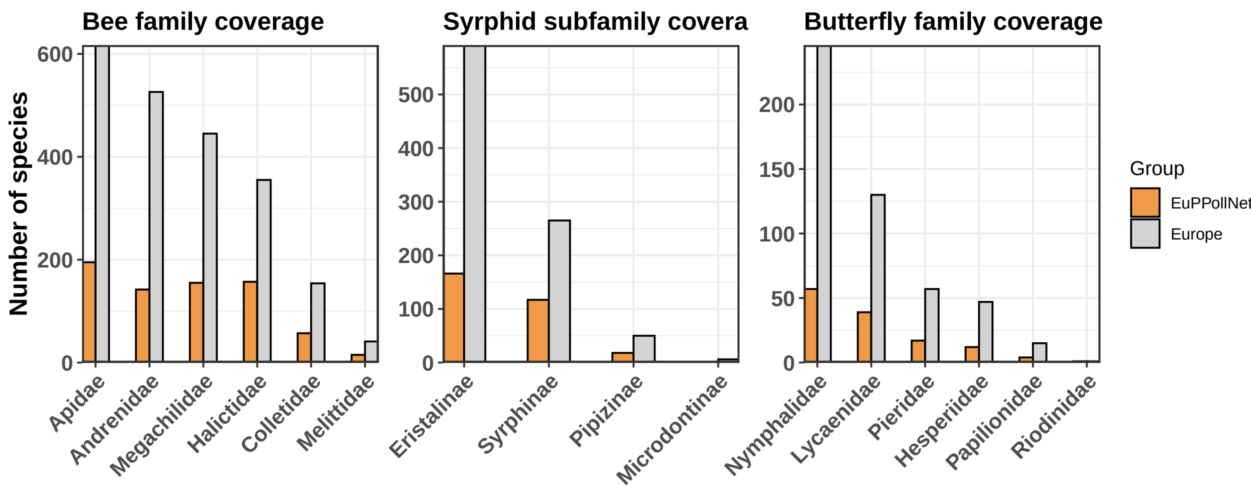

Figure S1. Coverage of the EuPPollNet species for bees (family level), syrphids (subfamily level) and butterflies (family level) in relation to the total number of European species within these taxonomic groups.

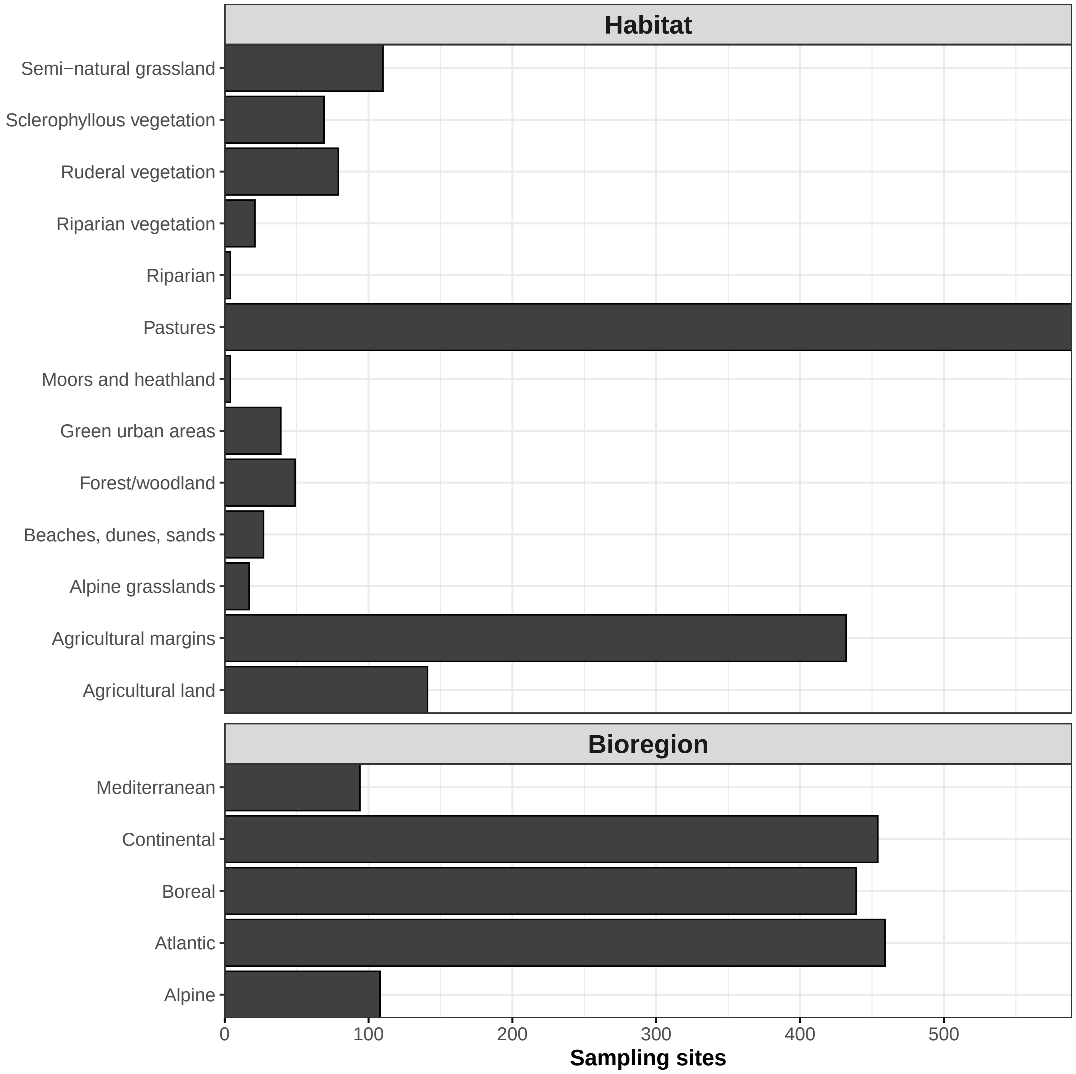

Figure S2. Barplot indicating the number of sampling sites by habitat and bioclimatic region within the database.

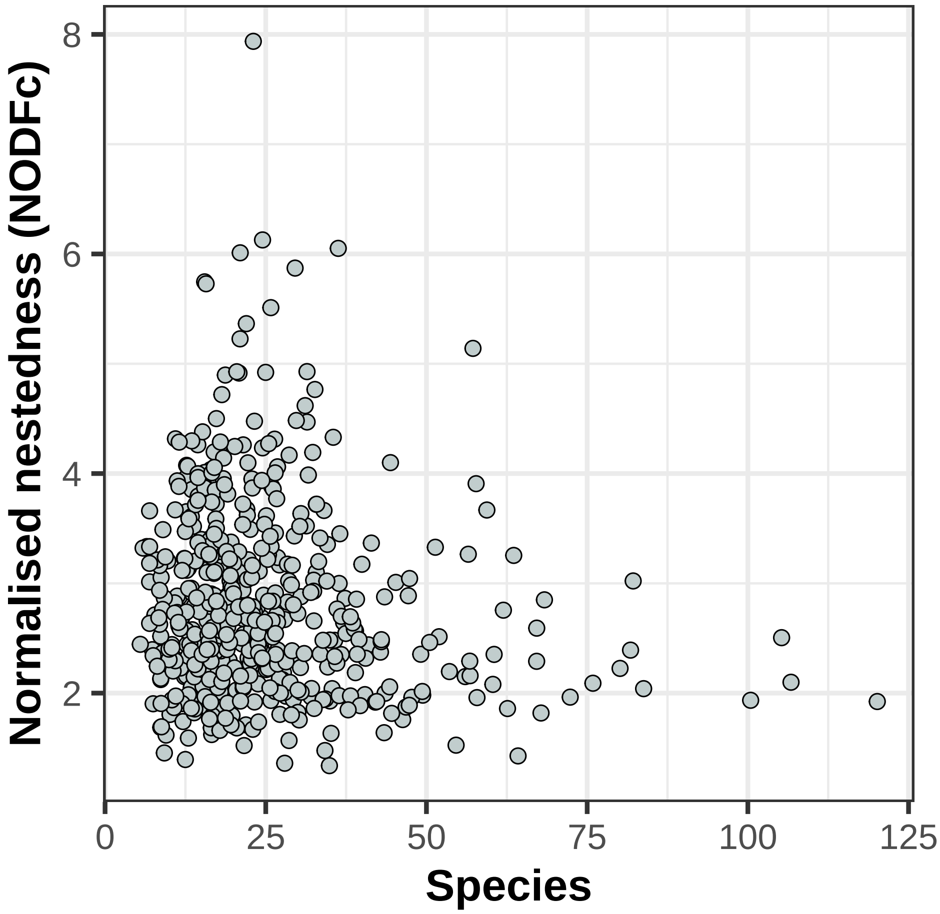

Figure S3. Association between nestedness (NODFc) and the geometric mean of plan and pollinator species per network