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. However, their diversity and role as pollinators are increasingly compromised by rapid human-induced environmental changes. One of the major challenges for pollinator conservation, is the lack of robust generalisable data across space and time to comprehend the conservation status and population trends among different pollinator species. Here, we present the EuPPollNet database, a fully 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 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 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 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. The main focus of this database are insect pollinators and accounts for 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 coevolutive 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 (González-Varo et al. 2013; 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), and has added relevant information of their interaction ecology of plant-pollinator networks across geographic regions (Olesen and Jordano 2002; Traveset et al. 2016) and 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 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 informative 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 to 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 allow to being reused and keep building on it over time. 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**).

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, the accumulation curve of pollinator species with increasing number plant species was also explored. 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 verify exact matches with the GBIF species checklist; (ii) select unmatched cases and fix orthographic errors; (iii) retrieve again taxonomic information for those unmatched cases, evaluate accuracy of fuzzing matching and programmatically fix records that are still not found; (iv) finally, we used the World Flora Taxonomic Backbone (Govaerts et

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
SafeNet_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

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.

Habitat type and bioclimatic region

The different sites per study were classified 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 get a general overview of some of the main aspects of these set of plant-pollinator networks, we evaluated how connectance and nestedness change across the latitudinal range of studies and bioclimatic regions. In addition, we explored the association between connectance and number of species per network (i.e., geometric mean of plants and pollinators), and if the different networks are more or less nested than expected by chance. Importantly, we implemented two different metrics of nestedness given the different analytical objectives. Common metrics of nestedness are highly correlated to network size, limiting our ability to compare this metric across networks. To avoid this, we implemented a normalised version of nestedness (NODFc) that 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. However, 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. In other words, interactions are reshuffled with almost equal probabilities to their relative abundances. Finally, connectance was 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 suggest 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.
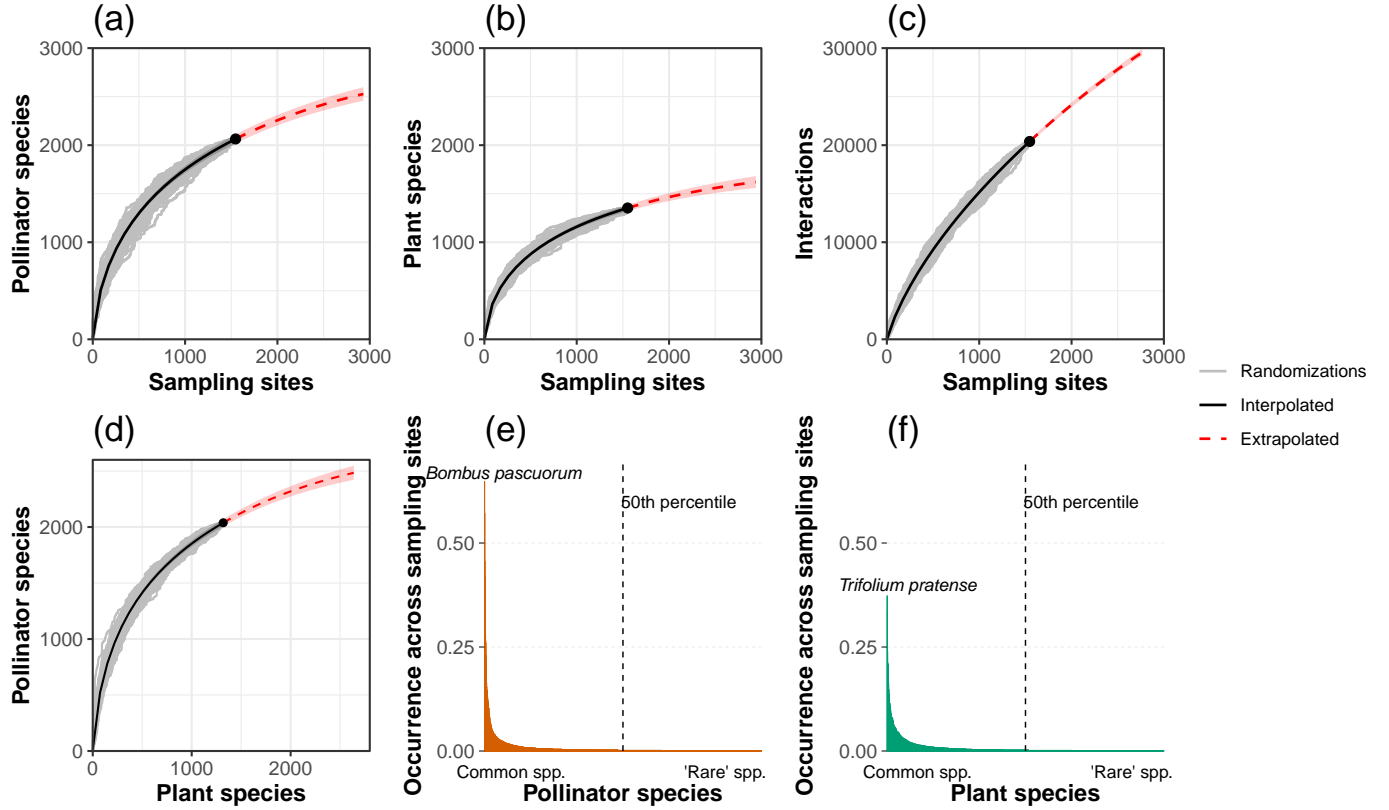
Figure 2. Graphs (a-b-c) indicate the accumulation curves for pollinators, plants, and their interactions across sampling sites. Grey solid lines represent 100 randomized accumulation curves, the black solid lines represents the interpolated curve (i.e., the mean across curves), and the red dashed lines illustrates 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 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.

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Taxonomic coverage

The database contains a total of 1,353 plant and 2,065 pollinator species. The coverage of plant species when considering all flowering plants occurring in Europe is 5.34% (**Figure 4**), and the average species coverage at plant family level is 9.04%.

The estimated sampling coverage of plant species at European level is x% (**Figure 4**). The three families with higher number of interactions within the database are xxxxx (%), xxxxxx (%) and xxxxx (%). Despite these species have a high number of interactions within the database, the number of species recorded within the database in comparison with the total number of species at European level reveals a low coverage of interactions for most of the species of these families.

The most common order of plants is Asterales with Asteraceae being the family with highest number of species within the database.

The database coverage of plants at European level is x% and the pollinator coverage when considering bees x%, syrphids x% and butterflies x%.

Most species of pollinators are Hymenoptera species (%), and most of these species are bees (%).

Figure 3 Figure 4 Figure S1

Provide number of species per taxonomic group and number of interactions Something always of interest: provide % of interactions of *Apis mellifera*?

Habitat type and bioclimatic region
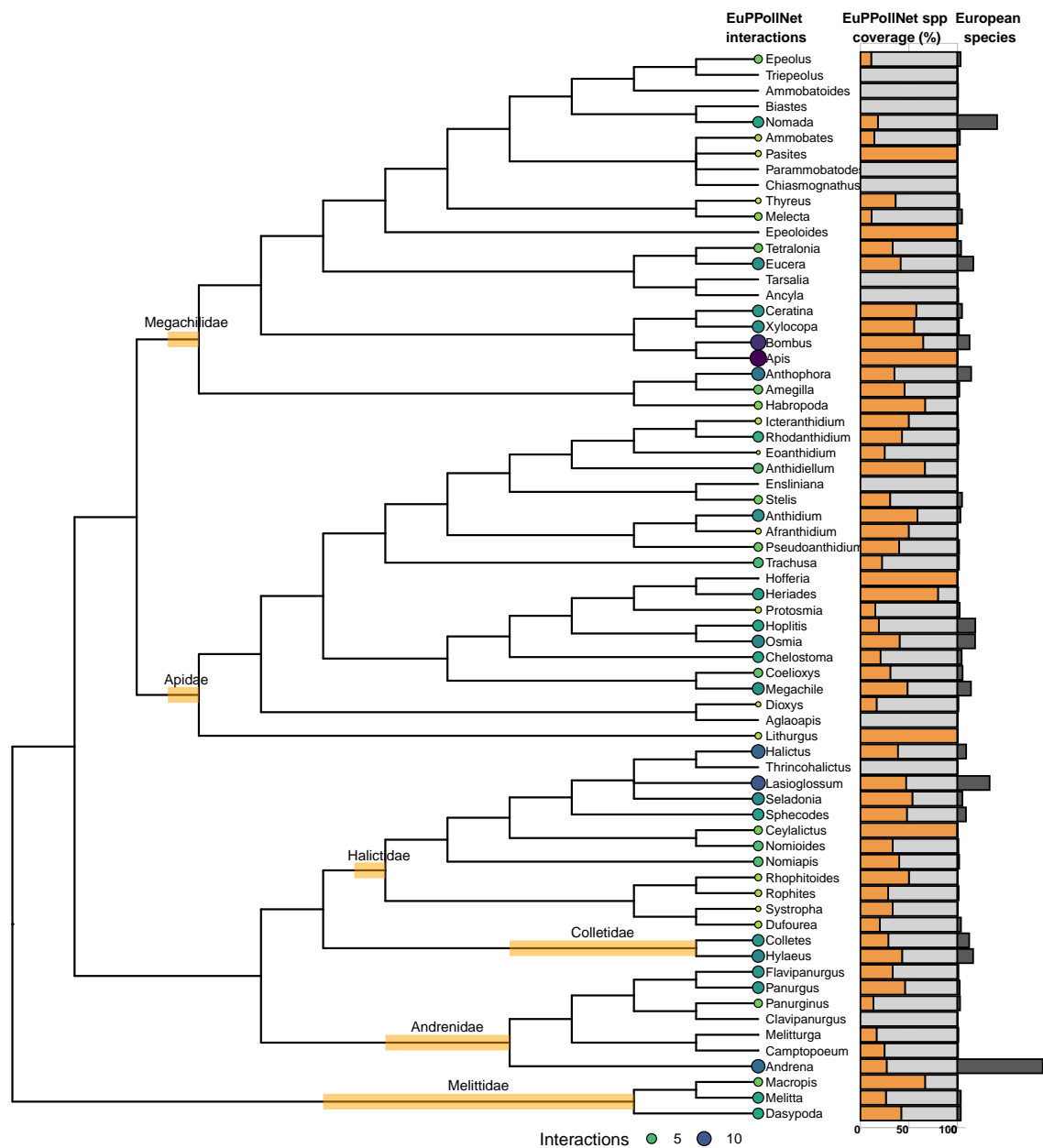
Network properties

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.
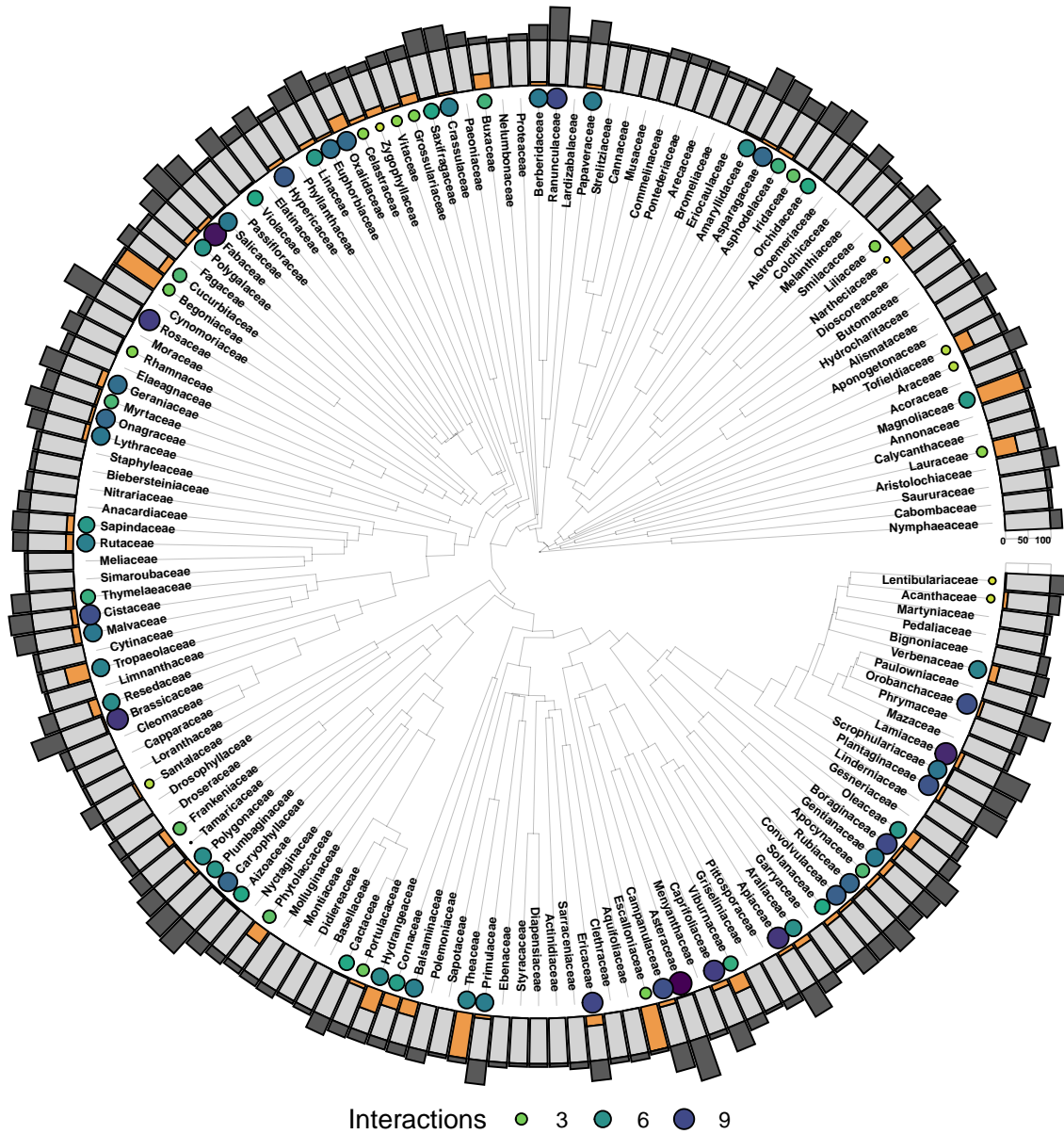
Figure 4. Phylogenetic representation of the plant families in the EuPPollNet database within the context of all flowering plant families occurring in Europe. The number of interactions recorded per genus in the database is illustrated using circles, with their sizes proportional to the number of interactions 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.

3 | DISCUSSION

Although Europe...

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

Networks, ref:

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

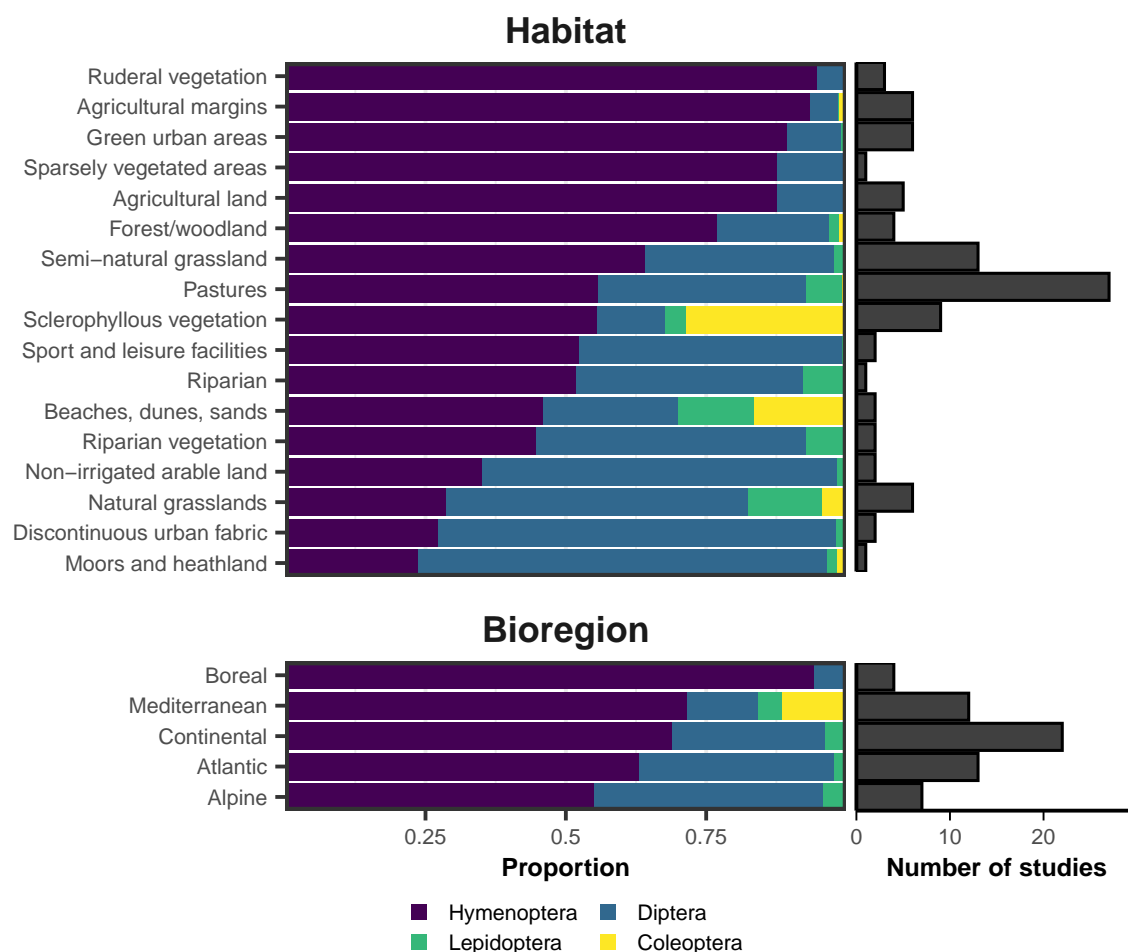Contextualise European diversity of plant and pollinator species with global biodiveristy

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 countribute 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.
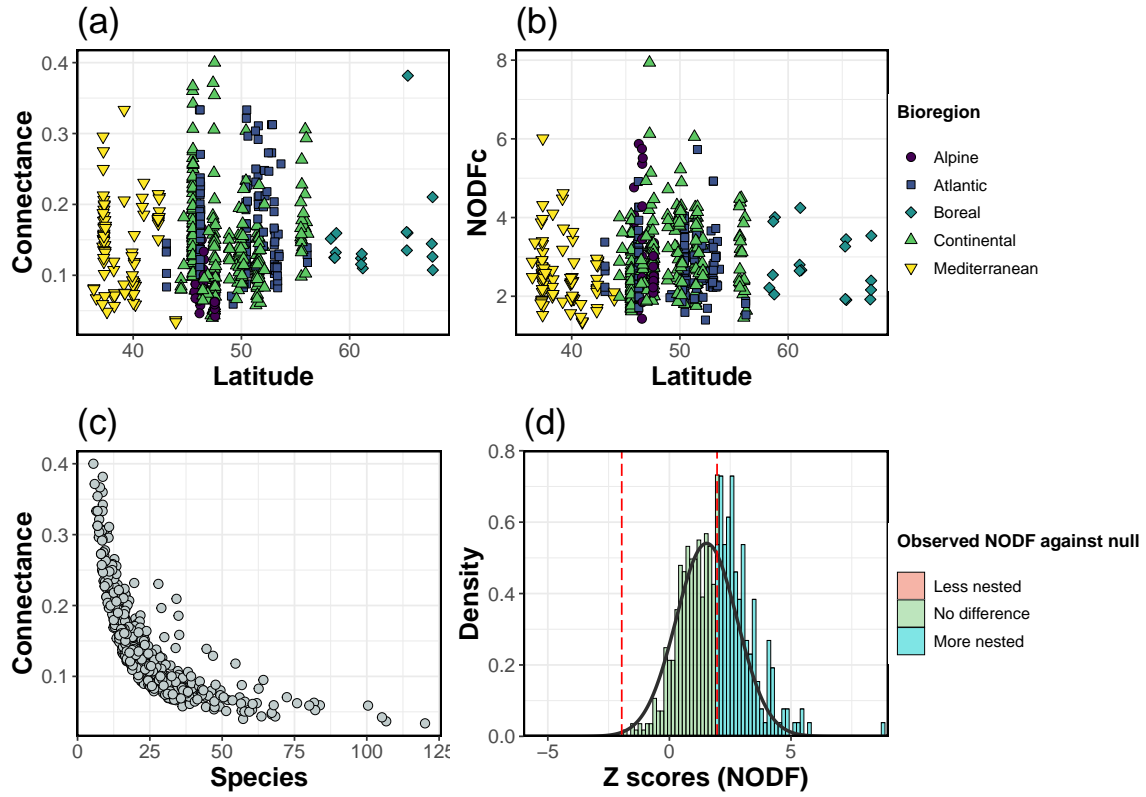
Figure 6. Graphs (a-b) indicate network connectance and nestedness across the latitudinal range of the studies from the database. In addition, the bioclimatic region where each network is located is indicated with points of different shapes and colours. Graph (c) shows the the association between network connectances and the geometric mean of plant and pollinator species per network. Graph (d) 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).

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Acknowledgments

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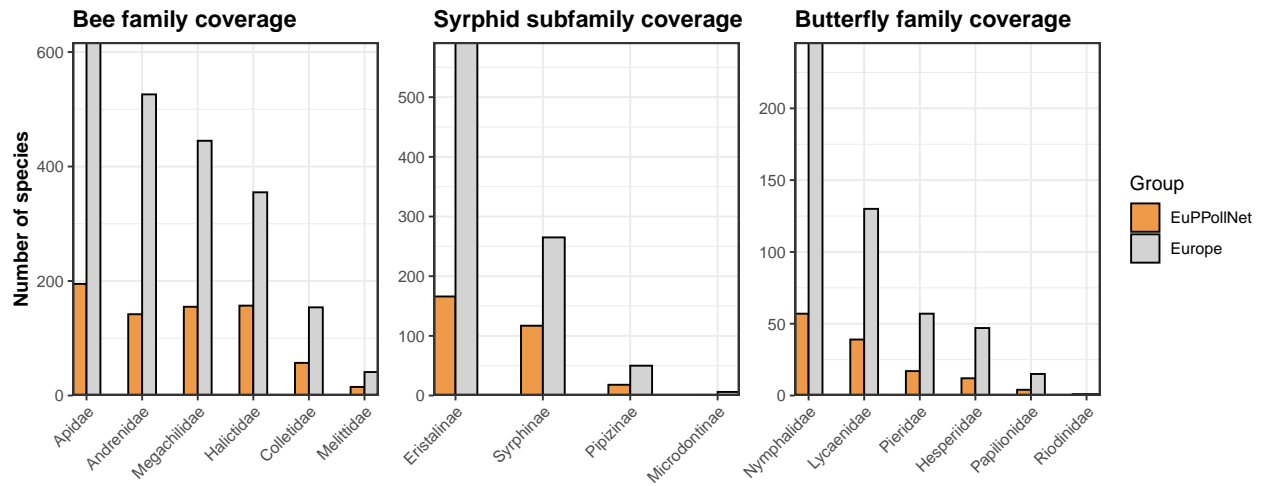
Figure S1. Coverage of the EuPPollNet species for bees (family level), syrphids (subfamily level) and butterflies (family level) in relation to the total number of European species within these taxonomic groups.