EuPPollNet: A European database of plant-pollinator networks

Jose B. Lanuza [1,2,3]| Tiffany M. Knight [3,2,4]| Nerea Montes-Perez [1]| Will Glenny [3,4]| Paola Acuña [5]| Matthias Albrecht [6]| Maddi Artamendi [7,8]| Isabelle Badenhausser [9,10,11]| Joanne M. Bennett [12]| Paolo Biella [13]| Ricardo Bommarco [14]| Andree Cappellari [15]| Sílvia Castro [16]| Yann Clough [17]| Pau Colom [18,19]| Joana Costa [16,20]| Natasha de Manincor [21,22]| Paula Dominguez-Lapido [7]| Christophe Dominik [4,3]| Yoko L. Dupont [23]| Reinart Feldmann [24]| Emeline Felten [25]| Victoria Ferrero [26]| William Fiordaliso [27]| Alessandro Fisogni [21]| Úna Fitzpatrick [28]| Marta Galloni [29]| Hugo Gaspar [16]| Elena Gazzea [15]| Irina Goia [30,31]| Carmelo Gómez-Martínez [32]| Miguel A. González-Estévez [32]| Juan Pedro González-Varo [33]| Ingo Grass [34]| Jiří Hadrava [35]| Nina Hautekèete [21]| Veronica Hederström [17]| Ruben Heleno [16]| Sandra Hervias-Parejo [32]| Jonna M. Heuschele [3,36,4]| Bernhard Hoiss [37]| Andrea Holzschuh [37]| Sebastian Hopfenmüller [38]| José M. Iriondo [39]| Birgit Jauker [40]| Frank Jauker [41]| Jana Jersáková [42]| Katharina Kallnik [37]| Reet Karise [43]| David Kleijn [44]| Stefan Klotz [4]| Theresia Krausl [17]| Elisabeth Kühn [45]| Carlos Lara-Romero [39]| Michelle Larkin [46]| Emilien Laurent [25]| Amparo Lázaro [32]| Felipe Librán-Embid [47,48]| Yicong Liu [4,2]| Sara Lopes [16]| Francisco López-Núñez [16,49]| João Loureiro [16]| Ainhoa Magrach [7,50]| Marika Mänd [43]| Lorenzo Marini [15]| Rafel Beltran Mas [32]| François Massol [21]| Corina Maurer [6]| Denis Michez [22]| Francisco P. Molina [1]| Javier Morente-López [39]| Sarah Mullen [51]| Georgios Nakas [52]| Lena Neuenkamp [53,54]| Arkadiusz Nowak [55,56]| Catherine J. O'Connor [16,57]| Aoife O'Rourke [51]| Erik Öckinger [14]| Jens M. Olesen [58,23]| Øystein H. Opedal [59]| Theodora Petanidou [52]| Yves Piquot [21]| Simon G. Potts [60]| Eileen F. Power [61]| Willem Proesmans [22,25]| Demetra Rakosy [4,3,62]| Sara Reverte [22]| Stuart P. M. Roberts [60]| Maj Rundlöf [63]| Laura Russo [64,51]| Bertrand Schatz [65]| Jeroen Scheper [44]| Oliver Schweiger [4,3]| Pau Enric Serra [32]| Catarina Siopa [16]| Henrik G. Smith [63,17]| Dara Stanley [66]| Valentin Ştefan [4,3]| Ingolf Steffan-Dewenter [37]| Jane C. Stout [61]| Louis Sutter [67]| Elena Motivans Švara [3,4,2]| Sebastian Świerszcz [55,68]| Amibeth Thompson [2,3,69]| Anna Traveset [32]| Annette Trefflich [70]| Robert Tropek [71,72]| Teja Tscharntke [47]| Adam J. Vanbergen [25]| Montserrat Vilà [1,73]| Ante Vujić [74]| Cian White [51]| Jennifer B. Wickens [60]| Victoria B. Wickens [60]| Marie Winsa [14]| Leana Zoller [2,3,75]| Ignasi Bartomeus [1]

Corresponding author= barragansljose@gmail.com

All authors excluding the first four and last are ordered alphabetically

[1] Doñana Biological Station (EBD-CSIC), Seville, Spain, [2] Martin Luther University Halle-Wittenberg, Institute of Biology, Halle, Germany, [3] German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, [4] Department of Community Ecology, Helmholtz Centre for Environmental

Research - UFZ, Halle, Germany, [5] Department of Plant Biology, Faculty of Science, University of Vigo, Vigo, Spain, [6] Agroecology and Environment, Agroscope, Zürich, Switzerland, [7] Basque Centre for Climate Change-BC3, Leioa, Spain, [8] University of the Basque Country, EuskalHerriko Unibertsitatea (UPV-EHU), Leioa, Spain, [9] Centre of Biological Studies of Chizé, La Rochelle University, Villiers en Bois, France, [10] LTSER "ZA Plaine & Val de Sèvre", CNRS, Villiers en Bois, France, [11] Multidisciplinary Research Unit for Grasslands and Forage Crops, INRAE, Lusignan, France, [12] Fenner School of Environment & Society, The Australian National University, Canberra, Australia, [13] ZooPlantLab, Department of Biotechnology and Biosciences, University of Milano-Bicocca, Milan, Italy, [14] Department of Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden, [15] Department of Agronomy, Food, Natural Resources, Animals and Environment, University of Padua, Padua, Italy, [16] Department of Life Sciences, Centre for Functional Ecology, University of Coimbra, Coimbra, Portugal, [17] Centre for Environmental and Climate Science, Lund University, Lund, Sweden, [18] Department of Evolutionary Biology, Ecology, and Environmental Sciences, University of Barcelona, Barcelona, Spain, [19] Biodiversity Research Institute (IRBio), Barcelona, Spain, [20] Linking Landscape, Environment, Agriculture and Food, School of Agriculture, University of Lisbon, Portugal, [21] Evo-Eco-Paleo, CNRS, University of Lille, Lille, France, [22] Laboratory of Zoology, Research Institute of Biosciences, University of Mons, Mons, Belgium, [23] Department of Ecoscience, University of Aarhus, Aarhus, Denmark, [24] Helmholtz Centre for Environmental Research - UFZ, Leipzig, Germany, [25] Agroecology, INRAE, Institut Agro, University of Burgundy, University of Burgundy Franche-Comté, Dijon, France, [26] Department of Biodiversity and Environmental Management, University of León, León, Spain, [27] Ecology of Interactions and Global Change, Research Institute in Biosciences, University of Mons, Mons, Belgium, [28] National Biodiversity Data Centre, County Waterford, Ireland, [29] Department of Biological, Geological and Environmental Sciences (BiGeA), University of Bologna, Bologna, Italy, [30] Faculty of Biology and Geology, Babeș-Bolyai University, Cluj-Napoca, Romania, [31] Centre for Systems Biology, Biodiversity and Bioresources (3B), Babeș-Bolyai University, Cluj-Napoca, Romania, [32] Mediterranean Institute for Advanced Studies (IMEDEA, UIB-CSIC), Esporles, Spain, [33] Department of Biology, Institute of Marine Research (INMAR), University of Cádiz, Puerto Real, Spain, [34] Department of Ecology of Tropical Agricultural Systems, University of Hohenheim, Stuttgart, Germany, [35] Department of Zoology, Faculty of Science, Charles University, Prague, Czechia, [36] Department of Biodiversity and People, Helmholtz Centre for Environmental Research - UFZ, Leipzig, Germany, [37] Department of Animal Ecology and Tropical Biology, Biocenter, University of Würzburg, Würzburg, Germany, [38] Cultural Landscape Günztal Foundation, Ottobeuren, Germany, [39] Area of Biodiversity and Conservation, ESCET, Rey Juan Carlos University, Madrid, Spain, [40] Justus Liebig University Giessen, Giessen, Germany, [41] Institute of Landscape Ecology and Resource Management, Justus Liebig University Giessen, Giessen, Germany, [42] Department of Ecosystems Biology, Faculty of Science, University of South Bohemia, České Budějovice, Czechia, [43] Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, Tartu, Estonia, [44] Nature Conservation and Plant Ecology Group, Wageningen University, Wageningen, The Netherlands, [45] Department of Conservation Biology & Social-Ecological Systems, Helmholtz Centre for Environmental Research - UFZ, Halle, Germany, [46] Botany and Plant Science, School of Natural Sciences and Ryan Institute, University of Galway, Galway, Ireland, [47] Agroecology, University of Göttingen, Göttingen, Germany, [48] Zoological Biodiversity, Institute of Geobotany, Leibniz University of Hannover, Hannover, Germany, [49] Research Centre for Natural Resources Environment and Society (CERNAS), Polytechnic Institute of Coimbra, Coimbra Agriculture School, Coimbra, Portugal, [50] IKERBASQUE, Basque Foundation forScience, Bilbao, Spain, [51] Botany Department, Trinity College Dublin, Dublin, Ireland, [52] Laboratory of Biogeography & Ecology, Department of Geography, University of the Aegean, Mytilene, Greece, [53] Department of Botany, Institute of Ecology and Earth Sciences, University of Tartu, Tartu, Estonia, [54] Institute of Landscape Ecology, Münster University, Münster, Germany, [55] Polish Academy of Sciences Botanical Garden, Center for Biological Diversity Conservation in Powsin, Warsaw, Poland, [56] Botanical Garden of the Wrocław University, Wrocław, Poland, [57] Cardif School of Biosciences, Cardif University, Cardif, UK, [58] Department of Biology, University of Aarhus, Aarhus, Denmark, [59] Division of Biodiversity and Evolution, Department of Biology, Lund University, Lund, Sweden, [60] Centre for Agri-Environmental Research, School of Agriculture, Policy and Development, University of Reading, Reading, UK, [61] Botany, School of Natural Sciences, Trinity College Dublin, Dublin, Ireland, [62] Thünen-Institute of Biodiversity, Braunschweig, Germany, [63] Department of Biology, Lund University, Lund, Sweden, [64] Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, TN, USA, [65] CEFE, CNRS, University of Montpellier, EPHE, IRD, Montpellier, France, [66] School of Agriculture and Food Science, University College Dublin, Dublin, Ireland, [67] Plant Productions Systems, Agroscope, Zürich, Switzerland, [68] Institute of Agroecology and Plant Production, Wrocław University of Environmental and Life Sciences, Wrocław, Poland, [69] University of Freiburg, Chair of Nature Conservation and Landscape Ecology, Freiburg, Germany, [70] State Institute of Agriculture and Horticulture Saxony-Anhalt, Bernburg, Germany, [71] Institute of Entomology, Biology Centre, Czech Academy of Sciences, České Budějovice, Czechia, [72] Department of Ecology, Faculty of Science, Charles University, Prague, Czechia, [73] Department of Plant Biology and Ecology, University of Seville, Seville, Spain, [74] Department of Biology and Ecology, Faculty of Sciences, University of Novi Sad, Novi Sad, Serbia, [75] Department of Ecology & Evolutionary Biology, University of Colorado, Boulder, CO, USA

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 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 the long-term persistence of plant-pollinator interaction networks. 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 (European Plant-Pollinator Networks) database, a fully open and reproducible European-level database containing harmonized taxonomic data on plant-pollinator interactions referenced in both space and time, along with other ecological variables of interest. This database offers an open workflow that allows researchers to track data-curation decisions and edit them according to their preferences. We present the taxonomic and sampling coverage of EuPPollNet, and summarize key structural properties in plant-pollinator networks. We hope EuPPollNet will stimulate future research that fills the taxonomic, ecological, and geographical data gaps on plant-pollinator interactions that we have identified. Further, the variation in the structure of the networks in EuPPollNet provides a strong basis for future studies aimed at quantifying drivers of plant-pollinator network change and guiding future conservation planning for plants and pollinators.

Main Types of Variables Included: EuPPollNet contains 1,162,913 interactions between plants and pollinators from 1,864 distinct networks (i.e., distinct sampling event in space or time), which belong to 54 different studies distributed across 23 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 (i.e., genus, family and order).

Spatial location and grain: The database contains 1,214 different sampling locations from natural and anthropogenic habitats that fall in 8 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 collected between 2004 and 2021. All records are time-referenced and most of the studies documented interactions within a single flowering season (68.52%).

Major taxa and level of measurement: The database contains interaction data at the species level for 94.39% of the records, including a total of 1,411 plant and 2,223 pollinator species. The database covers 5.56% of the European species of flowering plants, 34.38% of bees, 26.21% of butterflies, and 33.63% of syrphid species at the European level.

Software format: The database was built with the R programming language and is stored as ".rds" and ".csv" formats. The construction of the database is fully reproducible and can be accessed at the following link: https://github.com/JoseBSL/EuPPollNet.git.

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

1 | INTRODUCTION

Plant-pollinator interactions involve a great diversity of species, largely attributed to their co-evolutionary history (Ollerton, 2017), and are critically important for terrestrial biodiversity and economic productivity. The synergistic effects of climate change with other global change pressures are threatening worldwide biodiversity (Bellard et al., 2014; Sala et al., 2000), including plant and pollinator species as well as their interactions (Eichenberg et al., 2021; Goulson, Nicholls, Botías, & Rotheray, 2015; Settele, Bishop, & Potts, 2016). Under this scenario, the increasing availability of biodiversity data plays a major role in our ecological understanding of species status, trends, and conservation (Heberling, Miller, Noesgaard, Weingart, & Schigel, 2021; Zattara & Aizen, 2021). However, our knowledge of plant and pollinator species and their network of interactions still exhibits major temporal, spatial and taxonomic biases (Archer, Pirk, Carvalheiro, & Nicolson, 2014; Marshall et al., 2024; Poisot et al., 2021; Troia & McManamay, 2016), limiting our ability to effectively protect their biodiversity.

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, such as truncated power-law degree distributions (Jordano, Bascompte, & Olesen, 2003) or nestedness (Bascompte, Jordano, Melián, & Olesen, 2003). Large-scale analyses across multiple studies can quantify patterns across geographic regions (Olesen & Jordano, 2002; Traveset et al., 2016) or environmental gradients (Ramos-Jiliberto et al., 2010; Rech et al., 2016; Saunders et al., 2023) that cannot be examined in a single study. Although macro-ecological approaches that use ecological interactions make significant contributions to knowledge (Windsor, Hoogen, Crowther, & Evans, 2023), such synthesis work must consider variation across studies in the spatio-temporal nature of the data (Burkle & Alarcón, 2011; García et al., 2024). For instance, plant-pollinator studies tend to differ in sampling effort and methodology which affect the structure of the resulting plant-pollinator networks (Gibson, Knott, Eberlein, & Memmott, 2011; Jordano, 2016; Schwarz et al., 2020). Most plant-pollinator networks have unobserved interactions (Chacoff et al., 2012; Olesen et al., 2011), and thus research that attempts to synthesize across published studies must have access to raw data on interactions in order to statistically account for sampling effort and completeness. This emphasizes the importance of providing data in its rawest possible form in datasets that will be utilized for synthesis and macro-ecological studies.

Europe is one of the continents with a larger amount of available biodiversity data (Proença et al., 2017), yet still exhibits major gaps (Bennett et al., 2018; Wetzel 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 (Reverté et al., 2023), along with occurrence data (Zattara & Aizen, 2021), 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 biodiversity change (Jordano, 2016). Numerous works have studied plant-pollinator interactions in the last decades, generating 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, & 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 plant-pollinator interactions at a European level. For example, only over a dozen of European plant-pollinator networks are included in *Mangal*, while *GloBI* focuses on pairwise interactions disconnected from the community context. Assembling and curating the existing information on EU plant-pollinator networks will guide research efforts, conservation planning and will set a foundation for future global change research.

Here, we present the European Plant-Pollinator Networks database (EuPPollNet), which contains harmonized information on plant-pollinator interactions at the European level. The pollinator taxonomic groups include the main orders of entomofauna that visit and pollinate flowering plants in Europe. These comprise insect species from the orders Hymenoptera, Diptera, Lepidoptera, and Coleoptera, accounting for almost the totality of recorded interactions in EuPPollNet (99.86%). To understand the scope of the database, we examined the taxonomic and sampling coverage of the different plant and pollinator species at the European level with the help of the most up-to-date species checklists and rarefaction analyses. In addition, for bees and plants, we evaluated if there is a phylogenetic signal in the presence-absence of interaction data.

EuPPollNet contains one of the largest sets of plant-pollinator networks collated to date, providing a unique opportunity to examine the prevalence of key structural metrics across networks. For example, despite the large theoretical literature on the meaning of a nested structure in plant-pollinator networks (Bascompte & Jordano, 2007; Guimaraes, 2020), where specialists species interact only with subsets of generalists species, this pattern has only been empirically evaluated with a relatively small number of networks (Bascompte et al., 2003; Payrató-Borras, Hernández, & Moreno, 2019; Staniczenko, Kopp, & Allesina, 2013), and is still debated how structural metrics such as connectance and nestedness change across latitudes and bioclimatic regions (Olesen & Jordano, 2002; Song, Rohr, & Saavedra, 2017; Trøjelsgaard & Olesen, 2013).

Overall, EuPPollNet aims to cover a wide range of taxonomic groups and habitats, while also providing other variables of interest that define the ecological context and sampling methods of the study. In addition, EuPPollNet offers a transparent and accessible workflow of its data management and species harmonization that allows the database to be reused and to expand 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 EuPPollNet can be used to evaluate macro-ecological processes in plant-pollinator networks, guide conservation planning, and set a baseline for global change research.

2 | METHODS

Data acquisition

The EuPPollNet database includes published and unpublished studies compiled initially by a wide number of researchers and institutions within the European continent as defined by the European Environment Agency (Stanners & Bourdeau, 1995). As this database is the result of one of the work packages of the European project Safeguard (Safeguarding European wild pollinators; https://doi.org/10.3030/101003476), first, data was directly requested from members of the Safeguard project in May 2022. Second, the request was extended to data owners outside of the project, with data collection concluding in August 2024. These other data owners were identified by direct communication with colleagues suggested by Safeguard members and by directly searching for studies on Google Scholar of under-represented regions within the database. While Google Scholar lacks reproducibility (Gusenbauer & Haddaway, 2020), it still remains the most comprehensive search engine to date (Gusenbauer, 2019). This approach maximized the potential number of studies that could be incorporated in this database. The search strings used were "*plant-pollinator interactions*" and "*plant-pollinator networks*". To maintain high quality standards that will support robust future ecological research, we only included studies that met the following criteria: 1) studies containing time- and geo-referenced records of plant-pollinator interactions; and 2) studies that quantify interactions by documenting them as the contact between a floral visitor, referred to also as pollinators despite not evaluating pollination efficiency, and the reproductive structure of a specific plant being sampled (i.e., phyto-centric networks).

Dataset description

The database contains 54 independent published and unpublished studies conducted during the time period 2004 - 2021 in 23 different countries (**Figure 1a** and **Figure 1b**; see **Figure S1** for exact locations). The studies differ in sampling effort and methodology, and thus documenting sampling methods and sampling effort is an important feature of EuPPollNet. Most studies took place within a single flowering season (68.52%), sampled a given location for an average of 6.99 days, and exclusively sampled diurnal plant-pollinator interactions, with transects being the most common sampling method (64.81%). All the studies documented interactions with Hymenopterans (with 50.00% considering all Hymenopterans, 46.15% only wild bees and 3.85% only bumblebees), 92.31% documented interactions with Dipterans (with 46.15% considering all Dipterans, 46.15% only syrphids and 5.77% recorded syrphids plus bombylids or tachinid flies), 63.46% with Lepidopterans, and 32.69% with Coleopterans. The database includes a total of 1,162,913 distinct interactions. Most of the pollinator species belong to the orders Hymenoptera, Diptera, Lepidoptera and Coleoptera (89.11%), which account for nearly all interactions in this database (99.86%). Species that belong to other orders 10.89% are not explored in this study as they conduct a minor fraction of the total interactions (0.14%). Hymenoptera and Diptera contain the highest number of species comprising each approximately 1,000 species in the database. However, the majority of plant-pollinator interactions are from Hymenoptera species (90.15%; **Figure 1c**). Notably, the western honey bee, *Apis mellifera*, represents 69.89% of the total interaction records from the database and an average of 30.74% of the total interactions per network.

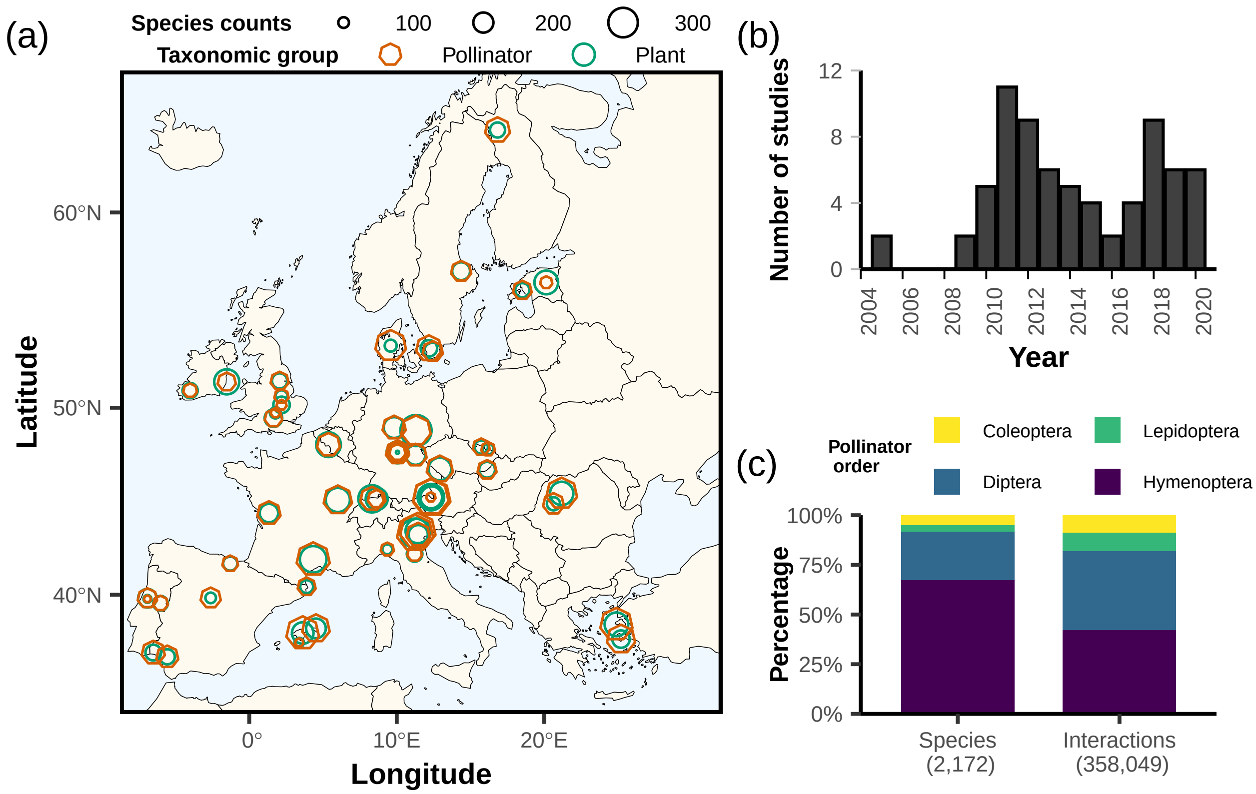

Figure 1. (**a**) Locations of the studies in EuPPollNet across the European continent, showing the total number of pollinator (i.e., orange heptagon) and plant (i.e., green circles) species per study. The sizes of these shapes are proportional to the respective species counts. For visualization purposes, we have selected only a single location per study. (**b**) Number of studies by year in EuPPollNet. (**c**) Proportion of species and interactions across the four main pollinator orders in EuPPollNet, excluding interactions from *Apis mellifera*. The total number of species and interactions is indicated in parentheses at the bottom.

Data structure

The EuPPollNet database is available in both .csv and .rds formats and contains a total of 31 columns (**Table 1**), where each row represents a single interaction between a plant and a pollinator species. These columns include information about the study and network identifiers (columns 1 and 2), sampling method (3), habitat type as described by the author, and a unified habitat classification across studies (4 and 5), bioregion where the network is located (6), country, locality, and latitude-longitude coordinates (7 to 10), date of the interaction (11), number of interactions (12), taxonomic information about plants (13 to 20), taxonomic information about pollinators (21 to 28), and information about the availability of floral count data (29). The flower count data is provided in a separate file (.csv or .rds) and can be merged with the interaction data through the "Flower_data_merger" column (30). Note that although two-thirds of studies include information on floral abundance, the methods and units vary greatly across studies. To construct a plant-pollinator network matrix within a single flowering season at the site level, users should group interactions by plant and pollinator species, site, study, and year. Finally, metadata at the study level is provided in a separate file, including information about the authors, digital object identifier (if available), sampling time, and taxonomic coverage of the main pollinator groups for each study.

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	North-south position of the observed interaction in decimal degrees
Longitude	East-west position 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_original_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_original_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

Taxonomic harmonization

All plant and pollinator species names were checked and harmonized in R using **rgbif** (Chamberlain, Oldoni, & Waller, 2022). 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 original species name, the new assigned name, and, if the name of the species is uncertain (e.g., species complex or species alike). In addition, taxonomic information at genus, family and order level was downloaded for each species.

For plants: (i) we initially verified the exact matches against the GBIF species checklist; (ii) we selected unmatched cases and fixed orthographic errors; (iii) we retrieved again taxonomic information for those unmatched cases, evaluated accuracy of fuzzy matching and programmatically fixed records that are still not found; (iv) finally, we used the World Flora Taxonomic Backbone (Govaerts, Nic Lughadha, Black, Turner, & Paton, 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 the European level by combining the most up to date published checklists of bees and syrphids (Reverté et al., 2023), and butterflies (Wiemers et al., 2018); (ii) 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 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. Coleoptera species names were only checked against the GBIF checklist.

Taxonomic coverage

To assess the completeness of plant and pollinator species in the EuPPollNet database at the European level, we used the aforementioned checklists for plants and pollinators. Specifically for plants, we refined the checklist to include only plants occurring in Europe 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, & 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 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 evaluated the taxonomic coverage of taxonomic groups with species checklists available in Europe (i.e., bees, syrphids and butterflies). While there is not a good understanding of pollinator diversity in other taxonomic groups, it was assumed that their coverage within the database is equal to the average coverage of bees, syrphids, and butterflies (mean coverage = 31.4; sd = 4.51). Therefore, the total number of of flower visiting species from other taxonomic groups (i.e., non-bee, non syrphid and non-butterfly flower visitors) at European level was extrapolated by assuming that their coverage is equal to the mean coverage of bees, syrphids, and butterflies. Consequently, we provide an estimate for the total number of pollinators across the European continent.

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, & Danforth, 2013) and processed it using the packages **ape** (Paradis et al., 2019), **MCMCglmm** (Hadfield, 2010) and **phytools**. For plants, the phylogenetic tree was obtained from a species level plant phylogeny (Smith & Brown, 2018) with the help of the **rtree** package (Li, 2023).

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 networks. In addition, we computed the accumulation curve of pollinator species with an increasing number of plant species as an indicator for how many pollinator species are likely responsible for the pollination of flowering plants (e.g., Kleijn et al., 2015 for crops). The rarefied and extrapolated sampling curves were obtained using the **iNEXT** package (Hsieh & Chao, 2016). The different rarefied curves were complemented with 100 bootstrapped accumulation curves.

Habitat type and bioclimatic region

We describe the habitat type for each site using information from Corine Land Cover (CLC, version 2018) extracted using the Terra package (Hijmans et al., 2022), visual inspection of Google Earth imagery and the habitat classification from the authors. These different habitat categories (see definitions in supplementary text) allow a quick comparison and understanding of the habitat types from the database. Moreover, Europe is characterized by a great variety of environmental conditions that harbor different biota. Thus, to allow authors to explore the set of studies that share similar environmental conditions and species, we assigned a biogeographical region to each site. The biogeographical regions were downloaded from the European Environment Agency (version 2016) and were matched to the different sites using a spatial joint from the **sf** package (Pebesma et al., 2018).

Network analyses

To provide a general overview of the structure of plant-pollinator networks in EuPPollNet, we quantified connectance and nestedness for each network, and examined how these network metrics change across latitude of studies and bioclimatic regions in Europe. We selected these two network metrics as they are commonly evaluated in plant-pollinator network studies and capture structural properties with a straightforward interpretation. We implemented "standardised" versions of connectance and nestedness to account for the effect of sampling effort on network metrics. 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. The relationship between residual connectance and species richness was investigated using a beta-regression implemented with the package **betareg** (Cribari-Neto & Zeileis, 2010). We used NODFc to compare nestedness across networks, as it corrects by connectance and the number of species

(Song et al., 2017). This metric was calculated using the **maxnodf** package (Hoeppke & Simmons, 2021). Both residual connectance and NODFc were used as dependent variables to evaluate their association with latitude. In addition, we quantified the association between connectance and nestedness with the number of species per network using a Kendall rank correlation coefficient to compare the strength of associations between network structures and species richness 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, Guimaraes, Guimaraes Jr, Loyola, & Ulrich (2008). The z-score approach allows 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, & Fründ, 2008). 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

Taxonomic coverage

Europe hosts approximately 5,000 species of pollinators and 25,000 species of plants that benefit from animal pollination. EuPPollNet contains a total of 2,223 pollinators and 1,411 plant species. The coverage of the main pollinator groups occurring in Europe is 34.38% for bees, 33.63% for syrphids and 26.21% for butterflies (see **Figure S2** for coverage at the family level for bees and butterflies, and at the subfamily level for syrphids). Bees (i.e., Anthophila) constitute 89.65% of the interactions in EuPPollNet, and 77.95% 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 of species at the bee genus level is 36.99% (**Figure 2**). The presence or absence of interaction records for bees does not follow a phylogenetic pattern ($\lambda = 0.07$; $P = 0.65$). The database coverage of all flowering plant species occurring in Europe is 5.56% (**Figure 3**), 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 does not follow a statistically relevant phylogenetic pattern ($\lambda = 0.26$; $P = 0.07$).

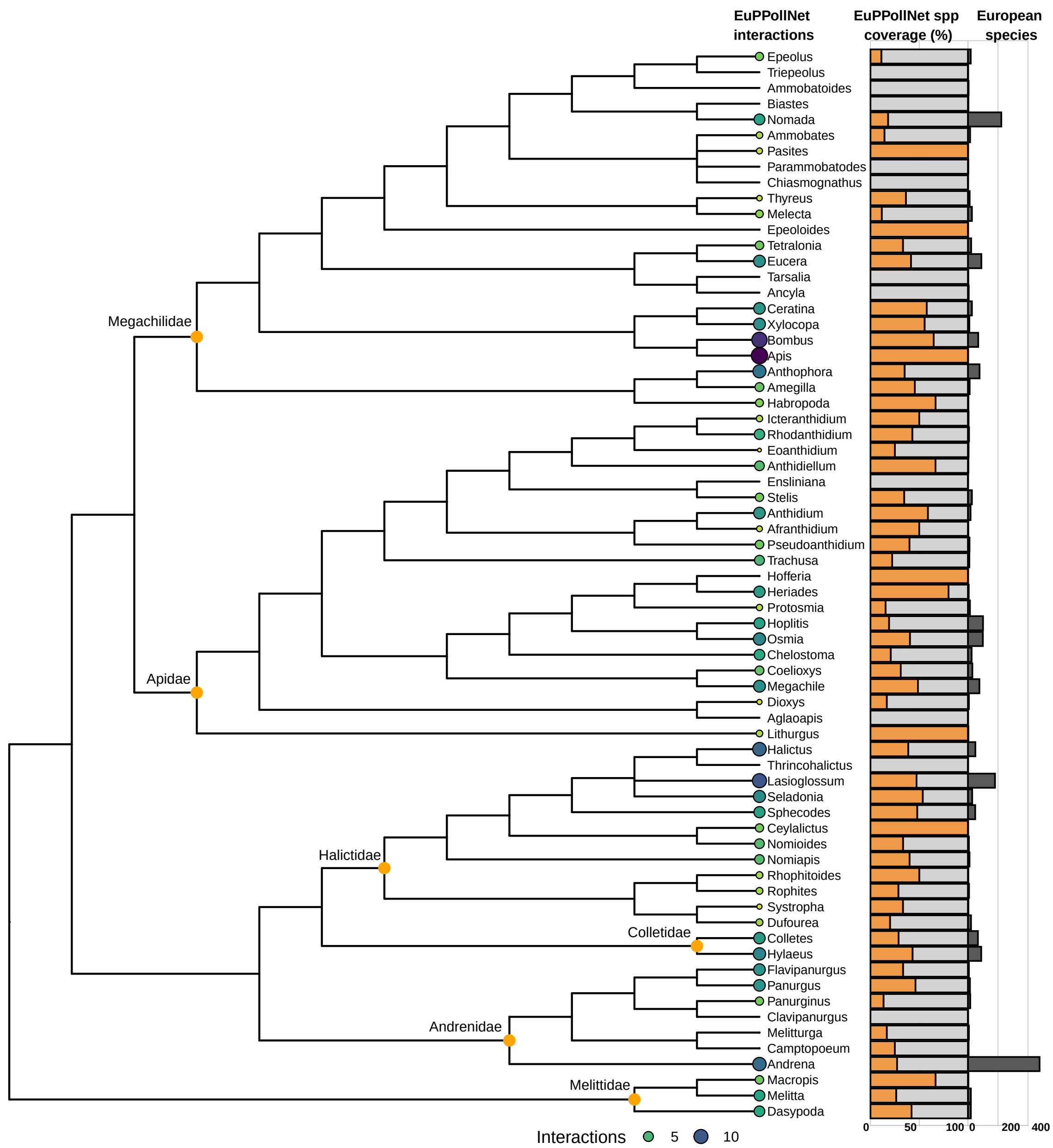

Figure 2. Phylogenetic and taxonomic coverage of the bee genera at European level. The number of interactions recorded per genus in the database is illustrated using circles, with their sizes proportional to the number of interactions on a logarithmic scale. Additionally, a gradient of colors ranging 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. Dark grey bars indicate the total number of species per genus at the European level.

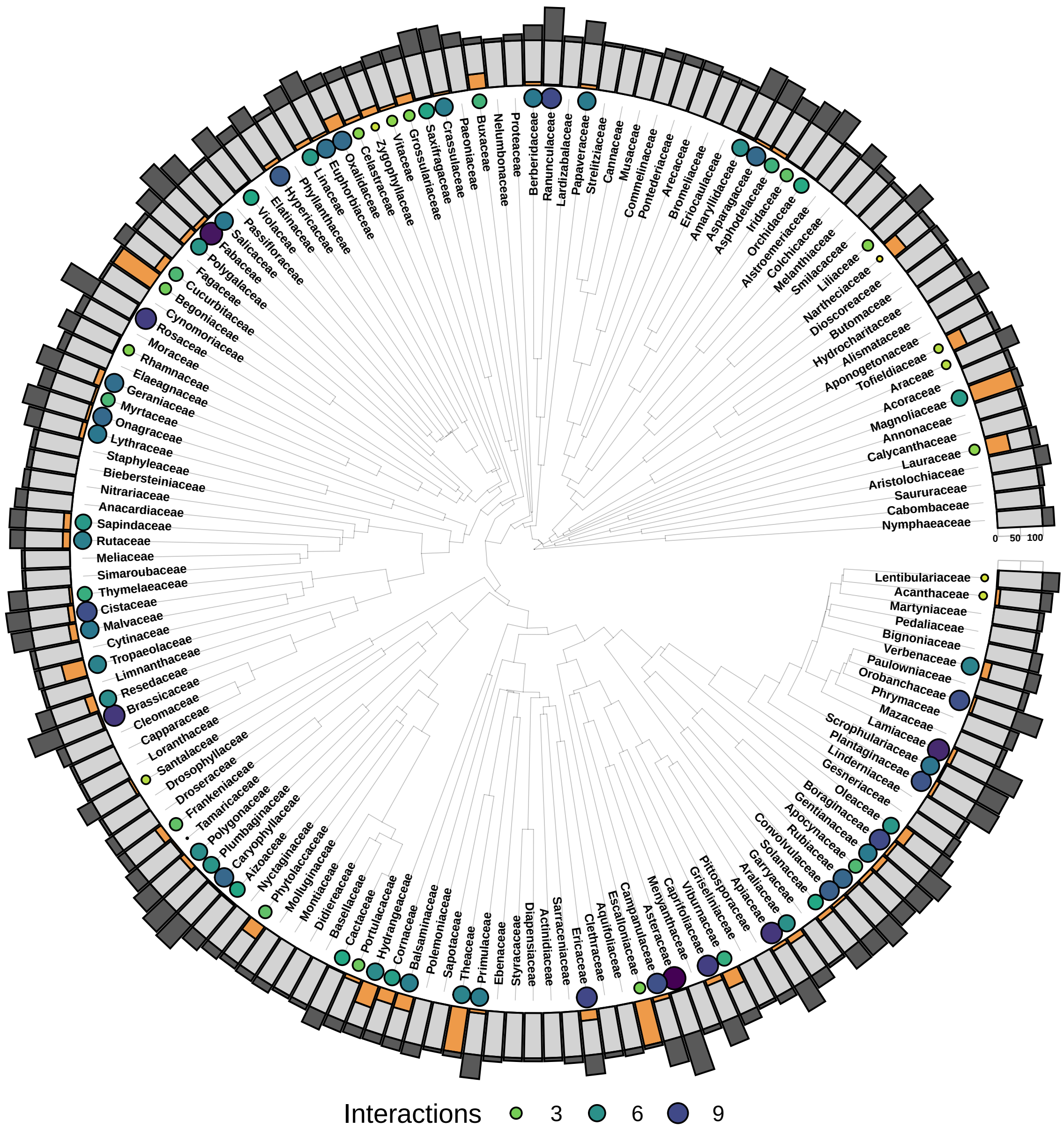

Figure 3. Phylogenetic and taxonomic coverage of the plant families at European level. The number of interactions recorded per genus in the database is illustrated using circles, with their sizes proportional to the number of interactions on a logarithmic scale. Additionally, a gradient of colors ranging 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.

Sampling coverage

The estimated sampling coverage of plant and pollinator species within EuPPollNet across the different networks 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 networks (**Figure 4a-4b**). 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 4c**). 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 4d**). We find that a small portion of plant species and pollinator species are shared across a broad range of networks and that most plant (85.68%) and pollinator (87.72%) species are exclusively found in less than 1% of networks (**Figures 4e-4f**). The most common plant (*Trifolium pratense*) and pollinator (*Bombus pascuorum* when excluding *Apis mellifera*) species are found in 36.07% and 62.70% of networks, respectively.

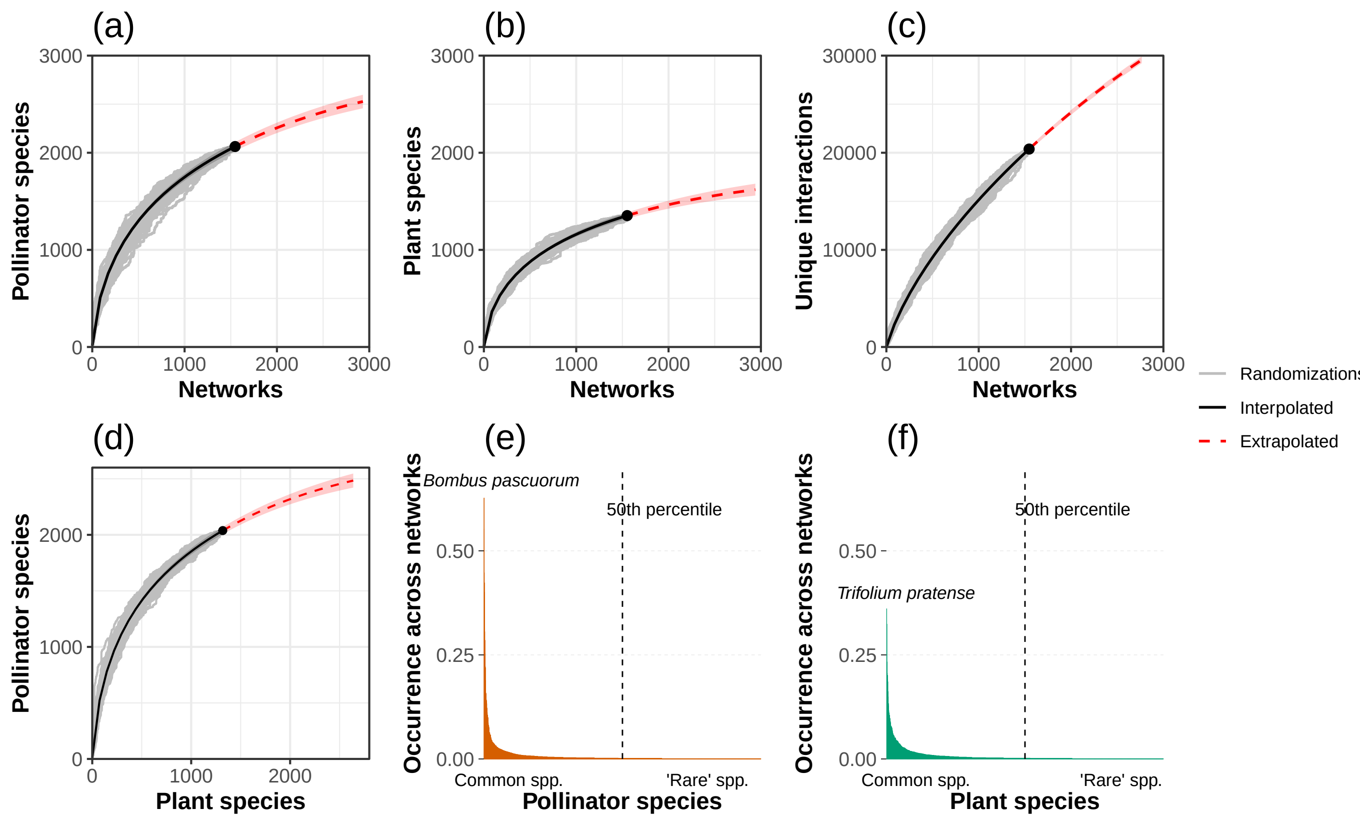

Figure 4. Graphs (a-b-c) indicate the accumulation curves for pollinators, plants, and their unique pairwise interactions across networks. Grey solid lines represent 100 randomized accumulation curves, the black solid lines represent the interpolated curve (i.e., the mean across curves), and the red dashed lines illustrate the extrapolated curve for approximately 3000 networks. 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 networks. Species on the left (i.e., common) are found in many networks, while species on the right (i.e., rare) are found in few or only a single network. Note that *Apis mellifera* is the most common pollinator but was excluded from this visualization.

Habitat type and bioclimatic region

The proportion of species from the major pollinator orders within the database differed across habitats and bioclimatic regions (**Figure 5**). Hymenoptera was the main taxonomic order in the majority of habitats, exceeded only by Diptera for the habitat categories of riparian vegetation, moors and heathland, and alpine grasslands. Overall, the proportion of flower visitors from Lepidoptera and Coleoptera were low across all habitats but Coleopteran flower visitors were notably more abundant in sclerophyllous vegetation and beaches, dunes and sands habitat categories. Similar patterns were observed when exploring the pollinator proportions by bioclimatic region. Hymenopterans were predominant across all bioclimatic regions and Dipterans were particularly abundant in the Alpine and Atlantic regions. Lepidopterans had low proportions across all bioclimatic regions and Coleopterans were only relevant in the Mediterranean region at European level. Notably, the number of studies (**Figure 5**) and sampling sites (**Figure S3**) also differed across habitats and bioclimatic regions. The habitats sampled by a higher number of studies in the database were intensive grasslands (28), semi-natural grasslands (12) and sclerophyllous vegetation (10). However, the habitats that contain a higher number of sampling sites were intensive grasslands (620), agricultural margins (432) and agricultural land (141). The bioclimatic regions with a higher number of studies were Continental (23), Atlantic (13) and Mediterranean (13); and those that contain a higher number of sampling sites were Continental (482), Atlantic (459) and Boreal (439).

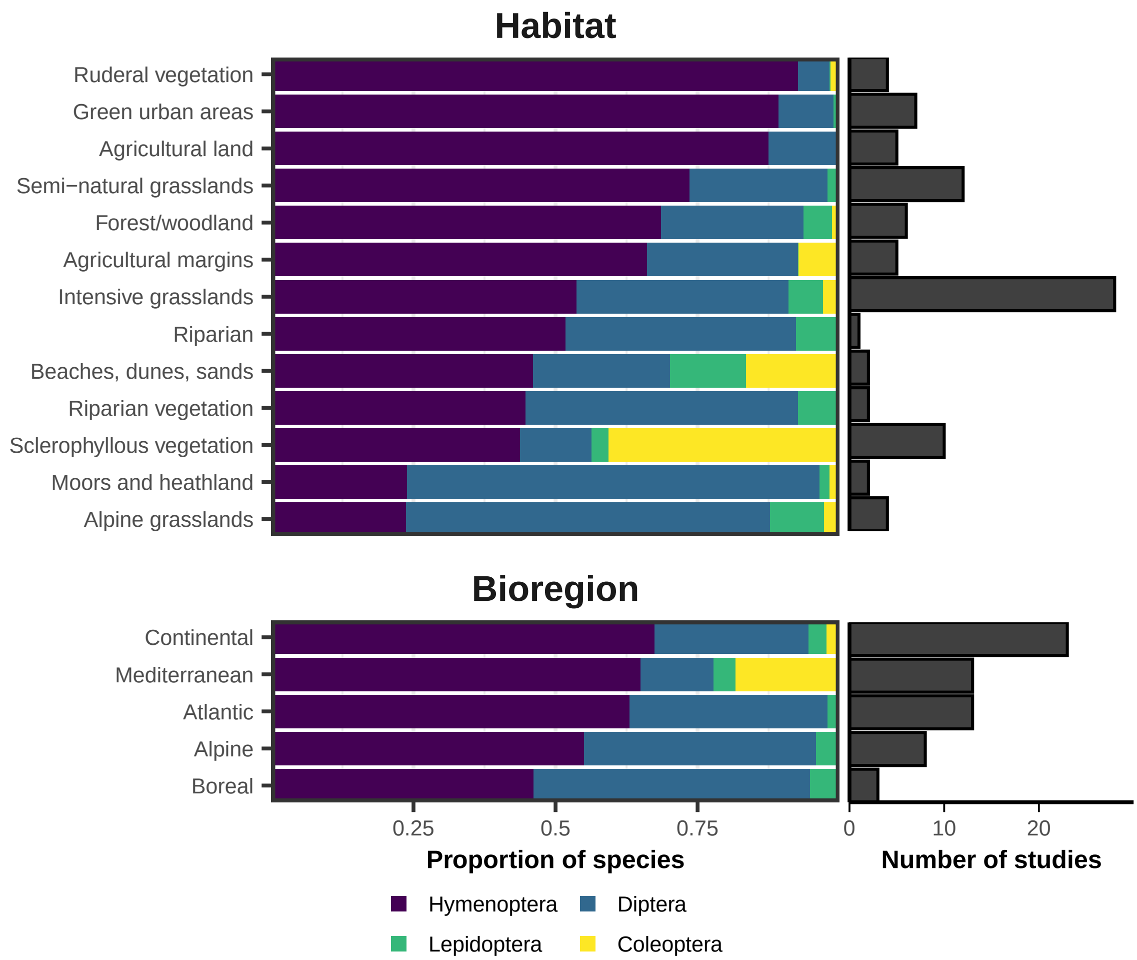

Figure 5. Proportion of species from the major pollinator orders by habitat types and bioclimatic regions in the EuPPollNet database. The orders, from left to right, include Hymenoptera, Diptera, Lepidoptera and Coleoptera. The horizontal barplot on the right indicates the number of studies that were 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 followed a 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 were independent of the mean number of species (Kendall τ = -0.06, $P = 0.03$; **Figure S4**). 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 than networks located at lower latitudes. Note that residual connectance and normalised nestedness showed a moderate negative correlation (Kendall τ = -0.46, $P =$ 0).

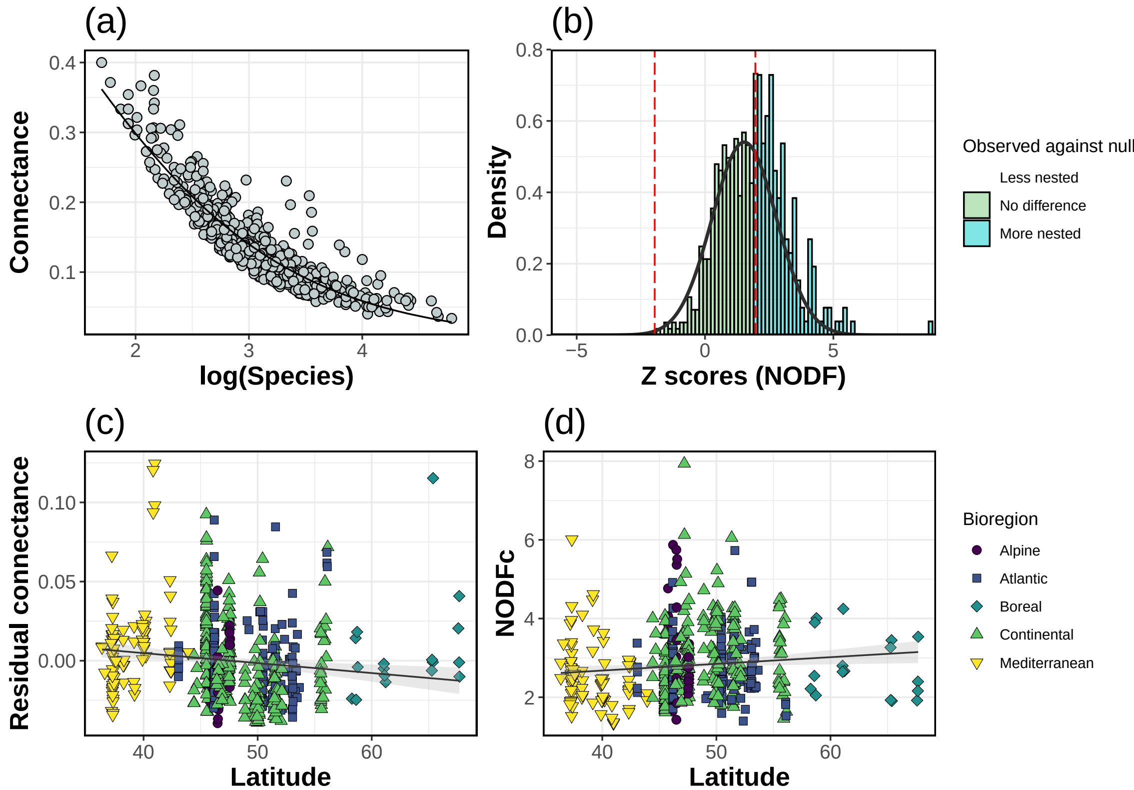

Figure 6. Graph (a) shows the association between network connectance and the geometric mean of plant and pollinator species per network on a log-scale with the respective fitted line from a Beta regression. Graph (b) shows the distribution of z-scores when comparing the nestedness from the empirical 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. 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 studies and networks compiled to date at European level. The database contains 1,411 plant and 2,223 pollinator species with over a million 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 (i.e., 5.6% for flowering plants and 34.4% for bee species). However, although our study likely has higher pollinator coverage, as we did not exclude non-pollinating species (e.g., predators, herbivores, parasites) from the checklists, this likely reflects that most plant and pollinator species are rare and geographically restricted. For example given that most of the plant-pollinator networks from the database are sampled on intensive grasslands, and habitat heterogeneity is a crucial factor in understanding pollinator diversity at European level (Hass et al., 2018; Kleijn et al., 2015; 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. Indeed, 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 & Withers, 2003). In other words, minimal sampling efforts are capturing a substantial number of species and interactions, but achieving a comprehensive inventory will require numerous sampling events within and across habitats, particularly for plant-pollinator interactions.

Bees are responsible for the majority of the sampled interactions at the metaweb level. As not all surveys included all pollinator groups, this result may partly be influenced by the taxonomic groups sampled across studies. However, the relevance of bees and other pollinator orders for network topology changed across habitats and bioclimatic regions in accordance to the literature. For instance, plant-pollinator communities in the Mediterranean were dominated by bees, while communities in Alpine or Boreal regions were fly species rich or fly-dominated. These patterns are consistent with our current understanding of bee diversity, which peaks in dry or temperate areas (Leclercq et al., 2023; Orr et al., 2021); 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 & Olesen, 1999; Lefebvre, Villemant, Fontaine, & Daugeron, 2018). In addition, beetles were only commonly documented as floral visitors in the Mediterranean region. This study cannot determine whether pollination ecologists traditionally document flower-beetle interactions only in the Mediterranean, or if there are fewer flower visitations by beetles outside this region. Nevertheless, the high proportion of beetles as floral visitors provides further support for their potential role as pollinators in the Mediterranean (Herrera, 2019; León-Osper & 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 of studies (~40%) 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 87% of networks and conducted on average a third of the total interactions per network. The proportion of honey bees in networks across Europe is higher than in natural communities (i.e., large unmanaged assemblages of plant species) across the world (~13%; Hung, Kingston, Albrecht, Holway, & Kohn, 2018), potentially reflecting the dominance of intensive grasslands habitats in EuPPollNet, the highly generalised nature of honeybees, the important role that honeybees are playing as pollinators in Europe, and/or because beekeeping is widely practiced in Europe (Herrera, 2020; Magrach, González-Varo, Boiffier, Vilà, & Bartomeus, 2017; Steffan-Dewenter & Tscharntke, 2000).

Although Europe contains a much larger number of flowering plants than pollinator species (~5 to 1 ratio according to our extrapolation from checklists), the observed number of pollinator species in the database was almost double that of the plants. 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-centered 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. In addition, we found that the accumulation curve of pollinators per plant species does not saturate, which indicates low redundancy of pollinators and that many are regionally "rare". Rare pollinators are functionally important for plant species at large scales (Simpson et al., 2022; Winfree et al., 2018), highlighting the need to conduct further sampling events to observe these rare species and to effectively understand and protect plant-pollinator biodiversity.

Consistent with Olesen & Jordano (2002), we find that residual connectance (i.e., the deviation from the expected connectance for a given network size) was lower at higher latitudes, while normalised nestedness increased towards higher latitudes. Networks at lower latitudes in Europe are exposed to higher temperatures, which can result in higher visitation rates (Arroyo, Armesto, & Primack, 1985; Classen et al., 2015; Herrera, 2019), and the overall level of pollinator generalization is known to be higher at lower latitudes (Schleuning et al., 2012). These factors should increase the number of possible connections that can be established between plants and pollinators for a given network size, resulting in more connected and less nested networks at lower latitudes. Finally, one third of networks were more nested than expected by chance. While this supports the idea that plant-pollinator networks tend to be nested (Bascompte et al., 2003), this result also suggests that nestedness could be a less prevalent feature than previously thought for plant-pollinator networks (Payrató-Borras et al., 2019).

Despite this database covering a wide range of habitats across 23 countries, it contains geographical biases that can impact our understanding of plant-pollinator communities (Hughes et al., 2021). For instance, most plant-pollinator networks are sampled from central Europe, while Eastern Europe and the Mediterranean region are underrepresented. This is consistent with previous studies which also report lack of plant-pollinator data for those regions (Bennett et al., 2018; Marshall et al., 2024), highlighting that this database shows existing patterns in data availability despite the absence of a systematic search for studies. This lack of data is especially relevant for Eastern Europe which has vast landscapes of high quality semi-natural grasslands but is experiencing rapid land use change (Sutcliffe et al., 2015), and the Mediterranean region is likely to be severely impacted by climate change (Duchenne et al., 2020; Jaworski et al., 2022; Pareja-Bonilla, Arista, Morellato, & Ortiz, 2023). These areas are well known for their rich pollinator diversity (Miličić, Vujić, & Cardoso, 2018; Reverté et al., 2023), and their under-representation is likely contributing to the low taxonomic coverage of this database at the European level. Although some of the most well studied countries in Europe (e.g., Belgium, The Netherlands) have already experienced land use change and biodiversity loss at the end of the 20th century (Carvalheiro et al., 2013), plant-pollinator communities in Europe and across the globe still face current and future threats from climate change (Bartomeus et al., 2011; Duchenne et al., 2020), land use change (Batáry, Dicks, Kleijn, & Sutherland, 2015; Reidsma, Tekelenburg, Van den Berg, & Alkemade, 2006), and the introduction of alien species (Vanbergen, Espíndola, & Aizen, 2018; Vilà et al., 2009). Therefore, continuous monitoring programs are needed in order to evaluate spatio-temporal changes of species and their interactions across different European habitats and regions. This will allow local and large scale analyses of the status and trends of plant-pollinator communities, effectively informing management and conservation actions.

In conclusion, the EuPPollNet database enables researchers to explore spatial, taxonomic and structural properties of plant-pollinator networks within Europe. In contrast to previous databases, EuPPollNet provides interaction data along with sampling information that could help researchers to better control for sampling effort and completeness and to select the most suitable networks for their research questions. Here, we have shown how connectance and nestedness change across their latitudinal range and that nestedness is not a ubiquitous feature of all plant-pollinator networks. These analyses aim to highlight the variability present across Europe in the structure of plant-pollinator networks and illustrate the opportunities available to develop and test questions about spatio-temporal network change using EuPPollNet. The reproducible workflow allows researchers to adapt and reuse this database, enabling the continuous addition of new networks to better evaluate the status and trends of plant-pollinator communities. Finally, we hope this database becomes an iterative resource that keeps growing and improving over time to better understand and conserve European biodiversity.

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ACKNOWLEDGEMENTS

We thank all the taxonomist and ecologist that has made this database possible by contributing with their fieldwork data.

FUNDING INFORMATION

This research was funded by the H2020 European project Safeguard (101003476) and by the Federal State of Saxony-Anhalt (MLU-BioDivFund). RT was supported by the Czech Science Foundation (Project No. 21-24186M). NDM, NH, YP and FM were financially supported by the ANR ARSENIC project (grant no. 14-CE02-0012), the ANR NGB project (grant no. 17-CE32- 011), the Region Nord-Pas-de-Calais, the CNRS, the French Ministère de l'Enseignement Supérieur et de la Recherche, the Hauts-de-France Region and the European Regional Funds.

CONFLICT OF INTEREST

None.

DATA AVAILABILITY

All data and code to produce of this database and manuscript are available at Zenodo (LINK) and Github (https://github.com/JoseBSL/EuPPollNet.git).

SUPPORTING INFORMATION

Title: EuPPollNet: A European database of plant-pollinator networks

Authors: Jose B. Lanuza [1,2,3]| Tiffany M. Knight [3,2,4]| Nerea Montes-Perez [1]| Will Glenny [3,4]| Paola Acuña [5]| Matthias Albrecht [6]| Maddi Artamendi [7,8]| Isabelle Badenhausser [9,10,11]| Joanne M. Bennett [12]| Paolo Biella [13]| Ricardo Bommarco [14]| Andree Cappellari [15]| Sílvia Castro [16]| Yann Clough [17]| Pau Colom [18,19]| Joana Costa [16,20]| Natasha de Manincor [21,22]| Paula Dominguez-Lapido [7]| Christophe Dominik [4,3]| Yoko L. Dupont [23]| Reinart Feldmann [24]| Emeline Felten [25]| Victoria Ferrero [26]| William Fiordaliso [27]| Alessandro Fisogni [21]| Úna Fitzpatrick [28]| Marta Galloni [29]| Hugo Gaspar [16]| Elena Gazzea [15]| Irina Goia [30,31]| Carmelo Gómez-Martínez [32]| Miguel A. González-Estévez [32]| Juan Pedro González-Varo [33]| Ingo Grass [34]| Jiří Hadrava [35]| Nina Hautekèete [21]| Veronica Hederström [17]| Ruben Heleno [16]| Sandra Hervias-Parejo [32]| Jonna M. Heuschele [3,36,4]| Bernhard Hoiss [37]| Andrea Holzschuh [37]| Sebastian Hopfenmüller [38]| José M. Iriondo [39]| Birgit Jauker [40]| Frank Jauker [41]| Jana Jersáková [42]| Katharina Kallnik [37]| Reet Karise [43]| David Kleijn [44]| Stefan Klotz [4]| Theresia Krausl [17]| Elisabeth Kühn [45]| Carlos Lara-Romero [39]| Michelle Larkin [46]| Emilien Laurent [25]| Amparo Lázaro [32]| Felipe Librán-Embid [47,48]| Yicong Liu [4,2]| Sara Lopes [16]| Francisco López-Núñez [16,49]| João Loureiro [16]| Ainhoa Magrach [7,50]| Marika Mänd [43]| Lorenzo Marini [15]| Rafel Beltran Mas [32]| François Massol [21]| Corina Maurer [6]| Denis Michez [22]| Francisco P. Molina [1]| Javier Morente-López [39]| Sarah Mullen [51]| Georgios Nakas [52]| Lena Neuenkamp [53,54]| Arkadiusz Nowak [55,56]| Catherine J. O'Connor [16,57]| Aoife O'Rourke [51]| Erik Öckinger [14]| Jens M. Olesen [58,23]| Øystein H. Opedal [59]| Theodora Petanidou [52]| Yves Piquot [21]| Simon G. Potts [60]| Eileen F. Power [61]| Willem Proesmans [22,25]| Demetra Rakosy [4,3,62]| Sara Reverte [22]| Stuart P. M. Roberts [60]| Maj Rundlöf [63]| Laura Russo [64,51]| Bertrand Schatz [65]| Jeroen Scheper [44]| Oliver Schweiger [4,3]| Pau Enric Serra [32]| Catarina Siopa [16]| Henrik G. Smith [63,17]| Dara Stanley [66]| Valentin Ştefan [4,3]| Ingolf Steffan-Dewenter [37]| Jane C. Stout [61]| Louis Sutter [67]| Elena Motivans Švara [3,4,2]| Sebastian Świerszcz [55,68]| Amibeth Thompson [2,3,69]| Anna Traveset [32]| Annette Trefflich [70]| Robert Tropek [71,72]| Teja Tscharntke [47]| Adam J. Vanbergen [25]| Montserrat Vilà [1,73]| Ante Vujić [74]| Cian White [51]| Jennifer B. Wickens [60]| Victoria B. Wickens [60]| Marie Winsa [14]| Leana Zoller [2,3,75]| Ignasi Bartomeus [1]

Contains:

- Supplementary text 1
- Figure S1
- Figure S2
- Figure S3
- Figure S4

Supplementary text 1

Habitat definitions:

1) **Ruderal vegetation**: Plants growing on highly disturbed sites such as road sides or mineral extraction sites.
2) **Agricultural margins**: 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 in this category 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) **Intensive grassland**: 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 included 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) **Alpine grasslands**: Low growing plant communities with little or none human disturbance. Often located at 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.

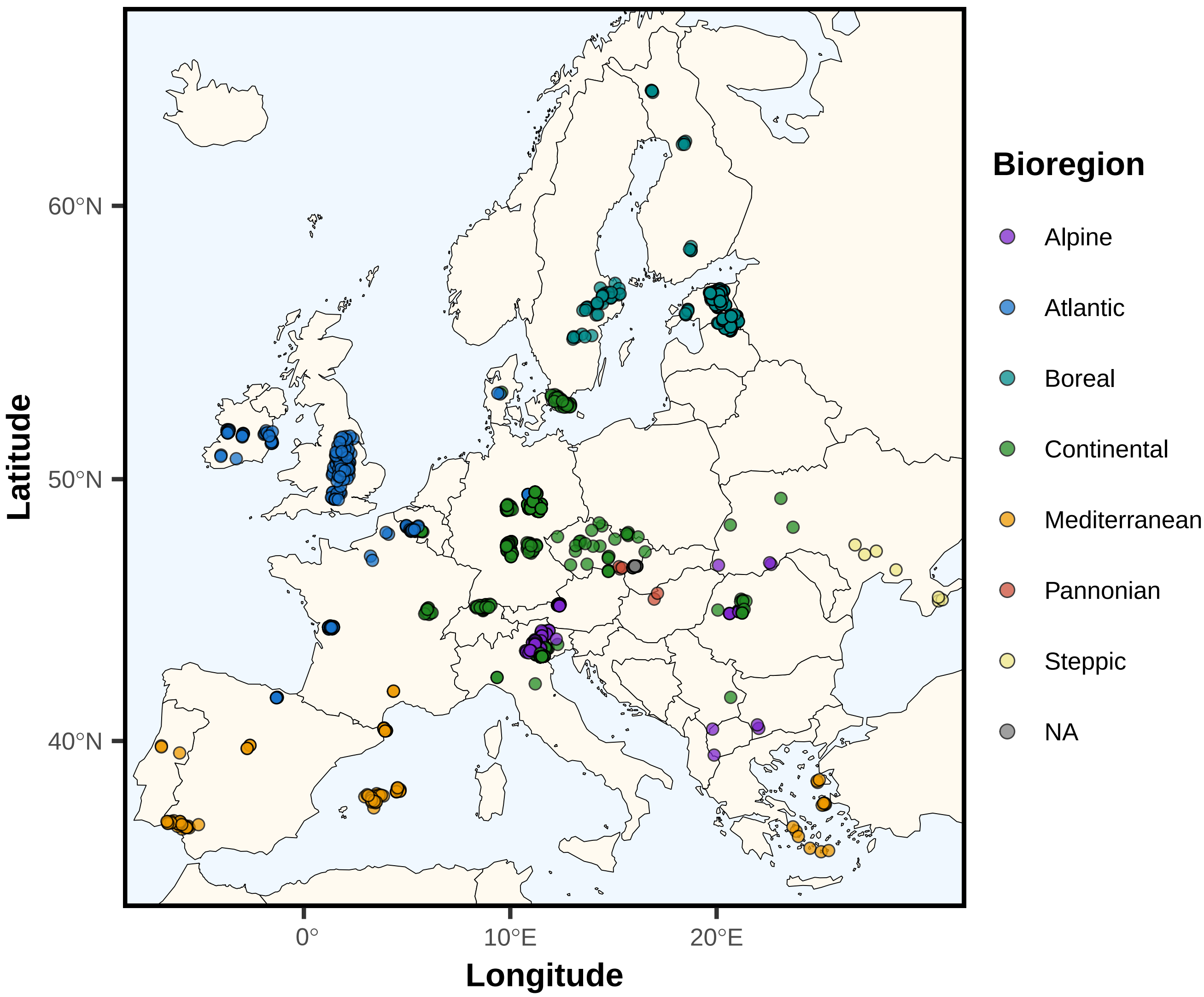

Figure S1. Geographical location of all networks in the EuPPollNet database coloured by bioregion.

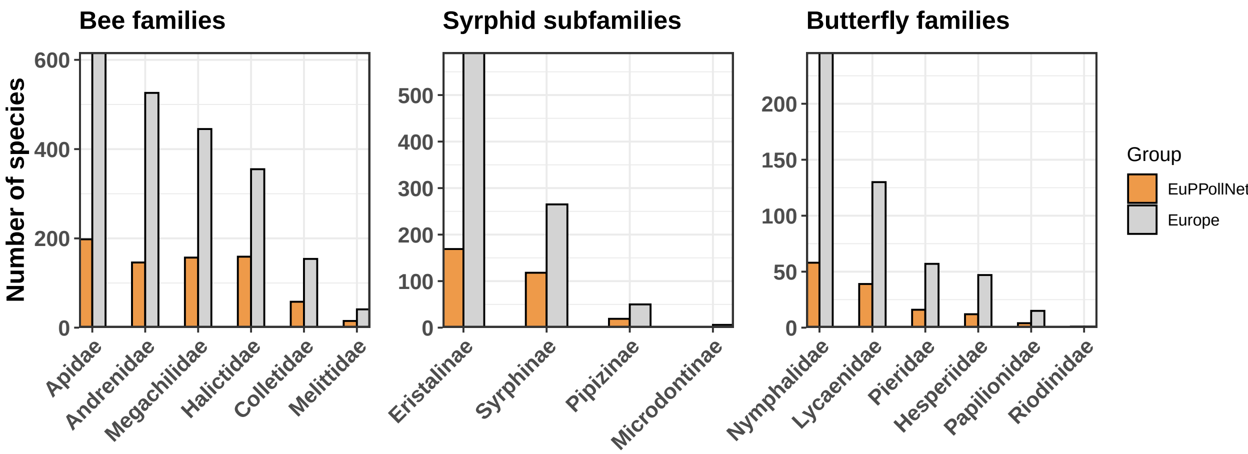

Figure S2. Coverage of the EuPPollNet species for bees (family level), syrphids (subfamily level) and butterflies (family level) in relation to the total number of European species within these taxonomic groups.

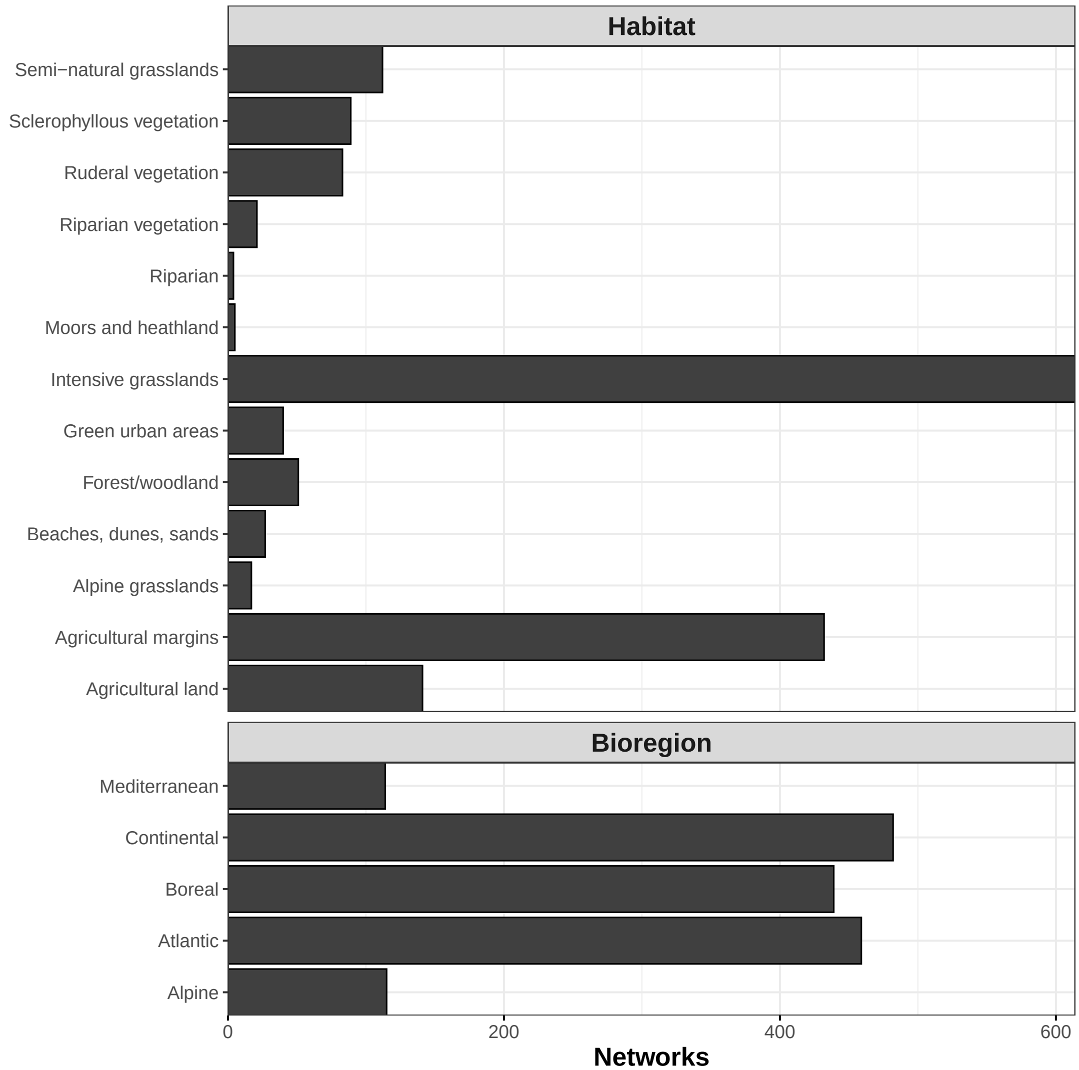

Figure S3. Barplot indicating the number of networks by habitat and bioclimatic region within the database.

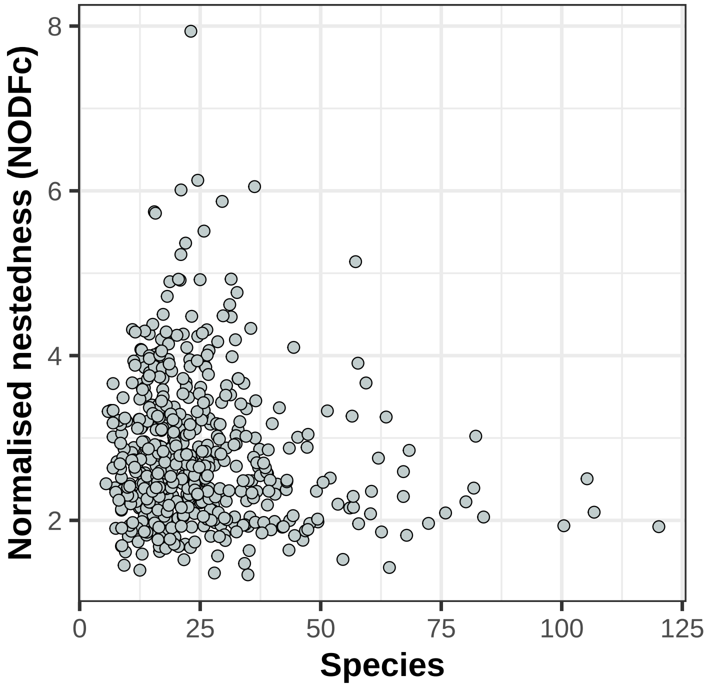

Figure S4. Association between nestedness (NODFc) and the geometric mean of plant and pollinator species per network