SAFEGUARD

Synthesis report on the impacts of multiple pressures on plant-pollinator networks and functional consequences on pollination and plant reproduction

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Safeguard
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Preface

Anthropogenic pressures such as landscape simplification and associated loss in floral diversity are responsible for the observed pollinator declines and induce profound changes in the pollinator and plant community and their interactions. These changes consequently also affect the pollination services the pollinators provide. Although pollinators and their services are well studied, we currently lack a systematic analysis that synthesises existing data to evaluate and better understand the direct and indirect effects of multiple pressures on plant-pollinator interaction networks and their function and stability. In Task 2.2 we addressed this knowledge gap and analysed plant-pollinator network data sets obtained from published studies in Europe, complementing them with data sets obtained in Task 2.3 and seed set data from Task 2.5. Here, we report about the main findings of this quantitative synthesis comprising 487 plant-pollinator networks and discuss the implications of the results.

Key results

- Landscape and local pressures affected network structure, function and stability mainly indirectly through changes in the pollinator community composition and changes in the foraging behaviour (i.e. specialisation) of pollinators.
- **Network structure:** High edge density (landscape pressure) and high local flower richness (local pressure) induced higher foraging specialisation of pollinators, which changed the structure of the networks towards higher modularity and lower nestedness.
- **Network function:** Increased amount of arable crop cover in a landscape (landscape pressure) filtered the pollinator community towards a dominance of common species and a loss of rare species. This change in community composition negatively affected the pollination service index (calculated based on the networks), which correlated with proportion of fertilised seeds and can thus be used as relevant proxy for network function.
- **Managed honeybees and network stability:** A high abundance of the managed honeybee (local pressure) increased modularity of the networks, indicating that wild pollinators shift their foraging niches in presence of high honeybee densities. A high modularity and low nestedness in turn are negatively affecting the stability of networks.
- The findings of this task provide insights on the complex interplay of how local and landscape pressures affect plant-pollinator network structure, functioning and robustness via multiple direct and indirect pathways. Our results thus suggest different actions depending on the conservation aim (pollination function or network stability).

Summary

The current pollinator declines, triggered by anthropogenic pressures, profoundly change plant and pollinator communities. Consequently, this also affects how plants and pollinators interact with each other and shapes the structure of the plant-pollinator interaction networks, which ultimately also affects the pollination function and stability of the networks. Despite a wealth of local studies, we lack a systematic analysis of the existing network data synthesising the direct and indirect effects of these multiple pressures on plant-pollinator

interaction networks. Here in Task 2.2, we analysed 487 plant-pollinator networks sampled in agricultural landscapes of 11 European countries, comprising 28 data sets from published studies and collected in Task 2.3. Using structural equation modelling, we investigated the direct and indirect pathways of how landscape pressures (percentage of arable crop cover as a proxy for landscape simplification and edge density as a proxy for landscape configuration) and local pressures (local flowering plant richness and honeybee abundance) affect the pollinator community and plant-pollinator network structure, functioning and stability. We found that landscape and local pressures affected network structure, functioning and stability mainly indirectly through changes in the pollinator community composition and changes in the foraging behaviour (i.e. specialisation) of pollinators. Pollinators were foraging more specialised in structure-rich landscapes (i.e. high edge density) and with a high local flower richness, which increased modularity and decreased nestedness of the networks. Additionally, a high honeybee abundance increased modularity of the networks as well, indicating that wild pollinators shift their foraging niches in presence of this competitor. A high modularity and low nestedness of networks was related to a lower stability of networks (i.e. lower robustness to secondary extinctions upon plant loss). Further, pollinator communities in simplified landscapes (i.e., high amount of arable crop cover) were dominated by common species, which negatively affected the mean pollination service index of the network (calculated based on the plant pollinator interactions). This pollination service index positively correlated with proportion of fertilised seeds of *Scabiosa ochroleuca* (seed set data obtained from Task 2.5), thus it can be used as a relevant proxy for plant reproductive success. The results of this task provide valuable insights into how local and landscape pressures indirectly affect pollination services and stability of networks across agricultural landscapes of Europe. Our results further suggest different actions depending on the conservation aim, as network function and stability were differently affected by the different pressures.

List of abbreviations

EU	**European Union**
pSEM	**Piecewise structural equation model**
PSI	**Pollination service index**
wNODF	**Weighted nestedness**
d’	**(Foraging) specialisation of pollinators**
HB	**Honeybees**

1. Introduction

Anthropogenic pressures such as landscape simplification, agricultural intensification and the associated loss of suitable semi-natural habitat are the main drivers for the observed pollinator decline (Dicks *et al.* 2021; IPBES 2016; Vanbergen & the Insect Pollinators Initiative 2013). Plants with pollen and nectar as food resource for pollinators, and pollinators providing pollination services to plants (Ollerton *et al.* 2011), are closely linked via mutualistic interactions. Thus, environmental changes affecting plant or pollinator communities are consequently also affecting their interactions and ultimately the important pollination function of these plant-pollinator networks. An improved general understanding of the direct and indirect effects and consequences of anthropogenic pressures on plant-pollinator interactions over a large spatial scale would thus not only help tailoring measures to conserve the species, but also the stability of their networks and the important ecosystem functions they provide.

Anthropogenic pressures are changing i) community composition, ii) abundances of species, and thus iii) the realised interactions between plants and pollinators (Tylianakis & Morris 2017). For example, pollinator communities in human-disturbed landscapes are generally dominated by common and/or generalist species (Burkle *et al.* 2013; Maurer *et al.* 2024; Weiner *et al.* 2014; Winfree *et al.* 2014). Additionally, the locally available floral resources shape the foraging specialisation of the pollinators present in the communities (Gómez-Martínez *et al.* 2022), which again alters the realised interactions found in a network. All these processes have consequences on plant-pollinator network structure (e.g., Grass *et al.* 2018; Martínez-Núñez *et al.* 2019; Proesmans *et al.* 2024), functions (Magrach *et al.* 2021; Peralta *et al.* 2023) and stability (e.g., Kaiser-Bunbury *et al.* 2010; Proesmans *et al.* 2024; Redhead *et al.* 2018). Despite the wealth of studies investigating these network structural changes, it is difficult to capture a common pattern due to the heterogeneity of drivers and network metrics assessed in the different study systems. For example, plant-pollinator networks in more intensive agricultural landscapes (a prime example for anthropogenic pressures) have been found to be more nested (i.e., specialist species interact with a subset of the species generalists interact with) and connected (Proesmans *et al.* 2024) and less modular (i.e., modularity describes sub-groups of species that interact more closely with each other than with other species) (Gómez-Martínez *et al.* 2022). In another study on the opposite, habitat loss has been found to increase network modularity (Spiesman & Inouye 2013). High local flower richness can reduce network connectance and increase pollinator specialisation, indicating higher niche complementarity of pollinators in these landscapes (Doublet *et al.* 2022; Gómez-Martínez *et al.* 2022), but the opposite was found by Theodorou et al. (2016). In addition, high densities of the managed honeybee (*Apis mellifera*) often pose a competitive pressure forcing wild pollinators to shift their foraging niches (Magrach *et al.* 2017; Page & Williams 2023), resulting in altered network structure as well. Generally, these changes in network structure have consequences on network stability: more modular, less nested and connected networks are found to be less stable (Memmott *et al.* 2004; Proesmans *et al.* 2024; Redhead *et al.* 2018). Such changes can also affect plant reproductive success (Magrach *et al.* 2021; Peralta *et al.* 2023), but general patterns of how network structure and functions are related remain to be established.

In Task 2.2 we aimed to advance our understanding of the mentioned processes and synthesise a general picture of how multiple pressures directly and indirectly affect plant-pollinator interaction networks and their functions and stability across the European scale. To accomplish this, we compiled 21 published plant-pollinator interaction data sets sampled in agricultural landscapes of Europe, complementing them with 8 data sets collected in Task 2.3. Using piecewise structural equation modelling, we evaluated the direct and indirect effects of landscape pressures (percentage arable crop cover and edge density) and local pressures (flower richness and honeybee abundance) on the plant-pollinator network structure, stability and proxies for network function (i.e., pollination). To understand how changes in plant-pollinator interactions affect plant reproductive success, we validated whether the proxies for network function (calculated solely based on plant-pollinator interactions) correlated with seed set data obtained from Task 2.5.

2. Methods

2.1 Study search and selection criteria

To compile plant-pollinator interaction data sets we screened the web of knowledge for studies that recorded plant-pollinator interactions in agricultural landscapes. We included the studies for our analyses if they conformed to the following selection criteria: The study was done in agricultural (non-mountainous) landscapes in Europe, recording plant-pollinator interactions in at least 6 independent study sites (i.e., distance among sites at least 1 km) via standardised transect-walks or plot/plant observations (excluding pollen-transport networks). To minimize heterogeneity of the data sets, we focused on studies recording plant-pollinator interactions in herbaceous habitats (defined as habitats dominated by herbaceous and grassy plant species, such as grasslands, road verges, field margins, or scrubland pastures in the Mediterranean, but excluding flower strips). The recorded species should include the most important groups of pollinators (i.e., at least wild bees). In addition to the studies from the literature search, we included studies authored by partners within the EU-Horizon project Safeguard that were collected within Task 2.3 and studies known by the authors of this paper but that did not appear in the search (see Table 1 for an overview of the studies).

2.2 Data preparation

We received 33 data sets suitable for our analyses (n = 636 sites). In most data sets, a study site was defined as one focal grassland, road verge or other herbaceous habitat that was sampled with the same sampling effort at each site (i.e., given transect length and/or given time spent sampling). Six studies sampled more than one habitat type per site and with variable sampling effort per habitat type. To improve comparability among studies and avoid confounding effects of habitat type, we thus selected only the herbaceous habitats from these studies. Additionally, to equalise sampling effort per site within these studies, we assured that the sampling effort per site was the same for each site (within a study) by selecting the transect sections accordingly or shortening the transects if necessary (i.e., to reach the same total transect length per site within a study). Further, when the sites within a study were less than 1 km apart from each other (the maximal foraging range of most pollinators, Greenleaf *et al.* 2007), we excluded one or a few sites in a way that assured this minimal distance among the remaining sites (accepting few exceptions were sites were >800 m apart from each other). After applying these selection criteria, all studies included at least 6 independent sites, all sites within a study had the same sampling effort and exclusively included herbaceous habitats (Table 1).

The studies varied in the recorded pollinator taxa. All of them identified wild bees (Hymenoptera: Anthophila) to species or morphospecies level, 17 studies also recorded hoverflies in addition, 5 studies included bees, hoverflies and butterflies, while 4 studies recorded all flower visitors. Since bees and hoverflies represent the most important pollinators in the study regions (IPBES 2016) and most studies recorded these taxa, we performed the analyses including only bees and hoverflies. Five studies did not record honeybees in their sampling, thus could not be used in the present analysis investigating honeybee abundance as a driver.

2.3 Landscape descriptors and flower richness

We used percentage of arable crop cover as a proxy for landscape simplification (Albrecht *et al.* 2020; Dainese *et al.* 2019) and edge density as a proxy for landscape configuration (Hass *et al.* 2018; Holzschuh *et al.* 2010). 14 studies provided values of arable crop cover within 1000 m radius around the study sites, 2 studies provided arable crop cover within a 500 m radius and 8 studies provided values of arable and perennial crop cover within 1000 m around the study sites. Additionally, we calculated percentage of arable land as well as edge density in a 1000 m radius for all studies based on CLC+ land cover raster data (10 m resolution), which is based on Sentinel time series from July 2017 to June 2019 (© European Union, Copernicus Land Monitoring 2018). We used the raster category “periodically herbaceous” as proxy for area covered by arable land and calculated percentage cover of arable land and edge density (m/ha) using R package landscapemetrics (Hesselbarth 2021). Before calculating edge density, we lumped the categories “Woody – needle leaved trees”, “Woody – broadleaved deciduous trees” and “Woody – broadleaved evergreen trees” into one category (“woodland”) since the discrimination among woodland types is irrelevant for pollinators sampled in the herbaceous layer. The values for percentage of arable crop calculated from the CLC+ raster and the values provided by the data holders correlated well (Pearson correlation coefficient r > 0.6, in most cases > 0.9). We thus used the values from CLC+ to complement the dataset for those 9 studies that did not provide data on percentage of arable crop cover. We used the edge density values calculated from CLC+ for all studies.

Local flower richness was calculated as the number of flowering entomophilous plant species recorded at a site (separate flower surveys). If the study had not done a separate flower survey in addition to the interaction sampling (3 studies), we calculated flower richness as number of plant species present in the plant-pollinator interactions.

Table 1: Summary of the data sets compiled for the quantitative synthesis. The four data sets marked with an asterisk (*) did not sample honeybees and thus could not be used for the present analysis using honeybee abundance as a driver. However, they may be included in follow-up analyses.

Study	Study ID	Country	Habitat	Sampling year	Taxa recorded	Crop cover provided
Li, Pengyao, et al. "The relative importance of green infrastructure as refuge habitat for pollinators increases with local land-use intensity." Journal of Applied Ecology 57.8 (2020): 1494-1503. https://doi.org/10.1111/1365-2664.13658	07_Scheper	south-western France	Grasslands	2015	Bees and hoverflies	arable
Noreika, Norbertas, et al. "Pollinator foraging flexibility mediates rapid plant-pollinator network restoration in semi-natural grasslands." Scientific Reports 9.1 (2019): 15473. https://doi.org/10.1038/s41598-019-51912-4	12_Ockinger	south-central Sweden	Semi-natural pastures	2012	Bees and hoverflies	arable
*Jauker, Frank, et al. "Partitioning wild bee and hoverfly contributions to plant–pollinator network structure in fragmented habitats." Ecology 100.2 (2019): e02569. https://doi.org/10.1002/ecy.2569	19_Jauker	Lower Saxony, Germany	Calcareous grasslands	2004	Wild bees and hoverflies (without honeybees)	arable
*Hopfenmüller, Sebastian, Ingolf Steffan-Dewenter, and Andrea Holzschuh. "Trait-specific responses of wild bee communities to landscape composition, configuration and local factors." PloS one 9.8 (2014): e104439. https://doi.org/10.1371/journal.pone.0104439	21_Hopfenmuller	Upper Franconia, Germany	Calcareous grasslands	2010	Wild bees (without honey bees)	arable

Holzschuh, Andrea, et al. "Mass-flowering crops dilute pollinator abundance in agricultural landscapes across Europe." Ecology letters 19.10 (2016): 1228-1236. https://doi.org/10.1111/ele.12657	23_Holzschuh	Würzburg, Germany	Semi-natural grasslands	2011 and 2012	Bees and hoverflies	arable + perennial
Sutter, Louis, et al. "Enhancing plant diversity in agricultural landscapes promotes both rare bees and dominant crop-pollinating bees through complementary increase in key floral resources." Journal of Applied Ecology 54.6 (2017): 1856-1864. https://doi.org/10.1111/1365-2664.12907	28_Sutter	Northern Switzerland	Herbaceous habitats	2014	Bees and hoverflies	arable
Magrach, Ainhoa, et al. "Honeybee spillover reshuffles pollinator diets and affects plant reproductive success." Nature Ecology & Evolution 1.9 (2017): 1299-1307. https://doi.org/10.1038/s41559-017-0249-9	29_Magrach	Huelva, Spain	Scrubland	2011 and 2012	Bees and hoverflies	arable + perennial
Holzschuh, Andrea, et al. "Mass-flowering crops dilute pollinator abundance in agricultural landscapes across Europe." Ecology letters 19.10 (2016): 1228-1236. https://doi.org/10.1111/ele.12657	30_Smith	Southern Sweden	Grasslands	2011 and 2012	Bees and hoverflies	arable + perennial
Holzschuh, Andrea, et al. "Mass-flowering crops dilute pollinator abundance in agricultural landscapes across Europe." Ecology letters 19.10 (2016): 1228-1236. https://doi.org/10.1111/ele.12657	31_Roberts	Sourthern England	Grasslands	2012 and 2013	Bees and hoverflies	arable + perennial

White, Cian D., et al. "Anthropogenic induced beta diversity in plant–pollinator networks: dissimilarity, turnover, and predictive power." Frontiers in Ecology and Evolution 10 (2022): 806615. https://doi.org/10.3389/fevo.2022.806615	37_White	East Leinster, Ireland	Herbaceous habitats	2018	Bees, hoverflies and butterflies	arable
Maurer, Corina, et al. "Landscape simplification leads to loss of plant–pollinator interaction diversity and flower visitation frequency despite buffering by abundant generalist pollinators." Diversity and Distributions (2024): e13853. https://doi.org/10.1111/ddi.13853	38_Maurer	Northern Switzerland	Herbaceous habitats	2020	Bees and hoverflies	arable
Maurer, Corina, ..., Heuschele, Jonna, et al. "Landscape simplification leads to loss of plant–pollinator interaction diversity and flower visitation frequency despite buffering by abundant generalist pollinators." Diversity and Distributions (2024): e13853. https://doi.org/10.1111/ddi.13853	39_Heuschele	Saxony-Anhalt, Germany	Herbaceous habitats	2021	Bees and hoverflies	arable
Szentgyörgyi, Hajnalka & Żmuda, Aleksandra, unpublished	40_Szentgyorgyi	Lesser Poland Voivodship	Herbaceous habitats	2020-2022	Bees and hoverflies	arable + perennial
Knauer, Anina, unpublished	41_Knauer	Northern Switzerland	Grasslands	2022	Bees	arable

McLaughlin, Gabrielle, unpublished (Safeguard T2.3)	42_McLaughlin	Nothern Switzerland	Calcareous grasslands	2022	Bees and hoverflies	arable + perennial
Weiner, Christiane Natalie, et al. "Land use intensity in grasslands: Changes in biodiversity, species composition and specialisation in flower visitor networks." Basic and Applied Ecology 12.4 (2011): 292-299. https://doi.org/10.1016/j.baae.2010.08.006	43_Weiner	South-western Germany	Grasslands	2007	All flower visiting insects	arable + perennial
Hadrava, Jiří, et al. "A comparison of wild bee communities in sown flower strips and semi-natural habitats: A pollination network approach." Insect Conservation and Diversity 15.3 (2022): 312-324. https://doi.org/10.1111/icad.12565	46_Hadrava	Central Bohemia, Czech Republic	Herbaceous habitats	2016	All flower visiting Aculeata	no
Michelot-Antalik, Alice, et al. "Comparison of grassland plant-pollinator networks on dairy farms in three contrasting French landscapes." Acta Oecologica 112 (2021): 103763. https://doi.org/10.1016/j.actao.2021.103763	50_Michelot	Western, eastern and central France	Permanent grasslands	2021	All flower visiting insects	arable
Librán-Embid, Felipe, et al. "A plant–pollinator metanetwork along a habitat fragmentation gradient." Ecology Letters 24.12 (2021): 2700-2712. https://doi.org/10.1111/ele.13892	53_Libran_Embid	Göttingen, Germany	Calcareous grasslands	2018	Bees and butterflies (Lepidoptera: Papilionidea and Zygaenidae)	arable

*Sydenham, Markus A. K. & Dupont, Yoko L., unpublished	55_Sydenham_ Norway	South-eastern Norway	Roadsides	2021	Wild bees (without honey bees)	arable
*Sydenham, Markus A. K. & Dupont, Yoko L., unpublished	55_Sydenham_ Denmark	Denmark	Roadsides	2021	Wild bees (without honey bees)	arable
Lázaro, Amparo, and Carmelo Gómez-Martínez. "Habitat loss increases seasonal interaction rewiring in plant–pollinator networks." Functional Ecology 36.10 (2022): 2673-2684. https://doi.org/10.1111/1365-2435.14160	56_Lazaro	Mallorca, Spain	Shrubland, natural Olea europaea communities	2018	All flower visiting insects	arable + perennial
Eeraerts, Maxime, et al. "Fruit orchards and woody semi-natural habitat provide complementary resources for pollinators in agricultural landscapes." Landscape Ecology 36 (2021): 1377-1390. https://doi.org/10.1007/s10980-021-01220-y	58_Eeraerts	Flanders, Belgium	Herbaceous habitats	2017 or 2018	Bees	arable
Walton, Richard E., et al. "Nocturnal pollinators strongly contribute to pollen transport of wild flowers in an agricultural landscape." Biology letters 16.5 (2020): 20190877. https://doi.org/10.1098/rsbl.2019.0877	59_Walton	Norfolk, England	Herbaceous pond border	2016 & 2017	All Hymenoptera, hoverflies, and Lepidoptera	arable

*Triquet, Coralie, et al. "Undestroyed winter cover crop strips support wild bee abundance and diversity in intensive cropping systems." Biodiversity and Conservation 33.1 (2024): 179-204. https://doi.org/10.1007/s10531-023-02741-5	60_Triquet	South-eastern France	Field margins	2019-2020	Wild bees (without honey bees)	no
Biegerl, Caroline, unpublished (Safeguard T2.3)	61_Biegerl	Würzburg, Germany	Natural grasslands	2022	Bees and hoverflies	no
Dominik, Christophe, unpublished (Safeguard T2.3)	62_Dominik	Saxony-Anhalt, Germany	Natural grasslands	2022	Bees and butterflies	no
Proesmans, Willem, unpublished (Safeguard T2.3)	63_Proesmans	Eastern France	Natural grasslands	2022	Bees, hoverflies and butterflies	no
Miličić, Marija, unpublished (Safeguard T2.3)	64_Milicic	Serbia	Natural grasslands	2022	Bees, hoverflies and butterflies	no

Morrison, Morgan, unpublished (Safeguard T2.3)	65_Morrison	Southern England	Natural grasslands	2022	Bees and hoverflies	no
Clough, Yann, unpublished (Safeguard T2.3)	68_Clough	Southern Sweden	Natural grasslands	2022	Bees and hoverflies	no
Montes, Nerea, unpublished (Safeguard T2.3)	69_Montes	Southern Spain	Scrubland	2022	Bees and hoverflies	no
Cano, Domingo & Rey, Pedro J., data set: https://doi.org/10.20350/digitalCSIC/15660	71_1_Cano_Saez	Southern Spain	Floral stands in olive groves	2020	All flower visiting insects	arable + perennial

2.4 Plant-pollinator networks

We pooled all sampling rounds per study site to create one plant-pollinator network per site (for each study). We excluded the honeybees from the interaction networks, because we aimed to investigate the effect of honeybee abundance on the interactions between wild pollinators and plants. Plant and wild pollinator species were the nodes, with their interaction frequencies as links. We excluded small networks with fewer than three plant or pollinator species from the analyses, because network metrics are not reliable anymore for such small networks (Dormann *et al.* 2009), resulting in n = 487 networks from 28 studies. To assess how specialised the pollinator species in the community forage given the available plant resources (based on the plant-pollinator interactions), we calculated specialisation d' for each pollinator species (d' ranges from 0 = no specialisation to 1 = perfect specialist, Blüthgen *et al.* 2006) and calculated the mean of d' of all pollinator species per site. We further calculated nestedness and modularity, two metrics that describe the structure of the networks. In a nested network, specialist species interact with species that are subsets of those species that interact with generalist species (Bascompte & Jordano 2007), while modularity describes a pattern where strongly interacting species form modules which are only weakly connected to other modules within the same network (Olesen *et al.* 2007). Nestedness was calculated as weighted NODF (Nestedness metric based on Overlap and Decreasing Fill) (Almeida-Neto & Ulrich 2011). Modularity was calculated from the weighted networks with the DIRTLPAwb+ algorithm from Beckett (2016). As proxies for functional consequences of landscape and local pressures on plant-pollinator interaction networks, we calculated functional complementarity, pollination service index (PSI) and robustness to secondary extinctions upon plant loss. We calculated functional complementarity of pollinators in regard to the plant species they visited (i.e. niche differentiation/complementarity of pollinators) based on the total branch length of a dendrogram based on qualitative differences in visited flower species assemblages between pollinators (Devoto *et al.* 2012). The pollination service index (PSI) describes the importance of all pollinators to a plant species and aims to estimate the proportion of conspecific pollen to a target plant (Dormann 2011). It is calculated as the product of the dependence of the plant i on pollinator j and the per visit efficiency (proportion of visits to i by j) (Dormann 2011). PSI ranges between 0 and 1, high PSI values are observed for pollinators that are either specialised and/or common (Dormann 2011). We calculated the mean PSI across all plant species in a network. Finally, to assess the stability of the networks, we calculated robustness as area below the secondary extinction curve (Memmott *et al.* 2004). We calculated robustness for the extinction scenario assuming that plant-pollinator interactions are driven by bottom-up effects (Ren *et al.* 2023; Schleuning *et al.* 2016), thus we removed subsequently plant species, always starting with the least abundant species, assuming that less abundant species have a higher probability to go extinct compared to abundant species. As Ren et al. (2023), we prefer this relatively simple, but clear assumption to calculate robustness as a relative index of network vulnerability to species loss over estimating “true” extinction sequences from empirical data.

To obtain standardised network metrics that can be compared across sites, we calculated z-scores for nestedness, modularity, functional complementarity and robustness based on 1000 null models for each network (using the Patefield algorithm which keeps marginal totals constant, Patefield 1981; Blüthgen & Staab 2024). All network metrics were calculated using R package bipartite (Dormann *et al.* 2008).

2.5 Commonness of pollinator species

We assessed the commonness of each species in the communities (i.e. studies) by using Fuzzy Quantification of Common and Rare Species in Ecological Communities (FuzzyQ) (Balbuena *et al.* 2021). This method estimates the probability of each species to be common or rare based on its abundance across and occupancy of sites via fuzzy clustering using R package FuzzyQ (Balbuena *et al.* 2021). The resulting commonness index ranges from 0 (rare) to 1 (common). We calculated the mean of the commonness indices of all pollinator species per site.

2.6 Statistical analyses

2.6.1 Sampling completeness

To assess sampling completeness of pollinator species and plant-pollinator interactions, we used asymptotic richness estimates based on Hill numbers calculated in R package iNEXT (Hsieh *et al.* 2016). Specifically, sampling completeness was calculated as the ratio of the observed species or interaction richness and the estimated species or interaction richness, following Chacoff et al. (2012). Mean sampling completeness per study ranged from 46 to 95 % (mean ± SE 62 ± 2) for pollinators and from 32 to 94 % (48 ± 2) for the interactions. Sampling completeness of pollinators and interactions was independent of landscape composition and configuration (pollinators: crop cover: $F_{1,528} = 0.575$, $p = 0.449$; edge density: $F_{1,528} = 0.082$, $p = 0.774$; interactions: crop cover: $F_{1,528} = 1.479$, $p = 0.225$; edge density: $F_{1,528} = 0.132$, $p = 0.716$, linear mixed effects models with study ID as random factor).

2.6.2 Structural equation modelling

All variables were z-transformed per study to improve comparability of the gradients between studies (Maurer *et al.* 2024; Riggi *et al.* 2024). Honeybee abundance and mean PSI were first log-transformed and then z-transformed. We used piecewise structural equation modelling (pSEM) (Lefcheck 2016) to assess the direct and indirect relationships of landscape (percentage crop cover and edge density) and local pressures (honeybee abundance and flower richness) on the structure of plant-pollinator interactions and consequences on network functions. To assess the hypothesised relationships between each response and the explanatory variables, we first built separate LMMs for each response variable with study ID as random factors (Table 2). The correlated errors between nestedness and modularity and between mean PSI and robustness were specified in the pSEM , otherwise, there was low collinearity among the explanatory variables (variance inflation factor VIF < 3, Zuur *et al.* 2010) and model assumptions were not violated as checked by inspection of residual plots using the R packages DHARMa (Hartig 2022) and performance (Lüdecke *et al.* 2020). For each of the nine models, we then selected the best combination of explanatory variables based on the Akaike information criterion (AIC). We built the piecewise structural equation model (pSEM) with these reduced models (Table 2) (Hulsmans *et al.* 2023). We evaluated the final pSEM using Shipley's tests of directed separation to detect missing paths. There was no significant missing path left, but we reduced the pSEM by omitting three relationships that did not explain patterns ($p > 0.1$, Table 2). Finally, the global goodness of fit was evaluated using Fisher's C statistic. The LMMs were run with the R package lme4 (Bates *et al.* 2015) and the pSEM with the R package piecewiseSEM (Lefcheck 2016). Data analysis was done in R version 4.4.2 (R Core Team 2022).

Table 2 Summary of the modelling approach.

Response	Hypothesised pathway	Variables after model selection	Pathways in final SEM
Flower richness	Crop cover + edge density	-	-
Honeybee abundance (log)	Crop cover + edge density + flower richness	Edge density	Edge density
Commonness index	Crop cover + edge density + flower richness	Crop cover	Crop cover
Mean d’	Crop cover + edge density + flower richness + honeybee abundance (log) + commonness index	Flower richness + edge density	Flower richness + edge density
Nestedness	Crop cover + edge density + flower richness + honeybee abundance (log) + commonness index + mean d’ +	Flower richness + honeybee abundance (log) + commonness index + mean d’	Flower richness + honeybee abundance (log) + mean d’
Modularity	Crop cover + edge density + flower richness + honeybee abundance (log) + commonness index + mean d’	Crop cover + flower richness + honeybee abundance (log) + mean d’	Crop cover + flower richness + honeybee abundance (log) + mean d’
Pollination service index (PSI) (log)	Crop cover + edge density + flower richness + honeybee abundance (log) + commonness index + mean d’ + nestedness + modularity	Flower richness + honeybee abundance (log) + mean d’ + nestedness + modularity	Flower richness + mean d’ + nestedness + modularity

Functional complementarity	Crop cover + edge density + flower richness + honeybee abundance (log) + commonness index + mean d’ + nestedness + modularity	Honeybee abundance + mean d’ + nestedness + modularity	Mean d’ + nestedness + modularity
Robustness upon plant loss	Flower richness + mean d’ + nestedness + modularity	Flower richness + mean d’ + nestedness + modularity	Flower richness + mean d’ + nestedness + modularity

2.6.3 Seed set data

We used seed set data obtained from Safeguard Task 2.5 (9 sites from Saxony-Anhalt, Germany) to validate whether mean PSI and functional complementarity calculated based on the plant-pollinator interactions are valid proxies for the pollination function of plant-pollinator networks. We used the proportion of fertilized seeds of the self-incompatible *Scabiosa ochroleuca* as response variable and either mean PSI or functional complementarity as explanatory variable in generalized linear mixed models (GLMMs) with binomial error structure and site ID as random factor.

3. Results

In total, the data set comprised 570 bee species (incl. *Apis mellifera*), 181 hoverfly species, which interacted with 756 plant species.

3.2 Direct and indirect effects of landscape and local pressures on the plant-pollinator network

Overall goodness of fit of the final pSEM was good with a Fisher’s C of 45.77 and a p-value of 0.83 (56 degrees of freedom) (Figure 1). The specified errors of nestedness and modularity were significantly correlated (estimate: -0.69, $p < 0.001$), as well as those of mean PSI and robustness (-0.24, $p < 0.001$).

3.2.1 Landscape pressures: percentage arable crop cover and edge density

Percentage of arable crop cover had a significant positive effect on the mean commonness index of the pollinators at a site (Figure 1; standardised path estimate ± standard error: 0.16 ± 0.04, $p < 0.001$), confirming the general prediction that pollinator communities in simple landscapes mainly consist of common species. Further, there was a positive trend of percentage of arable crop cover affecting modularity of networks (0.07 ± 0.04, $p = 0.083$). Edge density in turn positively affected honeybee abundance (0.1 ± 0.03, $p = 0.001$) and mean specialisation of the pollinator community (0.1 ± 0.04, $p = 0.024$).

3.2.2 Local pressures: flower richness and honeybee abundance

Flower richness had positive effects on mean specialisation of pollinators in a community (0.26 ± 0.04, $p < 0.001$), modularity (0.24 ± 0.04, $p < 0.001$) and robustness of a network (0.13 ± 0.03, $p = 0.001$; Figure 1). Further, flower richness tentatively negatively affected nestedness (-0.08 ± 0.05, p = 0.074) and had a negative effect on mean PSI (-0.28 ± 0.04, p < 0.001).

Abundance of honeybees significantly affected the structure of the plant-pollinator network: A higher number of honeybees increased the modularity of the network (0.09 ± 0.04, p = 0.033), while it slightly decreased nestedness (-0.08 ± 0.04, p = 0.058).

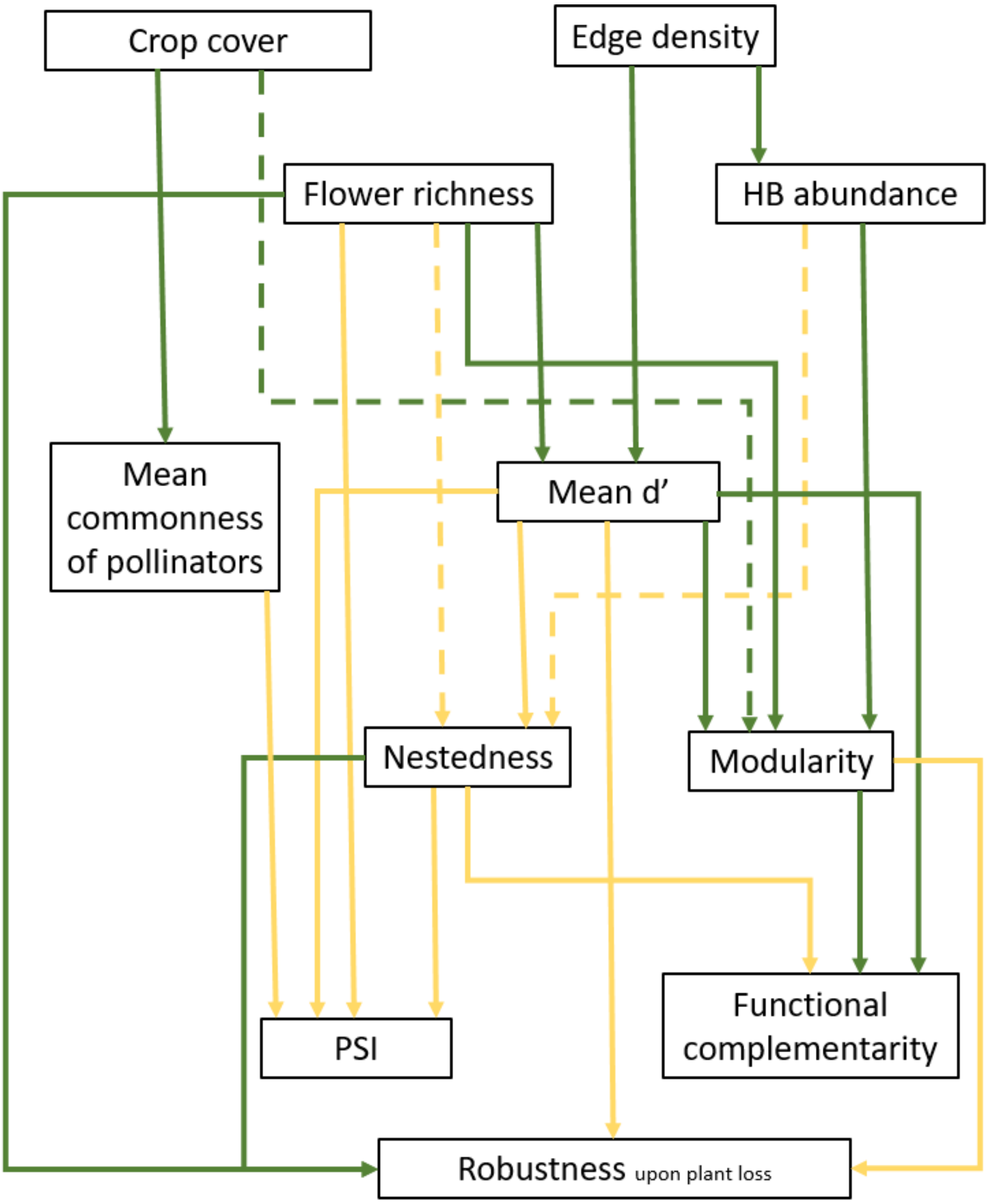

Figure 1: Relationships of the final pSEM. Green: positive relationships, yellow: negative relationships, dashed lines: non-significant trends (p < 0.1).

3.2.3 Commonness and specialisation of the pollinator community

The mean commonness of all pollinator species in a network had no effect on the structure (i.e., nestedness and modularity) or robustness of the network, but a negative effect on the functional proxy mean PSI (-0.17 ± 0.03, p < 0.001; Figure 1). The foraging behaviour of the pollinators (i.e., how specialised/selective they forage) played a central role in structuring the networks: Mean specialisation d’ of the pollinator community negatively affected nestedness of the network (-0.13 ± 0.05, p = 0.006), but positively affected modularity (0.14 ± 0.04, p = 0.002). Further, a specialised pollinator community (high mean d’) decreased the mean PSI (0.52 ± 0.04, p < 0.001) and but increased functional complementarity in pollinator foraging niches (0.11 ± 0.03, p < 0.001). Further, a high mean d’ decreased the robustness of networks upon plant loss (-0.33 ± 0.03, p < 0.001).

3.2.4 Network structure

As expected, nestedness and modularity had contrasting effects on network functional proxies and robustness: modularity negatively affected robustness of the network (-0.13 ± 0.05, p = 0.006), while it positively affected functional complementarity (0.70 ± 0.04, p < 0.001; Figure 1). On the contrary, nested networks are expected to have a higher robustness (0.49 ± 0.05, p < 0.001), but a lower functional complementarity of pollinators (-0.13 ± 0.04, p < 0.001) and a lower mean PSI (-0.28 ± 0.03, p < 0.001).

3.3 Seed set and functional network proxies

The mean pollination service index (PSI) of a network was marginally significantly positively related to the proportion of fertilized seeds per *Scabiosa ochroleuca* plant (likelihood ratio = 3.31, p = 0.069), while functional complementarity of the pollinator species in a network was not related to seed set (likelihood ratio = 0.02, p = 0.889).

4. Discussion

This synthesis of 487 plant-pollinator networks across 11 European countries provides to our knowledge the first European-wide synthesised insights on how multiple pressures act on plant-pollinator interactions with consequences on the pollination function and stability. Our results show that landscape simplification changed the pollinator communities towards the dominance of common species, which had negative consequences on the pollination services provided to plants in the network. Factors such as honeybee abundance and local flower richness additionally changed network structure via changes in foraging behaviour of pollinators, with consequences on network robustness.

4.1 Pressures on network structure and robustness

Landscape and local pressures (edge density and local flower richness) affected network structure mainly indirectly through changes in the foraging behaviour of pollinators. In a structure-rich landscape with a high local richness of floral resources, the pollinators foraged more specialised (higher mean specialisation d’). These results on the European scale confirm patterns already seen on local scales (Gómez-Martínez *et al.* 2022). This change towards more specialised foraging resulted in increased modularity and a decreased nestedness of networks, which overall increased functional complementarity of pollinator niches. These changes in network structure in turn decreased network robustness upon loss of plant species, which is in line with theory and previous findings (Kaiser-Bunbury *et al.* 2010; Memmott *et al.* 2004; Morrison *et al.* 2020).

Consequently, a loss in landscape structure and local flower richness likely leads to a loss of specialised plant-pollinator interactions, leading to more homogenised interactions and less modular networks. At the same time, the resulting increased redundancy of interactions in these networks makes them more robust. Thus, likely because vulnerable species already have been lost, and persisting species are generalists and less reliable on specific plant species, networks in more intensive agricultural landscapes are quite robust (Redhead *et al.* 2018).

4.2 Pressures on network function

Increased amount of crop cover, a proxy for landscape simplification, clearly filtered pollinator communities towards a dominance of common species and a loss of rare species, as hypothesised and shown previously for a single region (Winfree *et al.* 2014). Our results further show that these impoverished pollinator communities were not able to maintain the pollination function as measured with the pollination service index (PSI). The mean PSI calculated from the networks slightly positively correlated with proportion of fertilised seeds of the self-incompatible plant *Scabiosa ochroleuca*, and can thus likely be used as a proxy for plant reproductive success. Interestingly, a high plant richness, nestedness of networks and specialisation of pollinators were negatively affecting mean PSI. A locally high flower richness and nestedness of interactions might result in a higher proportion of heterospecific pollen brought to the focal plant (Arceo-Gómez & Ashman 2011; Evans *et al.* 2017). Although we would expect that specialisation of pollinators is related to a high flower constancy and thus advantageous for the plants (Allen-Perkins *et al.* 2024), we could not observe this effect here. In contrast, specialisation of pollinators and modularity (with indirect positive effects of edge density and flower richness) were positively affecting functional complementarity of pollinator niches, which was not correlated to proportion of fertilised seeds of *Scabiosa ochroleuca* (despite previous findings of a positive correlation with plant reproductive success, Magrach *et al.* 2021). We would thus suggest using PSI as a proxy for network functions, but this inconsistency also calls for more in-depth analyses of how network structure affects plant reproductive success.

In conclusion, plant reproductive success (measured via PSI) might be affected via two main pathways: i) via the pollinator community composition (i.e., how many common vs. rare species) and ii) via the foraging behaviour (i.e. specialisation) of the pollinators and the resulting network structure, which is likely governing the amount of conspecific pollen landing on the stigma. Both of these pathways are in turn affected by local and landscape pressures.

4.3 Impact of managed honeybees on networks

A high local abundance of managed honeybees at a site increased the modularity of the plant-pollinator networks (excluding the interactions involving honeybees). This demonstrates how managed honeybees pose a competitive pressure on the wild pollinators in the networks: The pollinators change their interaction pattern to segregate or shift their foraging niches in presence of the honeybee (Cappellari *et al.* 2022; Magrach *et al.* 2017; Page & Williams 2023), resulting in a change in network structure. Our results further show that through this change in network structure towards higher modularity, honeybees also indirectly decreased network robustness.

4.4 Conclusions and implications for policy and management

By synthesising 28 plant-pollinator network data sets collected in agricultural landscapes across Europe, the results of this task shed light on the complex interplay of how local and landscape pressures affect plant-pollinator network structure, functioning and robustness via multiple direct and indirect pathways. Our analyses showed that landscape and local pressures affect network structure and functions mainly through indirect pathways via changing pollinator community composition and their foraging specialisation. Our results suggest different actions depending on the conservation aim (preserving pollination function or network robustness): To preserve pollination services in agricultural landscapes, conservation measures should focus on preventing the loss of rare species. Alternatively, maintaining a high local flower richness and decreasing honeybee abundance to decrease modularity of networks should ensure robustness of the plant-pollinator network.

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