Received: 10 September 2024 | Accepted: 17 March 2026

DOI: 10.1111/1365-2664.70377

RESEARCH ARTICLE

Journal of Applied Ecology

Seasonal mass-flowering events dominate landscape effects on plant–pollinator network structure

Jonna M. Heuschele[1,2,3] | Oliver Schweiger[1,2] | Matthias Albrecht[4] | María R. Felipe-Lucia[2,5] | Hanna Honchar[6] | Yicong Liu[1,3] | Martin Musche[6] | Robert J. Paxton[2,3] | Josef Settele[2,3,6] | Hajnalka Szentgyörgyi[7] | Adam J. Vanbergen[8] | Tesfaye Wubet[1,2] | Christophe Dominik[1,2]

[1]Department of Community Ecology, UFZ—Helmholtz Centre for Environmental Research, Halle (Saale), Germany; [2]iDiv—German Centre for Integrative Biodiversity Research Halle-Jena-Leipzig, Leipzig, Germany; [3]Institute for Biology, Martin-Luther-University Halle-Wittenberg, Halle (Saale), Germany; [4]Agroscope, Agroecology and Environment, Zürich, Switzerland; [5]CSIC—Instituto Pirenaico de Ecología (IPE, CSIC), Jaca (Huesca), Spain; [6]Department of Conservation Biology, UFZ—Helmholtz Centre for Environmental Research, Leipzig, Germany; [7]Faculty of Biology, Institute of Botany, Jagiellonian University, Kraków, Poland and [8]Agroécologie, INRAE, Institut Agro, Univ. Bourgogne, Univ. Bourgogne Franche-Comté, Dijon, France

Correspondence
Jonna M. Heuschele
Email: jonna.heuschele@ufz.de

Funding information
Bundesministerium für Bildung und Forschung, Grant/Award Number: 01LC1905A; Deutsche Forschungsgemeinschaft, Grant/Award Number: DFG-FZT 118 202548816, PA 623/10-1 and PA 623/12-1; NextGenerationEU, Grant/Award Number: RYC2021-032828-I; Biodiversa+, Grant/Award Number: ANR-19-EBI3-0006, NCN UMO-2019/32/Z/NZ8/00006, Pa623/12 and SNSF 31BD30_186532/1

Handling Editor: Lorenzo Marini

Abstract

1. Agricultural landscapes feature marked seasonal changes in the quality and quantity of habitats and floral resources supporting pollinating insects. Seasonal dynamics can affect the structure of plant–pollinator interactions, yet the relative importance of both landscape elements with spatio-temporal dynamics and those elements that are more static in space and time remains largely unknown. Such an understanding is needed to identify resource-mediated modifications of plant–pollinator network structures and their functional and management implications.
2. To understand the spatio-temporal effects of landscape heterogeneity on the structure of plant–pollinator networks, we sampled plant–pollinator (Apiformes—except *Apis mellifera*; Syrphidae) communities over three seasonal periods in 12 landscapes in central Germany. The landscapes comprised spatial gradients in the proportion of semi-natural habitat cover and edge density. To assess temporal changes, we evaluated the cover of mass-flowering crops in bloom, floral diversity and honey bee density at each plant–pollinator sampling event.
3. Spatio-temporally dynamic characteristics, particularly the cover of mass-flowering crops, were more important than static characteristics in explaining variation in plant–pollinator network structure across the three seasonal periods. The richness of plants and pollinators was generally lower when the proportion of mass-flowering crops was high. Under such conditions, networks were more connected, with greater niche overlap among pollinators, and decreased network specialization (H2′). Richness was higher in landscapes with high edge density, with an increasing effect on network connectance up to a certain threshold.

The proportion of semi-natural habitat cover and floral diversity had differential effects on the richness of plants and pollinators, with strong effects on the dietary niche overlap of the pollinators, potentially indicating a decrease in competition when semi-natural habitat cover and flower diversity are high.

4. *Synthesis and application*. To better support plant–pollinator communities in agricultural-dominated landscapes, we suggest incentivizing the planting of complementary floral resources and preserving or restoring semi-natural habitat areas. Especially in intensively used agroecosystems, the negative effects of mass-flowering crops can be mitigated by maintaining flower-rich edge habitats and relatively small field sizes, which help support plant and pollinator communities, avoid potential negative effects of exploitative competition, and ensure the sustainability of pollination services via increased functional redundancy.

KEYWORDS
agrobiodiversity, mass-flowering crops, network analysis, plant–pollinator interactions, resource limitations, spatial configuration, temporal dynamics

1 | INTRODUCTION

Plant–pollinator interactions are the basis of pollination services provided to wild and crop plants, with considerable benefits for nature, human well-being and economies (Klein et al., 2018). Plant–pollinator interactions can be described in terms of their network properties (Bascompte & Jordano, 2007). This can reveal shifts in the composition and functioning of communities and ecosystems, such as levels of competition, complementarity and redundancy in pollination services (Tylianakis & Morris, 2017; more details in Table S1).

Pollinators and pollination services face multiple pressures, such as habitat loss, agrochemical use, climate change and invasive species (Kovács-Hostyánszki et al., 2017). Floral (pollen and nectar) resources are crucial for sustaining pollinator populations, yet they are unevenly distributed over space and time, particularly in homogenous agricultural landscapes with scarce wild floral resources (Mallinger et al., 2016). Globally, the increasing cultivation of mass-flowering crops has increased the reliance on pollination for agricultural production (Aizen et al., 2019), but this dependency has not been accompanied by a corresponding improvement of habitat resources supporting pollinator communities (Potts et al., 2016).

Mass-flowering crops offer large resource pulses in agricultural landscapes that mainly benefit generalist pollinators (Westphal et al., 2003), especially early in the season (Holzschuh et al., 2013). In landscapes dominated by intensive agriculture, where floral resources can become limited over the summer (Timberlake et al., 2019), alternatives to crops are often restricted to peripheral semi-natural habitat patches such as road and field verges (Phillips et al., 2020), hedges (von Königslöw et al., 2022) and agricultural weeds (Bretagnolle & Gaba, 2015). Therefore, resource pulses from mass-flowering crops provide temporally dynamic floral resources in intensive agricultural landscapes, highlighting the spatio-temporal dimension of floral resource limitation (Sponsler et al., 2023) and landscape heterogeneity, that may affect plant–pollinator networks (Ammann et al., 2024; Fahrig et al., 2011). For example, Souza et al. (2018) showed that lower seasonal resource availability increased specialization among pollinators (in tropical environments), caused by niche partitioning during intense pollinator competition for scarce resources. Therefore, high density of floral resources during crop mass-flowering may decrease competition among pollinators and subsequently increase niche overlap. However, mass-flowering crops might compete with wild flowering plants and concentrate pollinator activity and pollination services away from semi-natural habitat patches (Riggi et al., 2023). In addition, mass-flowering crops often attract abundant managed pollinators (e.g. honey bees, *Apis mellifera* L.). These can compete with wild pollinator communities for floral resources and alter the structure of wild plant–pollinator networks by displacing species and their mutualistic interactions with plants (Lindström et al., 2016; Weaver et al., 2022; Worthy et al., 2023).

Positive effects of floral resource diversity, driven by increased complementarity, have been shown for both rare and abundant pollinators (Sutter et al., 2017). At the network-level, floral richness can enhance specialization, likely due to niche partitioning of pollinators (Gómez-Martínez et al., 2022). Promoting the distribution and diversity of floral resources can support the restoration of plant–pollinator networks by improving network robustness through increased connectance and plant-niche overlap in isolated habitat patches (Cusser et al., 2019). For instance, Ebeling et al. (2011) showed that a gradient of floral diversity not only increases network complexity but also temporal stability in the frequency of flower visits.

Landscape composition can enhance network nestedness and robustness (Moreira et al., 2015). Diversity, temporal stability and a high proportion of semi-natural habitat cover may support more complex networks as opposed to a mere increase in floral resources, such as that achieved by planted flower strips with limited functional diversity (Hadrava et al., 2022). Although plant–pollinator networks are known to show temporal variability across the year (CaraDonna et al., 2021), few studies have investigated seasonal patterns in species interactions and how temporal dynamics of environmental factors relate to them (but see e.g. Chakraborty et al., 2021).

Here, we identified how landscape composition (semi-natural habitat cover) and configuration (edge density), and resource availability (mass-flowering crops, floral diversity) as well as honey bee density influence key properties of network structure and functioning: plant and pollinator richness, connectance, niche overlap of pollinators and network-level specialization (H2′). Richness of plant and pollinator species represent classical measures of diversity relevant for conservation. Connectance measures the ratio of realized to possible links in a network, ranging from 1 (*perfectly connected*) to 0 (*unconnected*). The level of network connectance can confer robustness against secondary extinctions (Dunne et al., 2002). Network specialization (H2′) quantifies how much observed interactions deviate from being perfectly specialized (0 = no specialization to 1 = perfect specialization). Highly specialized networks, where species interact with specific partners, are often considered more valuable for conservation because they support unique, interdependent relationships that are sensitive to habitat changes. High specialization thus highlights ecosystems that may require targeted management to preserve these unique interactions. It also allows unbiased comparisons between networks, enabling more accurate assessments of ecological resilience and management needs (Blüthgen et al., 2006). Niche overlap as Horn's index, focusing on pollinators, indicates functional redundancy with values near 1, and functional complementarity with values near 0 (Blüthgen & Klein, 2011). Functional redundancy can stabilize ecosystem function (Biggs et al., 2020; Winfree & Kremen, 2009) and benefit the pollination of agricultural crops (Woodcock et al., 2019). However, high niche overlap could also indicate higher competition for scarce floral resources between pollinator species.

In general, we expected that these network properties would vary across the season, mostly due to phenological turnover in the pool of flowering plant and flower visiting insect species, leading to the following hypotheses (Hi-iv). (Hi) Mass-flowering crop bloom attracts generalist species thereby reducing interspecific competition and allowing for more balanced foraging by less competitive pollinator species across wild plants, consequently increasing niche overlap and connectance, while decreasing specialization. (Hii) Greater wild plant floral diversity within a landscape allows for increased niche partitioning and therefore reduced niche overlap of pollinators and overall network specialization. (Hiii) Abundant managed honey bees can dominate networks and compete with wild insect pollinators for floral resources, leading to greater niche overlap and connectance. (Hiv) More pollinator-friendly landscape elements (semi-natural habitats, field margins and other edge habitats) buffer temporal floral resource fluctuations and potential competition from honey bees on the overall network structure.

2 | MATERIALS AND METHODS

2.1 | Study area

The study was conducted in the federal state of Saxony-Anhalt, Germany (Figure 1), where oilseed rape is the most abundant insect-pollinated crop; other crops such as sunflower, beans, asparagus and phacelia occur in lower proportions (STALA, 2022). Twelve landscapes of 1 km radius were selected along a gradient of arable land ranging from 22% to 97% (Figure 1, Table S2), which was highly correlated (Pearson $r = -0.92$) with the proportion of semi-natural habitat cover ranging from 0.8% to 66% (Figure 2). Our sites reflect typical European agricultural landscapes, with arable land cover ranging from 3.8% to 44.8% at the country level (Eurostat, 2025).

2.2 | Plant–pollinator networks

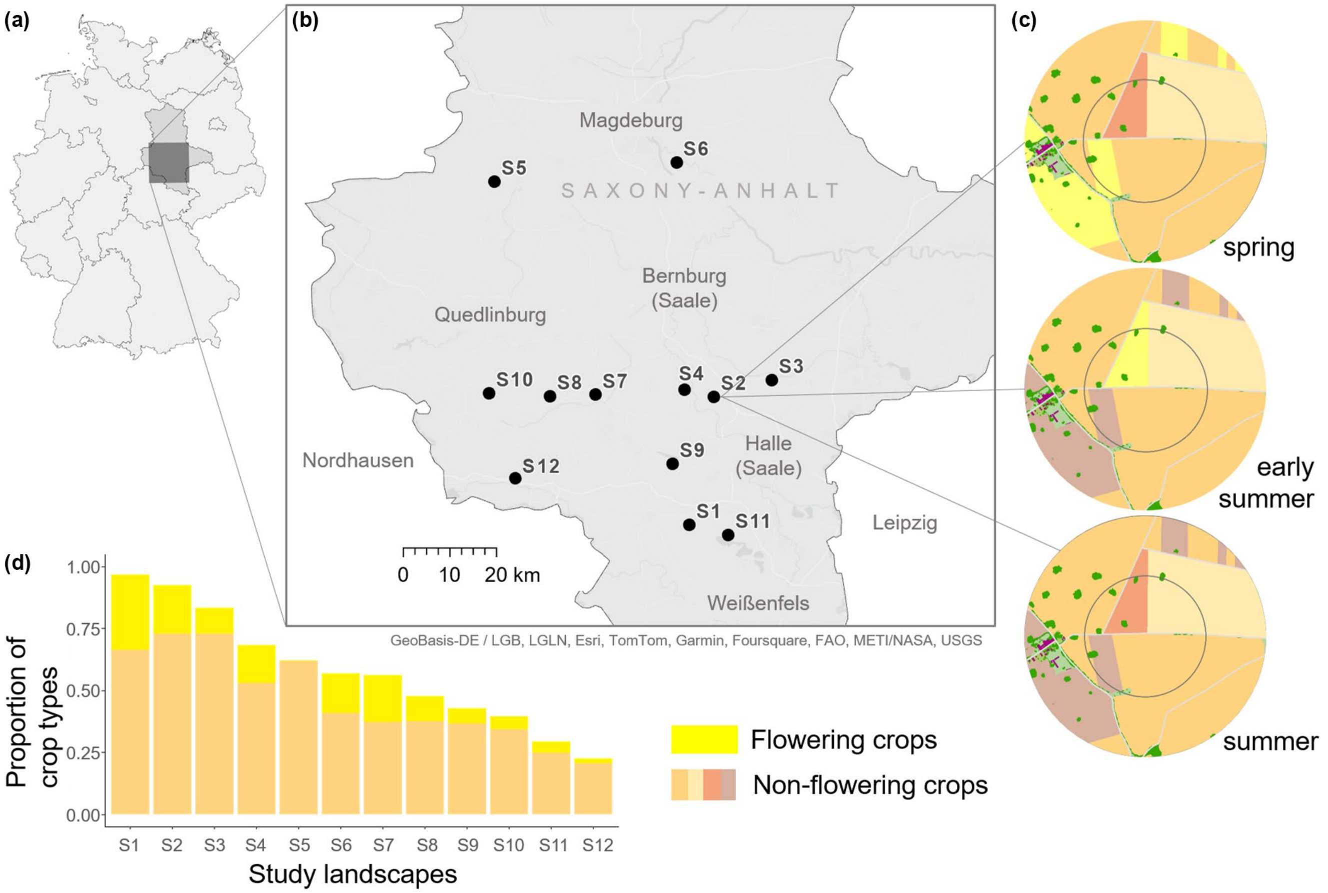
In 2021, plant–pollinator interactions were sampled three times in each landscape—spring (May), early summer (June–July) and late summer (August). Sampling was conducted between 9 am and 6 pm when favourable weather conditions were met (≥14°C, low wind speed <6 m/s, no precipitation).

In each landscape, 20 transect subsections of 50 m in length were established within a 500 m radius core area. To assess landscape-wide plant–pollinator networks, the subsections were proportionally distributed over all habitat types harbouring flowering plants. Sampling time was standardized at 120 min per landscape (6 min/50 m), excluding handling time.

While most studies focus on wild bees, we included hoverflies (Syrphidae), an often overlooked but functionally important group of pollinators (Doyle et al., 2020). All individuals observed visiting a flower were sampled and identified to species level by taxonomists. Cryptic species were identified via barcoding, except for the *Halictus simplex/longobardicus/compressus* complex, which was treated as a single group. Visited flowers were identified on-site using Flora Incognita (Mäder et al., 2021) or by expert botanists. If floral resources were depleted in a transect subsection (e.g. recently mowed), the subsection was relocated within the 500 m radius to maintain the proportional sampling of habitat types. Field data collection was conducted with a permit granted by the State Office for Environmental Protection in Saxony-Anhalt (licence number RL-0691). Data collection did not require ethical approval.

2.3 | Spatial landscape characteristics

Spatial aspects of landscape heterogeneity were quantified by calculating the proportion of semi-natural habitat cover and edge density. As these remained constant throughout the study period, we refer to them as ‘static’ throughout the manuscript. Landscape features were manually digitized at a 1:2500 scale within a 1 km radius, using



GeoBasis-DE / LGB, LGLN, Esri, TomTom, Garmin, Foursquare, FAO, METI/NASA, USGS

FIGURE 1 Location and characteristics of the 12 studied landscapes. (a) Study region in Saxony-Anhalt, Central Germany. (b) Twelve studied landscapes (S1–S12). (c) Example habitat map (S2) displaying the spatio-temporal variation of mass-flowering events in spring (May), early summer (June–July) and summer (August). (d) Gradient of arable land across the 12 landscapes, displaying proportions of non-flowering versus flowering crop types that provide pollen and nectar resources to pollinators.

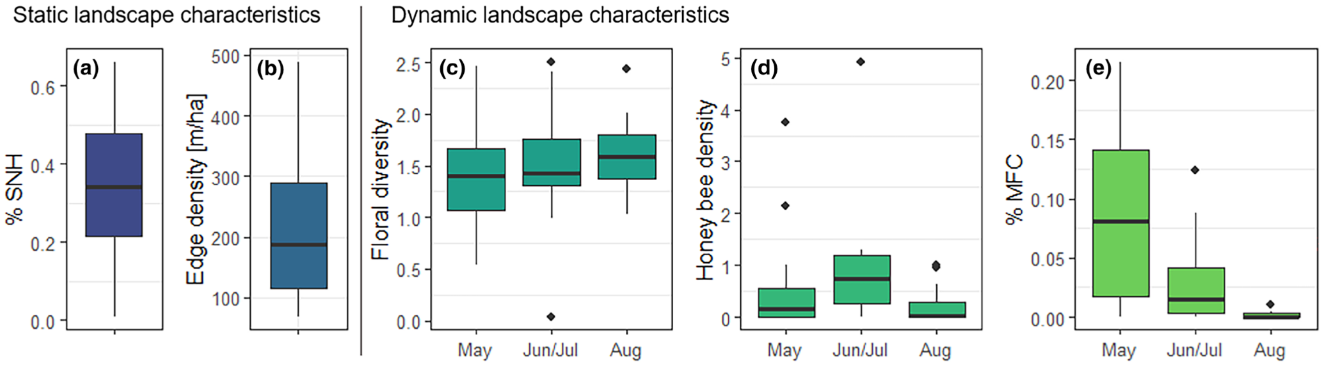


FIGURE 2 Landscape characteristics of the 12 study landscapes. (a, b) Boxplots of spatially static characteristics, that is the proportion of semi-natural habitat cover (% SNH) and edge density that did not vary across the seasonal periods in our study. (c–e) Boxplots of spatio-temporally dynamic characteristics, that floral diversity, honey bee density, and proportion of mass-flowering crops (% MFC), across the three seasonal periods (May, June–July, August). Exact means, standard deviations and ranges in Table S4.

remote sensing data (World Imagery, ESRI) and GIS tools (ArcGIS Pro 3.1.4 ESRI, 2012). Ground truthing of habitat maps was conducted during field visits. We differentiated habitat areas relevant to flowers and their visitors, applying an aggregated EUNIS habitat classification (EEA, 2012) with 12 distinct habitat classes. Semi-natural habitats included permanent grassland, woodland and the margins of fields and roads. The proportion of semi-natural habitat cover was calculated relative to the entire area of the studied landscapes. Landscape edge density was calculated as the ratio of boundary habitat to total landscape area. Landscape metrics were calculated using the R package 'landscapemetrics' (Hesselbarth et al., 2019; R Core Team, 2022).

2.4 | Spatio-temporal landscape characteristics

In contrast to the spatial characteristics, the spatio-temporal landscape characteristics were re-assessed during each sampling period, therefore referred to as 'dynamic'. The cover of mass-flowering crops in bloom was measured at the 1 km scale. Along the transect within the 500 m core area, a floral survey was performed using vegetation plots of 2 m × 0.5 m with flowering species and inflorescence counts recorded. Three plots were sampled in heterogeneous plant communities, whereas only one plot was sampled in mass-flowering crops. Shannon diversity was calculated using the 'vegan' package (Oksanen et al., 2020), with the mean values per habitat type weighed by the length of the respective transect. The sum of weighted floral diversity was calculated to derive a landscape-level diversity index. Additionally, honey bee densities were estimated by recording their abundance for 1 min per transect subsection and calculating the mean at the landscape-level.

2.5 | Data analysis

2.5.1 | Plant–pollinator interaction networks

Statistical analyses were performed in R v. 4.0.1. (R Core Team, 2022). Thirty-six quantitative plant–pollinator networks were compiled (3 periods × 12 landscapes) with the R package 'bipartite' (Dormann et al., 2008). Managed honey bees were excluded to focus on interactions between wild pollinators and flowering plants as honey bee densities depend more on beekeeping than landscape factors.

Network metrics were calculated with the function 'networklevel' ('bipartite'). Since network size can influence these metrics (Blüthgen & Staab, 2024), we calculated *z*-scores for each of the metrics based on 10,000 null models computed with the Patefield algorithm, 'r2d-table', which maintains row and column sums but randomizes cell values (Patefield, 1981).

2.5.2 | Modelling effects on plant–pollinator networks

Following a multimodel inference approach, we assessed the importance of explanatory variables for each network metric and the richness of plants and pollinators through linear mixed-effects models with the 'lmer' function ('lme4' package, Bates et al., 2015). Calculated z-scores of the network metrics were response variables, with landscape characteristics as explanatory variables. Spatially static variables included the proportion of semi-natural habitat cover and edge density. Spatio-temporally dynamic variables included the cover of mass-flowering crops, floral resource diversity and honey bee densities. Similarly, the richness of plants and pollinators was analysed separately. In the model of plant richness, honey bee density and floral resource diversity were excluded. An ANOVA tested the differences in spatio-temporal variables across seasonal periods. Interaction effects between each static and dynamic variable were included. Quadratic terms were added to capture potential non-linear relationships, based on visual inspection of scatter plots indicating curvilinear patterns. We included 'site' as a random effect term to account for the repeated sampling in the study landscapes. Continuous explanatory variables were *z*-transformed (mean of zero, standard deviation of one) to facilitate comparison of coefficient estimates. All model assumptions were tested following Zuur et al. (2010), and models were checked for multicollinearity and outliers using the 'performance' package (Lüdecke et al., 2021). The final model for each network metric and richness value was selected from a global model using the 'dredge' function from 'MuMIn' (Bartoń, 2026), ranking models by the lowest Akaike information criterion (AIC). Included terms were limited to eight to avoid overfitting. Coefficients were averaged across the subset of models whose cumulative AIC weights summed to 95% ('model.avg' in 'MuMIn'), and the relative importance of variables was calculated as the summed AIC weights (ω_i) (Giam & Olden, 2016).

3 | RESULTS

3.1 | Plant–pollinator networks

The 36 landscape-scale networks contained 195 pollinator and 173 plant species (Figure S1, Table S3). We observed 2846 interactions of 1092 unique links, varying considerably among each landscape and seasonal period (range = 13–186 interactions) (Figure S2, Table S4).

3.2 | Influence of landscape characteristics on network structure

While both spatio-temporally dynamic and spatially static factors were important, dynamic variables generally had a greater impact on network structure (Figure 3, variation of landscape characteristic in Table S5). The strongest influence was from mass-flowering crops, appearing in all top models with the highest relative importance ($\omega_i = 0.97–1$). High cover of mass-flowering crops was negatively related to plant and pollinator richness, and H2′ network specialization, and positively related to connectance and niche overlap of pollinators (Figure 4). We found positive relationships edge density and both pollinator richness ($\omega_i = 0.65$, Figure 5a) and plant richness ($\omega_i = 0.22$, Figure 5d). The proportion of semi-natural habitat cover ($\omega_i = 0.38$, Figure 5b) and floral diversity ($\omega_i = 0.28$, Figure 5c) showed a negative correlation with pollinator richness, whereas plant richness was positively influenced by the proportion of semi-natural habitat cover ($\omega_i = 0.24$, Figure 5e). In contrast, edge density showed a hump-shaped relationship with connectance ($\omega_i = 0.46$, Figure 6a), peaking at intermediate levels, and was slightly negatively related to niche overlap ($\omega_i = 0.15$, Figure 6d). We did not find interactions between semi-natural habitat cover and dynamic variables. However, the proportion of semi-natural habitat

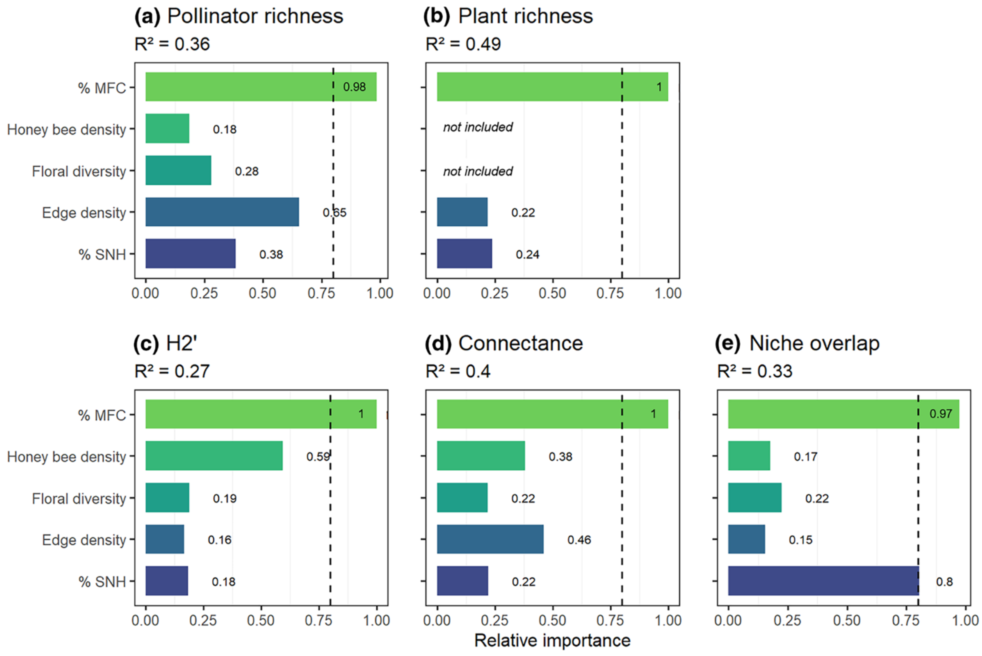


FIGURE 3 Relative importance of the landscape characteristics on plant and pollinator richness (a, b) and three plant–pollinator network metrics (c–e). The dashed line represents a conventional threshold at 0.8, identifying important variables. R^2 value of the models, including the listed variables is given. % MFC = cover of mass-flowering crops; % SNH = proportion of semi-natural habitat cover.

cover showed a hump-shaped relationship with niche overlap (ω_i=0.8, Figure 6e), and was negatively related to connectance (ω_i=0.22, Figure 6b). Floral diversity was negatively related to both connectance and niche overlap (Figure 6c,f), albeit with a relatively low importance (ω_i=0.22, 0.22). H2′ specialization was weakly negatively related with the proportion of semi-natural habitat cover (ω_i=0.18, Figure S3a) and edge density (ω_i=0.16, Figure S3c), and weakly positively related with floral diversity (ω_i=0.19, Figure S3b). Except for the positive relationship with H2′ network specialization (ω_i=0.59, Figure S4a), honey bee density generally showed weak relationships with network metrics and pollinator richness, associated with wide confidence intervals, and appeared to be strongly influenced by three data points (Figure S4). Although formal tests indicated that these points were not statistical outliers, their leverage suggests that the overall effect of honey bee density should be interpreted with caution (additional analysis of variation partitioning in Table S6).

4 | DISCUSSION

Our study revealed that spatio-temporal dynamics in floral resource density and diversity have a predominant influence on the structure of plant–pollinator networks across seasonal periods compared to the effects of spatially static landscape characteristics.

In accord with our hypothesis (Hi), we found that high cover of mass-flowering crops produced smaller networks (lower plant and pollinator richness) with greater network connectance and pollinator niche overlap, whereas network specialization decreased. Previous studies have shown that mass-flowering crops particularly attract and benefit generalist pollinators (Magrach et al., 2018), such as bumblebees (Westphal et al., 2003) and mason bees (Holzschuh et al., 2013), and can affect the overall functional composition of pollinators (Beyer et al., 2021). Our results suggest that in landscapes with high cover of mass-flowering crops (dominated by oilseed rape in our case), the attraction of generalist and often highly competitive pollinators may reduce competition among species. This concentration of generalists on mass-flowering crops leads to highly connected networks, which may increase redundancy among pollinator species and potentially community robustness to coextinctions (Dunne et al., 2002, but see Vieira & Almeida-Neto, 2015). However, the concurrent reduction in plant and pollinator richness during mass-flowering events also indicates a simplification of landscape-scale interaction networks. Therefore, while high mass-flowering crop cover may produce more robust networks, it does not necessarily promote species conservation.

The spatio-temporal sequence of flowering of different crops can be facilitative or competitive in terms of pollination services (Grab et al., 2017). However, aside from their short-term beneficial effects on certain species groups, mass-flowering crops can also contribute to the dilution of pollinators at the landscape scale (Holzschuh et al., 2016), potentially leading to a decrease in pollination function for other crops and wild flowering plants. This aligns with the need to maintain landscape-scale habitat diversity to support diverse pollinator communities (Maurer et al., 2022) and to implement temporally complementary measures to sustain pollinators and plants in landscapes dominated by mass-flowering crops (von Königslöw et al., 2022). Altogether, our results indicate that mass-flowering

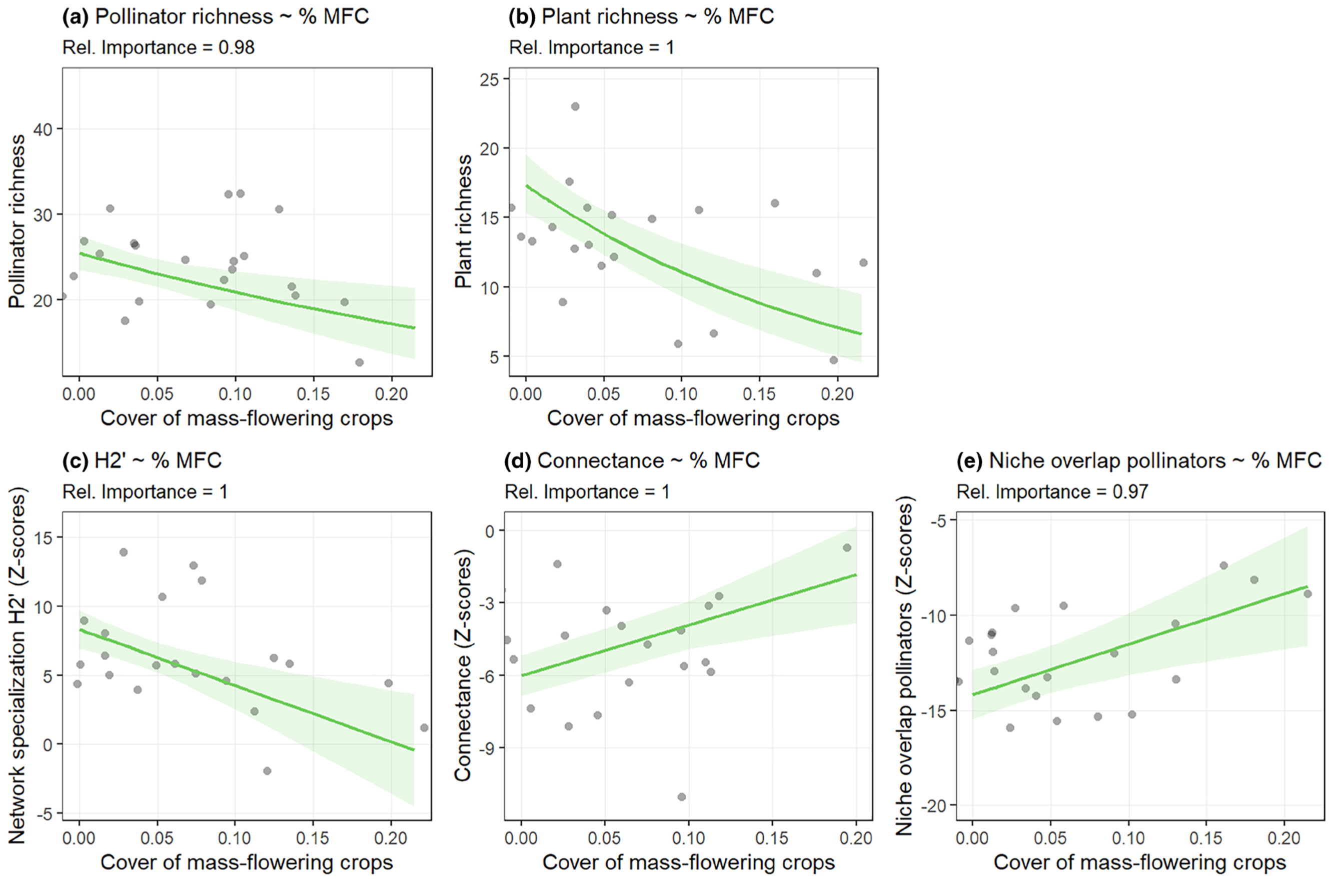
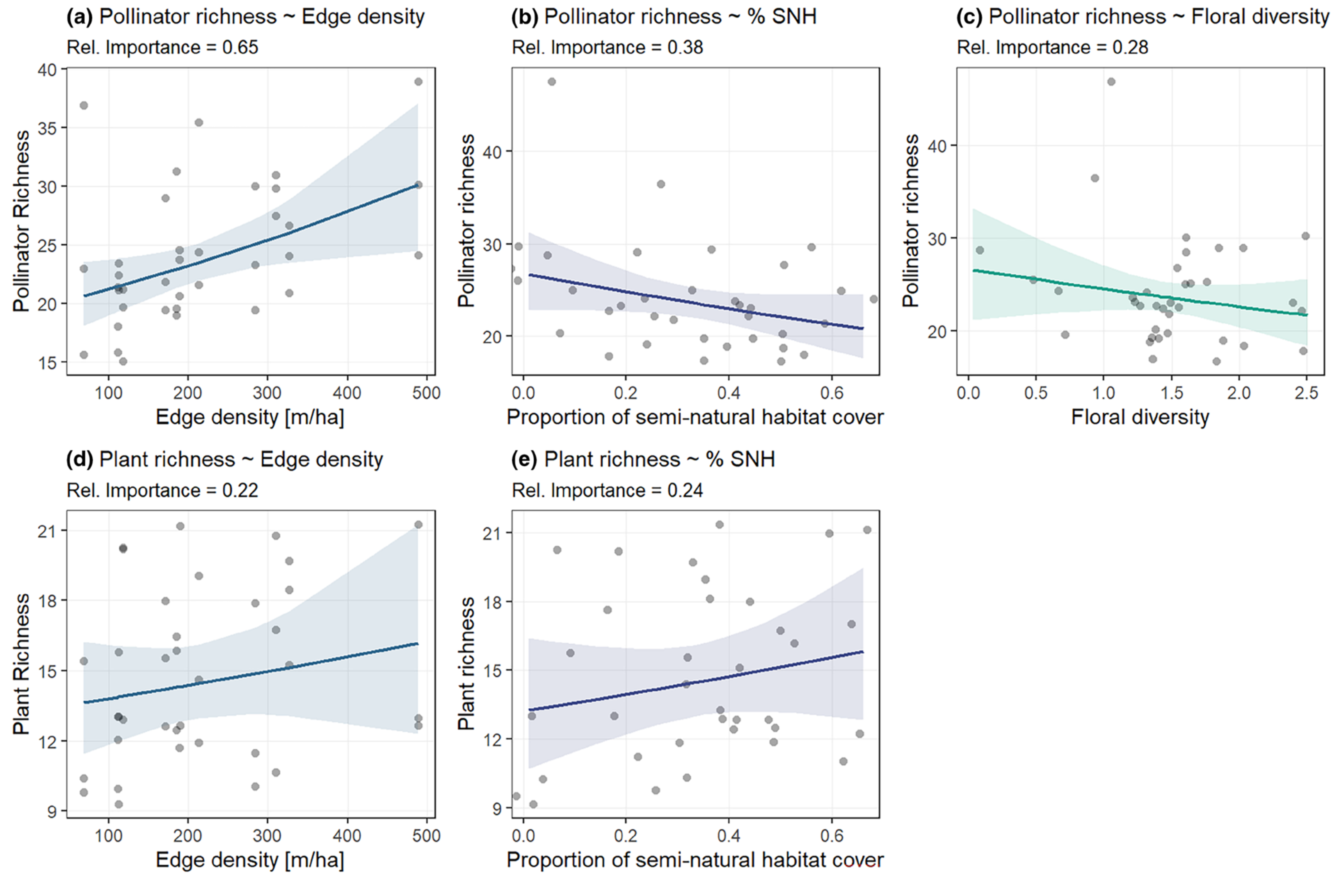


FIGURE 4 Effects of the cover of mass-flowering crops (% MFC) on richness (a, b) and three network metrics (c–e). Plots display partial residuals and model predictions with respective 95% confidence intervals (light green bands). Relative importance ('Rel. Importance') was calculated as the sum of Akaike (AIC) weights (ω_i) of all models including the respective covariate, within a multimodel inference approach, considering the subset of models with a cumulative AIC weight of 95%.

crops can lead to less complex yet more robust networks, emphasizing the need to mitigate network simplification through complementary management approaches.

We did not find interacting effects of dynamic and static landscape characteristics in our models contrary to our expectation (Hiv). However, we found counteracting effects for example of edge density on network specialization and richness of plants and pollinators compared to the negative influence of the proportion of mass-flowering crops. This might suggest that landscape structural properties can provide a certain level of compensation for plant–pollinator networks pressured in landscapes with high cover of mass-flowering crops. While increased pollination specialization has been shown to benefit plants through higher flower constancy and reduced heterospecific pollen deposition (Labonté et al., 2023; Valdovinos et al., 2013), others indicate that greater network specialization may increase the vulnerability of specialized interactions, making them more susceptible to disruption (Blüthgen et al., 2006). This may negatively affect the pollination of wild plants during the bloom of mass-flowering crops such as oilseed rape (Holzschuh et al., 2011). Furthermore, after mass-flowering events end, an increase in generalist pollinators may exacerbate competition for wild flowers, as these generalists return to the semi-natural flowering habitats. Similarly, González-Varo and Vilà (2017) observed an increase in honey bee density in semi-natural habitat areas following mass-flowering blooms. While wild plants could benefit from the increased densities of pollinators, there could be an increase in interspecific competition among pollinators, potentially leading to niche partitioning (Gómez-Martínez et al., 2022). To counteract these potential risks, increasing landscape configuration, such as edge density, can provide stabilizing effects. Such improvements can be achieved by maintaining small field sizes where they still occur, establishing structural landscape elements such as hedgerows, and managing edge habitats to support both plants and pollinators in intensively used agricultural landscapes. All these measures will contribute to meet the requirements of the European Nature Restoration Regulation (Regulation (EU), 2024/1991).

High floral diversity and a high proportion of semi-natural habitat cover reduced niche overlap of pollinators as we hypothesized (Hii). However, the hump-shaped effect of the proportion of semi-natural habitat cover might suggest that niche differentiation occurs both at low and high levels of proportion of semi-natural habitat cover, potentially due to either very strong or reduced competition for floral resources and habitat. We found a negative effect of the proportion of semi-natural habitat cover and of floral


(a) Pollinator richness ~ Edge density
Rel. Importance = 0.65

(b) Pollinator richness ~ % SNH
Rel. Importance = 0.38

(c) Pollinator richness ~ Floral diversity
Rel. Importance = 0.28

(d) Plant richness ~ Edge density
Rel. Importance = 0.22

(e) Plant richness ~ % SNH
Rel. Importance = 0.24

FIGURE 5 Effects of edge density and proportion of semi-natural habitat cover (% SNH) on pollinator richness (a, b) and plant richness (d, e), and the effect of floral diversity on pollinator richness (c). Plots display partial residuals and model predictions with 95% confidence intervals. Relative importance ('Rel. Importance') was calculated as the sum of Akaike (AIC) weights (ω_i) of all models including the respective covariate within a multimodel inference approach, considering the subset of models with a cumulative AIC weight of 95%.

diversity on pollinator richness in contrast to previously published research (e.g. Cole et al., 2017). In our study, this unexpected result could stem from dilution of pollinator species in landscapes with high proportion of semi-natural habitat and increased niche partitioning, indicating that the average number of pollinator species visiting a flower decreases with increased cover of semi-natural habitat and floral diversity (Wenninger et al., 2016). Landscapes with low semi-natural habitat cover had higher pollinator richness but low plant richness, as expected by the species–area relationship, resulting in a high ratio of pollinator per plant species. In these conditions, pollinators might increase their diet breadth, potentially across sub-optimal floral resources due to resource limitation. The relatively high network connectance might reflect these patterns. Although, the presence of potential competition-avoidance mechanisms is indicated by low niche overlap, which is driven by interaction frequency. As the proportion of semi-natural habitat increases, floral richness rises relative to pollinator richness, reducing the number of pollinators per plant species. This may relax resource competition, allowing greater niche overlap without the need to exploit sub-optimal floral resources, consistent with the observed decrease in connectance. At very high levels of semi-natural habitat (>40%), the number of pollinators per plant species becomes sufficiently low that pollinators can largely forage on preferred plant species. This pattern is reflected in low network connectance and a corresponding decline in niche overlap.

While our results regarding the impact of honey bee density on the network structure (Hiii) remain inconclusive, we observed that honey bee density peaked in the second seasonal period (Figure 2d) after the flowering of oilseed rape (Figure 2e). This likely drove honey bees to forage in semi-natural habitats, which in turn may have led other pollinators to narrow their dietary niches. Previous studies have shown that competitive effects of honey bees negatively affect wild bee populations (Lindström et al., 2016; Weaver et al., 2022) and that the provision of continuous, diverse floral resources can promote niche differentiation of managed and wild bee populations (Bernhardsson et al., 2024).

Studies considering an inter-annual temporal scale have shown that pollination network metrics are relatively constant across years, although the number and identity of interactions and nodes may be highly variable (Petanidou et al., 2008; Resasco et al., 2021). We chose a within season time scale because crop cycles in central European agricultural systems are primarily composed of annual crops. However, including legacy effects of crop rotations,

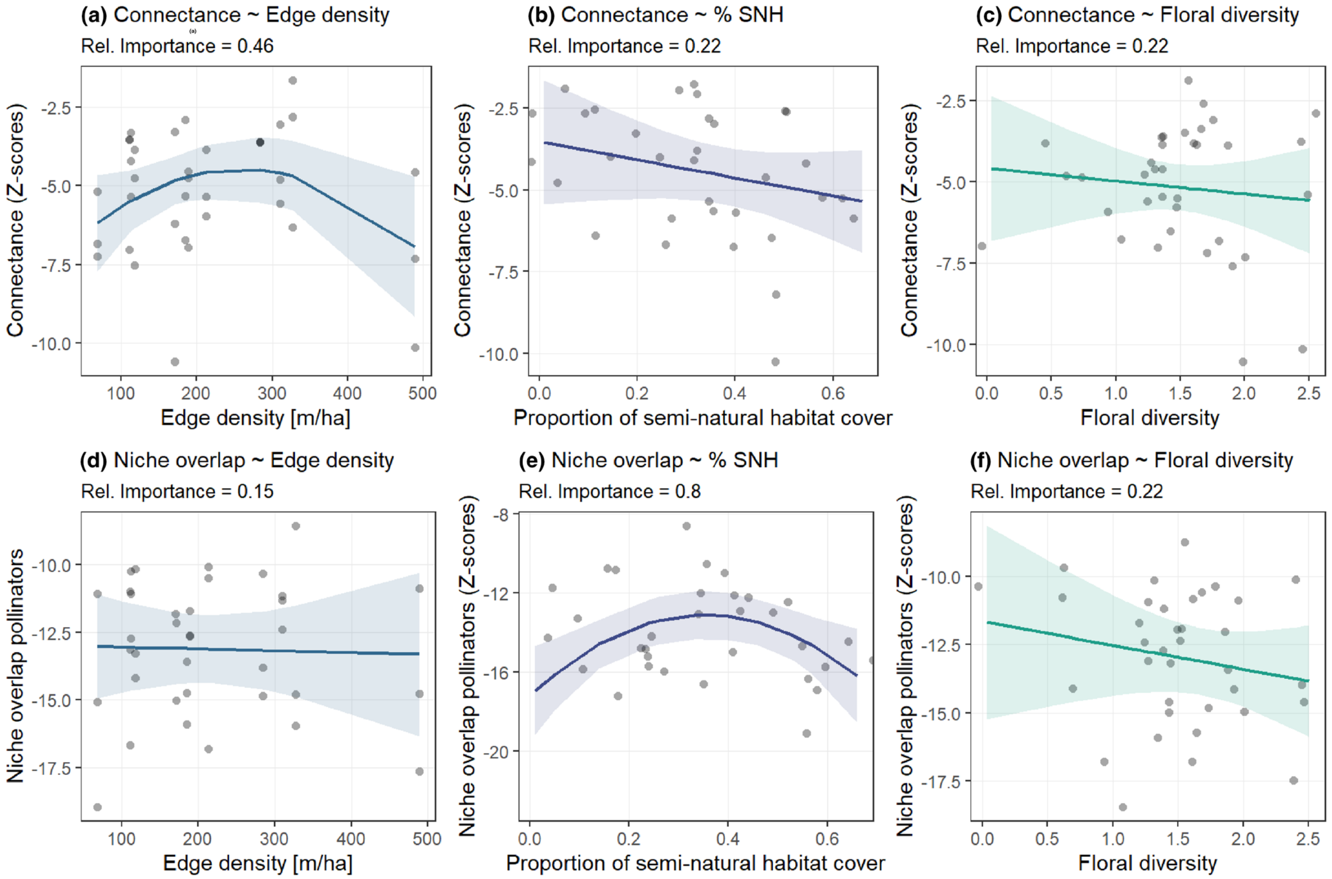


FIGURE 6 Effects of edge density, proportion of semi-natural habitat cover (% SNH), and floral diversity on connectance (a–c) and niche overlap of pollinators (d–f). Plots display partial residuals and model predictions with 95% confidence intervals. Relative importance ("Rel. Importance") was calculated as the sum of Akaike (AIC) weights (ω_i) of all models including the respective covariate, within a multimodel inference approach, considering the subset of models with a cumulative AIC weight of 95%.

such as pesticide applications, general turn-over of biomass and soil disturbances, might help identify important drivers of interaction networks (Raderschall et al., 2022). Therefore, future research combining intra- and inter-annual variability to fully understand the spatio-temporal dimensions of plant–pollinator network interactions is needed.

4.1 | Management and policy implications

To better support robust and diverse plant–pollinator communities and networks, avoid potential negative effects of competition and increase the sustainable provision of pollination in agricultural-dominated landscapes via increased functional redundancy, we make the following recommendations. To mitigate fluctuations from short-term mass-flowering crops, policies should incentivize plantings providing diverse and continuous complementary floral resources, and conserve semi-natural habitats in agricultural landscapes. Measures to increase the diversity and amount of pollinator-friendly habitats will also support managed bees (Decourtye et al., 2010), while minimizing the risk of interspecific competition. For instance, an increase of floral diversity by one unit (1–2 Shannon diversity) decreased potentially competitive shared use of floral resources by ~7%. Additionally, edge density can partly compensate negative effects of mass-flowering crops on network structure, which underscores the role of landscape configuration in influencing plant and pollinator richness and their network properties, potentially affecting pollination dynamics. For example, a threefold increase in edge density increased the diversity of the pollinator community by ~20% (Figure 5a) and of plants by ~8.5% (Figure 5b). While a reduction in the proportional cover of mass-flowering crops by 5% increased the number of pollinator species in the network by ~10% (Figure 4a) and of plants by ~20% (Figure 4b). Niche overlap of pollinators decreased by ~10% with a reduction of the proportional cover of mass-flowering crops (Figure 4e). Incentives to maintain small field sizes and restoration and maintenance of flower-rich green infrastructure are recommended and coherent with the European Nature Restoration Regulation objectives to protect and restore agroecosystems and pollinator habitats (Regulation (EU), 2024/1991, art. 10).

Landscape-scale management approaches that consider both the spatial and temporal dynamics of plant–pollinator community interactions are essential to transform intensive agricultural landscapes from a major pressure on pollinators into a positive force for restoring pollination as an integral part of healthy agroecosystems.

AUTHOR CONTRIBUTIONS

All authors contributed to the study conception and design. Field work and data collection were conducted by Jonna M. Heuschele and Yicong Liu. Data preparation and analysis were performed by Jonna M. Heuschele and Oliver Schweiger. The first draft of the manuscript was written by Jonna M. Heuschele. Oliver Schweiger, Matthias Albrecht, Marìa R. Felipe-Lucia, Hanna Honchar, Yicong Liu, Martin Musche, Robert J. Paxton, Josef Settele, Hajnalka Szentgyörgyi, Adam J. Vanbergen, Tesfaye Wubet, and Christophe Dominik commented on subsequent versions of the manuscript. All authors read and approved the final manuscript.

ACKNOWLEDGEMENTS

We thank Frank Creutzburger (wild bees) and Walter Durka (plants) for their help with the morpho-species identification of indicated species groups. We thank Anja Manigk, Henriette Kühnert, and Karima Bassit for DNA-barcoding cryptic bee species. Open Access funding enabled and organized by Projekt DEAL.

FUNDING INFORMATION

This work was carried out within the framework of the UFZ PhD consortium INTERCEDE. JMH and MFL gratefully acknowledge the support of iDiv funded by the Deutsche Forschungsgemeinschaft (DFG–FZT 118, 202548816). MFL acknowledges that her current contract is part of the RYC2021-032828-I grant, financed by MCIN/AEI/10.13039/501100011033 and by the European Union 'NextGenerationEU'/PRTR. This is an output of the Biodiversa project VOODOO (Viral eco-evolutionary dynamics of wild and domestic pollinators under global change, www.voodoo-project.eu) and its funders in Switzerland: SNSF 31BD30_186532/1, France: ANR-19-EBI3-0006, Germany: Pa623/12 and Poland: NCN UMO-2019/32/Z/NZ8/00006. German Research Foundation (DFG) PA 623/10-1, PA 623/12-1 (RP) and the Federal Ministry of Education and Research (BMBF) and German Aerospace Research and Technology Centre (as executing organization), grant no. 01LC1905A (OS).

CONFLICT OF INTEREST STATEMENT

The authors have no relevant financial or non-financial interests to disclose.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.9s4mw6mxm (Heuschele et al., 2026).

ORCID

Jonna M. Heuschele https://orcid.org/0009-0005-3242-9412
Matthias Albrecht https://orcid.org/0000-0001-5518-3455
Yicong Liu https://orcid.org/0009-0003-2573-8132
Hajnalka Szentgyörgyi https://orcid.org/0000-0002-5753-800X
Christophe Dominik https://orcid.org/0000-0001-6310-1632

REFERENCES

Aizen, M. A., Aguiar, S., Biesmeijer, J. C., Garibaldi, L. A., Inouye, D. W., Jung, C., Martins, D. J., Medel, R., Morales, C. L., Ngo, H., Pauw, A., Paxton, R. J., Sáez, A., & Seymour, C. L. (2019). Global agricultural productivity is threatened by increasing pollinator dependence without a parallel increase in crop diversification. *Global Change Biology*, *25*(10), 3516–3527. https://doi.org/10.1111/gcb.14736

Ammann, L., Bosem-Baillod, A., Herzog, F., Frey, D., Entling, M. H., & Albrecht, M. (2024). Spatio-temporal complementarity of floral resources sustains wild bee pollinators in agricultural landscapes. *Agriculture, Ecosystems & Environment*, *359*, 108754. https://doi.org/10.1016/j.agee.2023.108754

Bartoń, K. (2026). MuMIn: Multi-model inference. R package version 1.48.11. https://CRAN.R-project.org/package=MuMIn

Bascompte, J., & Jordano, P. (2007). Plant-animal mutualistic networks: The architecture of biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, *38*(1), 567–593. https://doi.org/10.1146/annurev.ecolsys.38.091206.095818

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Bernhardsson, O., Kendall, L., Olsson, O., Olsson, P., & Smith, H. G. (2024). Shared use of a mass-flowering crop drives dietary niche overlap between managed honeybees and bumblebees. *Journal of Applied Ecology*, *61*(9), 2135–2145. https://doi.org/10.1111/1365-2664.14743

Beyer, N., Kirsch, F., Gabriel, D., & Westphal, C. (2021). Identity of mass-flowering crops moderates functional trait composition of pollinator communities. *Landscape Ecology*, *36*(9), 2657–2671. https://doi.org/10.1007/s10980-021-01261-3

Biggs, C. R., Yeager, L. A., Bolser, D. G., Bonsell, C., Dichiera, A. M., Hou, Z., Keyser, S. R., Khursigara, A. J., Lu, K., Muth, A. F., Negrete, B., Jr., & Erisman, B. E. (2020). Does functional redundancy affect ecological stability and resilience? A review and meta-analysis. *Ecosphere*, *11*(7), e03184. https://doi.org/10.1002/ecs2.3184

Blüthgen, N., Menzel, F., & Blüthgen, N. (2006). Measuring specialization in species interaction networks. *BMC Ecology*, *6*, 9. https://doi.org/10.1186/1472-6785-6-9

Blüthgen, N., & Klein, A.-M. (2011). Functional complementarity and specialisation: The role of biodiversity in plant–pollinator interactions. *Basic and Applied Ecology*, *12*(4), 282–291. https://doi.org/10.1016/j.baae.2010.11.001

Blüthgen, N., & Staab, M. (2024). A critical evaluation of network approaches for studying species interactions. *Annual Review of Ecology, Evolution, and Systematics*, *55*(2024), 65–88. https://doi.org/10.1146/annurev-ecolsys-102722-021904

Bretagnolle, V., & Gaba, S. (2015). Weeds for bees? A review. *Agronomy for Sustainable Development*, *35*(3), 891–909. https://doi.org/10.1007/s13593-015-0302-5

CaraDonna, P. J., Burkle, L. A., Schwarz, B., Resasco, J., Knight, T. M., Benadi, G., Blüthgen, N. [. N.]., Dormann, C. F., Fang, Q., Fründ, J., Gauzens, B., Kaiser-Bunbury, C. N., Winfree, R., & Vázquez, D. P. (2021). Seeing through the static: The temporal dimension of plant-animal mutualistic interactions. *Ecology Letters*, *24*(1), 149–161. https://doi.org/10.1111/ele.13623

Chakraborty, P., Chatterjee, S., Smith, B. M., & Basu, P. (2021). Seasonal dynamics of plant pollinator networks in agricultural landscapes: How important is connector species identity in the network? *Oecologia*, *196*(3), 825–837. https://doi.org/10.1007/s00442-021-04975-y

Cole, L. J., Brocklehurst, S., Robertson, D., Harrison, W., & McCracken, D. I. (2017). Exploring the interactions between resource availability and the utilisation of semi-natural habitats by insect pollinators in an intensive agricultural landscape. *Agriculture, Ecosystems & Environment*, *246*, 157–167. https://doi.org/10.1016/j.agee.2017.05.007

Cusser, S., Neff, J. L., & Jha, S. (2019). Landscape context differentially drives diet breadth for two key pollinator species. *Oecologia*, *191*(4), 873–886. https://doi.org/10.1007/s00442-019-04543-5

Decourtye, A., Mader, E., & Desneux, N. (2010). Landscape enhancement of floral resources for honey bees in agro-ecosystems. *Apidologie*, *41*(3), 264–277. https://doi.org/10.1051/apido/2010024

Dormann, C. F., Gruber, B., & Fründ, J. (2008). Introducing the bipartite package: Analysing ecological networks. *R News*, *8*(2), 8–11.

Doyle, T., Hawkes, W. L. S., Massy, R., Powney, G. D., Menz, M. H. M., & Wotton, K. R. (2020). Pollination by hoverflies in the Anthropocene. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1927), 20200508. https://doi.org/10.1098/rspb.2020.0508

Dunne, J. A., Williams, R. J., & Martinez, N. D. (2002). Network structure and biodiversity loss in food webs: Robustness increases with connectance. *Ecology Letters*, *5*(4), 558–567. https://doi.org/10.1046/j.1461-0248.2002.00354.x

Ebeling, A., Klein, A.-M., & Tscharntke, T. (2011). Plant–flower visitor interaction webs: Temporal stability and pollinator specialization increases along an experimental plant diversity gradient. *Basic and Applied Ecology*, *12*(4), 300–309. https://doi.org/10.1016/j.baae.2011.04.005

ESRI. (2012). ArcGIS Pro (Version 3.1) [Computer software].

European Environment Agency (EEA). (2012). EUNIS habitat classification. https://eunis.eea.europa.eu/habitats.jsp

Eurostat. (2025). Land cover statistics. https://ec.europa.eu/eurostat/statistics-explained/index.php?title=Land_cover_statistics#Land_cover_in_EU_countries

Fahrig, L., Baudry, J., Brotons, L., Burel, F. G., Crist, T. O., Fuller, R. J., Sirami, C., Siriwardena, G. M., & Martin, J.-L. (2011). Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology Letters*, *14*(2), 101–112. https://doi.org/10.1111/j.1461-0248.2010.01559.x

Giam, X., & Olden, J. D. (2016). Quantifying variable importance in a multimodel inference framework. *Methods in Ecology and Evolution*, *7*(4), 388–397. https://doi.org/10.1111/2041-210X.12492

Gómez-Martínez, C., González-Estévez, M. A., Cursach, J., & Lázaro, A. (2022). Pollinator richness, pollination networks, and diet adjustment along local and landscape gradients of resource diversity. *Ecological Applications*, *32*(6), e2634. https://doi.org/10.1002/eap.2634

González-Varo, J. P., & Vilà, M. (2017). Spillover of managed honeybees from mass-flowering crops into natural habitats. *Biological Conservation*, *212*, 376–382. https://doi.org/10.1016/j.biocon.2017.06.018

Grab, H., Blitzer, E. J., Danforth, B., Loeb, G., & Poveda, K. (2017). Temporally dependent pollinator competition and facilitation with mass flowering crops affects yield in co-blooming crops. *Scientific Reports*, *7*, 45296. https://doi.org/10.1038/srep45296

Hadrava, J., Talašová, A., Straka, J., Benda, D., Kazda, J., & Klečka, J. (2022). A comparison of wild bee communities in sown flower strips and semi-natural habitats: A pollination network approach. *Insect Conservation and Diversity*, *15*(3), 312–324. https://doi.org/10.1111/icad.12565

Hesselbarth, M. H., Sciaini, M., With, K. A., Wiegand, K., & Nowosad, J. (2019). Landscapemetrics: An open-source R tool to calculate landscape metrics. *Ecography*, *42*, 1648–1657. (v1.5.4).

Heuschele, J. M., Schweiger, O., Albrecht, M., Felipe-Lucia, M. R., Honchar, H., Liu, Y., Musche, M., Paxton, R. J., Settele, J., Szentgyörgyi, H., Vanbergen, A. J., Wubet, T., & Dominik, C. (2026). Seasonal mass-flowering events dominate landscape effects on plant-pollinator network structure [dataset]. *Dryad*. https://doi.org/10.5061/dryad.9s4mw6mxm

Holzschuh, A., Dainese, M., González-Varo, J. P., Mudri-Stojnić, S., Riedinger, V., Rundlöf, M., Scheper, J., Wickens, J. B., Wickens, V. J., Bommarco, R., Kleijn, D., Potts, S. G., Roberts, S. P. M., Smith, H. G., Vilà, M., Vujić, A., & Steffan-Dewenter, I. (2016). Mass-flowering crops dilute pollinator abundance in agricultural landscapes across Europe. *Ecology Letters*, *19*(10), 1228–1236. https://doi.org/10.1111/ele.12657

Holzschuh, A., Dormann, C. F., Tscharntke, T., & Steffan-Dewenter, I. (2011). Expansion of mass-flowering crops leads to transient pollinator dilution and reduced wild plant pollination. *Proceedings. Biological sciences*, *278*(1723), 3444–3451. https://doi.org/10.1098/rspb.2011.0268

Holzschuh, A., Dormann, C. F., Tscharntke, T., & Steffan-Dewenter, I. (2013). Mass-flowering crops enhance wild bee abundance. *Oecologia*, *172*(2), 477–484. https://doi.org/10.1007/s00442-012-2515-5

Klein, A.-M., Boreux, V., Fornoff, F., Mupepele, A.-C., & Pufal, G. (2018). Relevance of wild and managed bees for human well-being. *Current Opinion in Insect Science*, *26*, 82–88. https://doi.org/10.1016/j.cois.2018.02.011

Kovács-Hostyánszki, A., Li, J., Pettis, J., Settele, J., Aneni, T., Espíndola, A., Kahono, S., Szentgyörgyi, H., Thompson, H., Vanbergen, A., & Vandame, R. (2017). Drivers of change of pollinators, pollination networks and pollination. In S. G. Potts, V. Imperatriz-Fonseca, & H. T. Ngo (Eds.), *The assessment report on pollinators, pollination and food production of the intergovernmental science-policy platform on biodiversity and ecosystem services* (pp. 27–149). Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES).

Labonté, A., Monticelli, L. S., Turpin, M., Felten, E., Laurent, E., Matejicek, A., Biju-Duval, L., Ducourtieux, C., Vieren, E., Deytieux, V., Cordeau, S., Bohan, D., & Vanbergen, A. J. (2023). Individual flowering phenology shapes plant–pollinator interactions across ecological scales affecting plant reproduction. *Ecology and Evolution*, *13*(1), e9707. https://doi.org/10.1002/ece3.9707

Lindström, S. A. M., Herbertsson, L., Rundlöf, M., Bommarco, R., & Smith, H. G. (2016). Experimental evidence that honeybees depress wild insect densities in a flowering crop. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1843), 20161641. https://doi.org/10.1098/rspb.2016.1641

Lüdecke, D., Ben-Shachar, M., Patil, I., Waggoner, P., & Makowski, D. (2021). Performance: An R package for assessment, comparison and testing of statistical models. *The Journal of Open Source Software*, *6*(60), 3139. https://doi.org/10.21105/joss.03139

Mäder, P., Boho, D., Rzanny, M., Seeland, M., Wittich, H. C., Deggelmann, A., & Wäldchen, J. (2021). The Flora incognita app—Interactive plant species identification. *Methods in Ecology and Evolution*, *12*(7), 1335–1342. https://doi.org/10.1111/2041-210X.13611

Magrach, A., Holzschuh, A., Bartomeus, I., Riedinger, V., Roberts, S. P. M., Rundlöf, M., Vujić, A., Wickens, J. B., Wickens, V. J., Bommarco, R., González-Varo, J. P., Potts, S. G., Smith, H. G., Steffan-Dewenter, I., & Vilà, M. (2018). Plant-pollinator networks in semi-natural grasslands are resistant to the loss of pollinators during blooming of mass-flowering crops. *Ecography*, *41*(1), 62–74. https://doi.org/10.1111/ecog.02847

Mallinger, R. E., Gibbs, J., & Gratton, C. (2016). Diverse landscapes have a higher abundance and species richness of spring wild bees by providing complementary floral resources over bees' foraging periods. *Landscape Ecology*, *31*(7), 1523–1535. https://doi.org/10.1007/s10980-015-0332-z

Maurer, C., Sutter, L., Martínez-Núñez, C., Pellissier, L., & Albrecht, M. (2022). Different types of semi-natural habitat are required to sustain diverse wild bee communities across agricultural landscapes. *Journal of Applied Ecology*, *59*(10), 2604–2615. https://doi.org/10.1111/1365-2664.14260

Moreira, E. F., Boscolo, D., & Viana, B. F. (2015). Spatial heterogeneity regulates plant-pollinator networks across multiple landscape scales. *PLoS One*, *10*(4), e0123628. https://doi.org/10.1371/journal.pone.0123628

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens,

M. H. H., Szoecs, E., & Wagner, H. (2020). *vegan* (v2.5-7) [computer software]. https://CRAN.R-project.org/package=vegan

Patefield, W. M. (1981). Algorithm AS 159: An efficient method of generating random R × C tables with given row and column totals. *Applied Statistics*, *30*(1), 91–97. https://doi.org/10.2307/2346669

Petanidou, T., Kallimanis, A. S., Tzanopoulos, J., Sgardelis, S. P., & Pantis, J. D. (2008). Long-term observation of a pollination network: Fluctuation in species and interactions, relative invariance of network structure and implications for estimates of specialization. *Ecology Letters*, *11*(6), 564–575. https://doi.org/10.1111/j.1461-0248.2008.01170.x

Phillips, B. B., Wallace, C., Roberts, B. R., Whitehouse, A. T., Gaston, K. J., Bullock, J. M., Dicks, L. V., & Osborne, J. L. (2020). Enhancing road verges to aid pollinator conservation: A review. *Biological Conservation*, *250*, 108687. https://doi.org/10.1016/j.biocon.2020.108687

Potts, S. G., Imperatriz-Fonseca, V., Ngo, H. T., Aizen, M. A., Biesmeijer, J. C., Breeze, T. D., Dicks, L. V., Garibaldi, L. A., Hill, R., Settele, J., & Vanbergen, A. J. (2016). Safeguarding pollinators and their values to human well-being. *Nature*, *540*(7632), 220–229. https://doi.org/10.1038/nature20588

R Core Team. (2022). *R: A language and environment for statistical computing [computer software]*. R Foundation for Statistical Computing. https://www.R-project.org/

Raderschall, C. A., Lundin, O., Aguilera, G., Lindström, S. A., & Bommarco, R. (2022). Legacy of landscape crop diversity enhances carabid beetle species richness and promotes granivores. *Agriculture, Ecosystems & Environment*, *340*, 108191. https://doi.org/10.1016/j.agee.2022.108191

Regulation (EU). (2024). 2024/1991 of the European Parliament and of the Council of 24 June 2024 on Nature Restoration and Amending Regulation (EU) 2022/869 (Text with EEA Relevance). http://data.europa.eu/eli/reg/2024/1991/oj/eng

Resasco, J., Chacoff, N., & Vázquez, D. (2021). Persistence of plant–pollinator interactions in time and space. *Ecology*, *102*(6), e03359. https://doi.org/10.1002/ecy.3359

Riggi, L. G. A., Raderschall, C. A., Fijen, T. P. M., Scheper, J., Smith, H. G., Kleijn, D., Holzschuh, A., Aguilera, G., Badenhausser, I., Bänsch, S., Beyer, N., Blitzer, E. J., Bommarco, R., Danforth, B., González-Varo, J. P., Grab, H., Le Provost, G., Poveda, K., Potts, S. G., … Lundin, O. (2023). Early-season mass-flowering crop cover dilutes wild bee abundance and species richness in temperate regions: A quantitative synthesis. *Journal of Applied Ecology*, *61*(3), 452–464. https://doi.org/10.1111/1365-2664.14566

Souza, C. S., Maruyama, P. K., Aoki, C., Sigrist, M. R., Raizer, J., Gross, C. L., & de Araujo, A. C. (2018). Temporal variation in plant-pollinator networks from seasonal tropical environments: Higher specialization when resources are scarce. *Journal of Ecology*, *106*(6), 2409–2420. https://doi.org/10.1111/1365-2745.12978

Sponsler, D., Iverson, A., & Steffan-Dewenter, I. (2023). Pollinator competition and the structure of floral resources. *Ecography*, *2023*(9), e06651. https://doi.org/10.1111/ecog.06651

STALA. (2022). Wachstumsstand und Ernte: Anbaufläche und Ernte von Feldfrüchten und Grünland, Obst und Gemüse. https://statistik.sachsen-anhalt.de/fileadmin/Bibliothek/Landesaemter/StaLa/startseite/Themen/Land_und_Forstwirtschaft__Fischerei/Berichte/Wachstumsstand_und_Ernte/6C202_2021-A.pdf

Sutter, L., Jeanneret, P., Bartual, A. M., Bocci, G., & Albrecht, M. (2017). 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), 1856–1864. https://doi.org/10.1111/1365-2664.12907

Timberlake, T. P., Vaughan, I. P., & Memmott, J. (2019). Phenology of farmland floral resources reveals seasonal gaps in nectar availability for bumblebees. *Journal of Applied Ecology*, *56*(7), 1585–1596. https://doi.org/10.1111/1365-2664.13403

Tylianakis, J. M., & Morris, R. J. (2017). Ecological networks across environmental gradients. *Annual Review of Ecology, Evolution, and Systematics*, *48*(1), 25–48. https://doi.org/10.1146/annurev-ecolsys-110316-022821

Valdovinos, F. S., Moisset de Espanés, P., Flores, J. D., & Ramos-Jiliberto, R. (2013). Adaptive foraging allows the maintenance of biodiversity of pollination networks. *Oikos*, *122*(6), 907–917. https://doi.org/10.1111/j.1600-0706.2012.20830.x

Vieira, M. C., & Almeida-Neto, M. (2015). A simple stochastic model for complex coextinctions in mutualistic networks: Robustness decreases with connectance. *Ecology Letters*, *18*(2), 144–152. https://doi.org/10.1111/ele.12394

von Königslöw, V., Fornoff, F., & Klein, A.-M. (2022). Wild bee communities benefit from temporal complementarity of hedges and flower strips in apple orchards. *Journal of Applied Ecology*, *59*(11), 2814–2824. https://doi.org/10.1111/1365-2664.14277

Weaver, J. R., Ascher, J. S., & Mallinger, R. E. (2022). Effects of short-term managed honey bee deployment in a native ecosystem on wild bee foraging and plant–pollinator networks. *Insect Conservation and Diversity*, *15*(5), 634–644. https://doi.org/10.1111/icad.12594

Wenninger, A., Kim, T. N., Spiesman, B. J., & Gratton, C. (2016). Contrasting foraging patterns: Testing resource-concentration and dilution effects with pollinators and seed predators. *Insects*, *7*(2), 23. https://doi.org/10.3390/insects7020023

Westphal, C., Steffan-Dewenter, I., & Tscharntke, T. (2003). Mass flowering crops enhance pollinator densities at a landscape scale. *Ecology Letters*, *6*(11), 961–965. https://doi.org/10.1046/j.1461-0248.2003.00523.x

Winfree, R., & Kremen, C. (2009). Are ecosystem services stabilized by differences among species? A test using crop pollination. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1655), 229–237. https://doi.org/10.1098/rspb.2008.0709

Woodcock, B. A., Garratt, M. P. D., Powney, G. D., Shaw, R. F., Osborne, J. L., Soroka, J., Lindström, S. A. M., Stanley, D., Ouvrard, P., Edwards, M. E., Jauker, F., McCracken, M. E., Zou, Y., Potts, S. G., Rundlöf, M., Noriega, J. A., Greenop, A., Smith, H. G., Bommarco, R., … Pywell, R. F. (2019). Meta-analysis reveals that pollinator functional diversity and abundance enhance crop pollination and yield. *Nature Communications*, *10*(1), 1481. https://doi.org/10.1038/s41467-019-09393-6

Worthy, S. H., Acorn, J. H., & Frost, C. M. (2023). Honey bees (*Apis mellifera*) modify plant-pollinator network structure, but do not alter wild species' interactions. *PLoS One*, *18*(7), e0287332. https://doi.org/10.1371/journal.pone.0287332

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, *1*(1), 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Ecological dimensions of plant–pollinator interaction networks.

Table S2. List of proportions of crop types at the 12 landscapes.

Table S3. Lists of all recorded pollinator and plant species.

Table S4. Plant–pollinator network metrics across three seasonal periods.

Table S5. Characteristics of the 12 studied landscapes.

Table S6. Results of variation partitioning of honey bee density, mass-flowering crop cover, and floral diversity.

Figure S1. Plant–pollinator interaction network plots for three exemplary landscapes across the three seasonal periods (May, June–July, August).

Figure S2. Observed values of network structural properties.

Figure S3. Effect plots of modelled environmental variables and H2′ network specialization.

Figure S4. Effect plots of honey bee density and three network metrics.

How to cite this article: Heuschele, J. M., Schweiger, O., Albrecht, M., Felipe-Lucia, M. R., Honchar, H., Liu, Y., Musche, M., Paxton, R. J., Settele, J., Szentgyörgyi, H., Vanbergen, A. J., Wubet, T., & Dominik, C. (2026). Seasonal mass-flowering events dominate landscape effects on plant–pollinator network structure. *Journal of Applied Ecology*, *63*, e70377. https://doi.org/10.1111/1365-2664.70377