









RESEARCH ARTICLE

Urbanisation and agricultural intensification modulate plant–pollinator network structure and robustness

Willem Proesmans¹  | Emeline Felten¹ | Emilien Laurent¹ | Matthias Albrecht²  | Nathan Cyrille^{1,3} | Audrey Labonté¹  | Corina Maurer²  | Robert Paxton⁴  | Oliver Schweiger⁵  | Hajnalka Szentgyörgyi⁶  | Adam J. Vanbergen¹ 

¹Agroécologie, INRAE, Institut Agro, Université de Bourgogne, Université de Bourgogne Franche-Comté, Dijon, France; ²Agroscope, Agroecology and Environment, Zürich, Switzerland; ³Biogéosciences, UMR 6282 CNRS, Université de Bourgogne, Dijon, France; ⁴General Zoology, Institute of Biology, Martin Luther University Halle-Wittenberg, Halle (Saale), Germany; ⁵UFZ Helmholtz Centre for Environmental Research, Halle (Saale), Germany and ⁶Institute of Botany, Faculty of Biology, Jagiellonian University, Kraków, Poland

Correspondence

Willem Proesmans

Email: willem.proesmans@inrae.fr

Funding information

BiodivERsA 2018–2019 CALL
'BIODIVERSITY AND ITS INFLUENCE
ON ANIMAL, HUMAN, AND PLANT
HEALTH', Grant/Award Number:
ANR-19-EBI3-0006, BMBF16LC1905A,
DFGPA632/10-1,12/1, NCN
UMO-2019/32/Z/NZ8/00006 and
NSF31BD30_186532/1

Handling Editor: Alison Brody

[Correction added on 10 April 2024, after first online publication: The copyright line was changed.]

Abstract

1. Land use change is a major pressure on pollinator abundance, diversity and plant–pollinator interactions. Far less is known about how land-use alters the structure of plant–pollinator networks and their robustness to plant–pollinator coextinctions.
2. We analysed the structure of plant–pollinator networks sampled in 12 landscapes along an urbanisation and agricultural intensity gradient, from early spring to late summer 2021, and used a stochastic coextinction model to correlate plant–pollinator coextinction risk with network structure (species and network-level metrics) and landscape context.
3. Networks in intensively managed (i.e., agricultural and urban) landscapes had a lower risk of initiating a coextinction cascade, while networks in less intensively managed landscapes may be less robust. Network structure modulated the frequency and severity of coextinctions and species loss, while the strength of species interactions increased robustness.
4. Urban networks were more species rich and symmetrical due to the high diversity of ornamental plants, while intensively managed agricultural landscapes had smaller, more tightly connected and nested networks.
5. Network structure modulated the frequency of extinctions, which was decreased by greater linkage density, interaction asymmetry and interaction dependence in the networks, while once an extinction occurred, nestedness and linkage density propagated the degree of the coextinction cascade and species loss. At the species level, species strength was inversely correlated with extinction risk, implying that generalist species with a high number of interactions with specialists had the lowest extinction risk.

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2024 The Authors. *Functional Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.

6. An interplay between land-use and network structure affects community robustness to coextinctions with implications for pollination services and plant reproduction. Land-use change or other global change pressures by reorganising species interactions can alter communities and their potential functioning.

KEYWORDS

bees, bipartite networks, extinction cascade, flower visitors, land use, landscape structure, Nestedness, SCM

1 | INTRODUCTION

Urbanisation and agricultural intensification are global land-use trends impacting pollinators through modification of habitat and floral resources (Geslin et al., 2017; Vanbergen & The Insect Pollinators Initiative, 2013; Weiner et al., 2014). Intensively managed agricultural monocultures produce deficits in semi-natural habitat and floral resources supporting pollinators (Le Féon et al., 2010), only partly offset by mass-flowering crops that provide transient pulses of pollen and nectar (Riedinger et al., 2014). Limited floral resource availability and diversity reduces pollinator species richness (Baude et al., 2016), and plant-pollinator networks in intensive agricultural landscapes are structurally simple and dominated by generalist species (Redhead et al., 2018). The extent of unfavourable (artificial surfaces) and favourable (gardens, allotments, waste ground, parks, etc.) habitats in urban landscapes dictates the availability of floral and nesting resources supporting pollinators (Baldock et al., 2019; Jha & Kremen, 2013). Additionally, managed honeybees can dominate urban pollinator communities (Renner et al., 2021), influencing wild pollinator foraging and abundance (Magrath et al., 2017; Theodorou et al., 2017; Valido et al., 2019). Conversely, complex landscape mosaics of semi-natural and anthropogenic habitats support greater floral nutrient diversity, which in turn supports greater pollinator biodiversity (Jha & Kremen, 2013; Maurer et al., 2022).

Such land-use-driven heterogeneity in floral resources serves as a species filter, affecting the structure of plant-pollinator networks (e.g., nestedness and linkage density) and their potential robustness to extinction cascades (Martínez-Núñez et al., 2019; Redhead et al., 2018; Thébault & Fontaine, 2010). Generally, the intrinsic structure of plant-pollinator communities, such as the tendency for specialist species to interact with generalist species in nested interaction networks, aids species persistence (Bastolla et al., 2009; Memmott et al., 2004). However, species extinctions driven by anthropogenic pressures (Vanbergen & The Insect Pollinators Initiative, 2013) can disrupt network structure (Kaiser-Bunbury et al., 2010; Traveset et al., 2017). A species extinction can lead to multiple coextinctions through its interspecific interactions (Colwell et al., 2012; Vieira & Almeida-Neto, 2015). The risk of initiating such a coextinction

cascade and multiple species extirpations are influenced by various network structures, for example, nestedness and connectance (Thébault & Fontaine, 2010; Vanbergen et al., 2017; Vieira & Almeida-Neto, 2015). Coextinction risks may be imbalanced among plant and pollinator species (Schleuning et al., 2016; Traveset et al., 2017) according to their level of life-history dependence on mutualism (Vanbergen et al., 2017; Vieira & Almeida-Neto, 2015). For example, apomictic flowering plants (e.g., *Taraxacum* sp.), perennial ornamental plants and agricultural crops can be crucial floral resources for pollinators (Baude et al., 2016) yet do not rely on pollinators for gene flow and persistence. Generalist pollinator species may have sufficient dietary or foraging plasticity to exploit these modified floral resources (Cusser et al., 2019), while others may undergo coextinction when specific foraging plants are extirpated (Kaiser-Bunbury et al., 2010; Prendergast & Ollerton, 2021).

Although their effects on pollinator species composition and diversity are established (e.g., Le Féon et al., 2010; Morrison & Dirzo, 2020; Prendergast & Ollerton, 2021), the impacts of urbanisation and agricultural intensification on landscape-scale plant-pollinator network structure and robustness remain less understood (Baldock et al., 2019; Theodorou et al., 2017). We analysed the structure of plant-pollinator networks throughout the season along a landscape-scale gradient of urbanisation and agricultural intensification to assess the effect of species extinctions on network robustness through a Stochastic Coextinction Model (SCM). Overall, we expected that the coextinction probabilities of plant-pollinator networks would be modified by land-use type and intensity, via effects on floral nectar resources and assemblage structure at network (e.g., linkage density and nestedness) and species (e.g., centrality and species strength) levels.

Specifically, we predicted that:

1. Urban landscapes would support speciose, densely linked plant-pollinator networks dominated by generalist species (lower specialisation), while intensive agricultural landscapes contain more nested networks with fewer species and rural mosaic networks are less nested.
2. Nested networks or those dominated by generalists are expected to be more robust against coextinction cascades, while at the species level, coextinction risk was expected to be highest in more

specialised species (i.e., species with fewer links in networks) and those with obligate dependence on mutualism.

2 | METHODS

Replication statement: Scale of inference, spatial scale and number of replicates that were used for the experiment.

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Insect pollinator and plant assemblages (networks)	Landscape (1 km radius)	12 landscapes × 3 sampling periods

2.1 | Study region and replication

The study was carried out in Côte d'Or, Eastern France (Figure 1). This region is characterised by a temperate oceanic climate

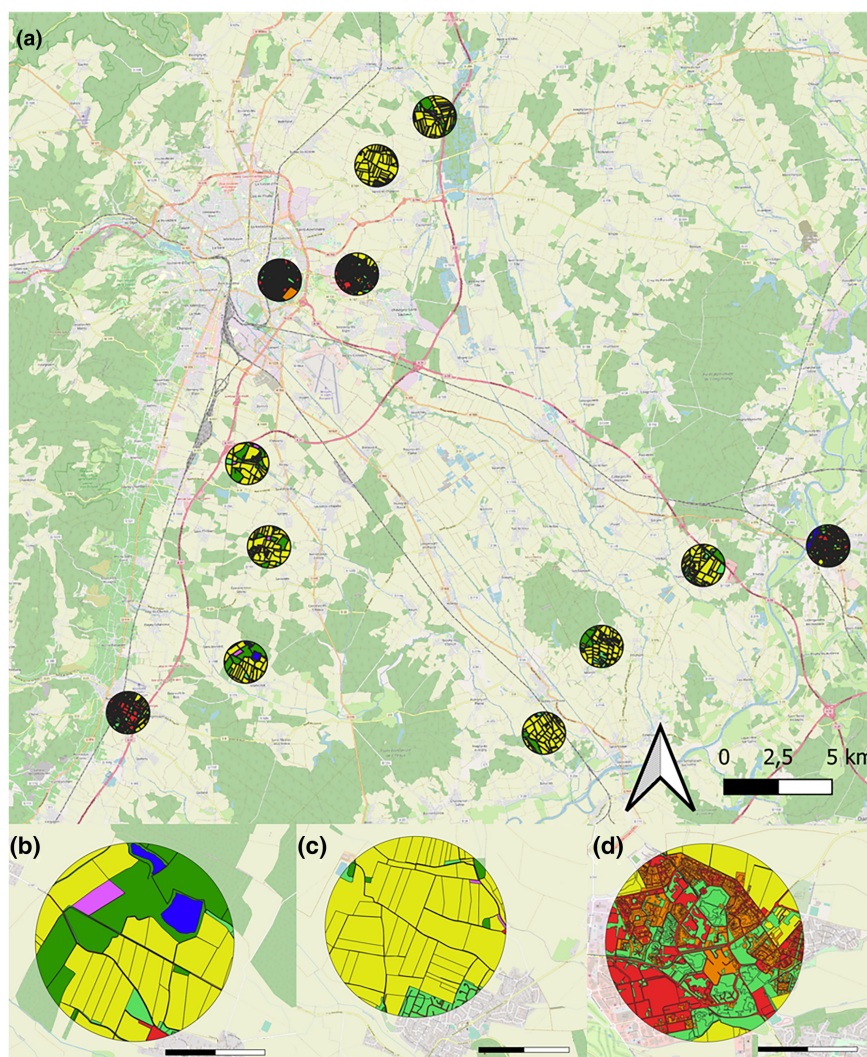
(Köppen–Geiger climate classification—Cfb) and land cover is dominated by agricultural fields (37%), forest (36%) and grasslands (17.2%), while 3% of the land area consists of urban environment.

2.2 | Gradient in landscape structure

We selected a priori and characterised 12 landscapes (1000 m radius) assigned to three landscape categories ($n=3 \times 4$) and following EUNIS (level 3) Habitat Classification (European Environment Agency 2021). Landscapes categories were as follows: Intensive agricultural = $\geq 75\%$ cover of arable crop and intensively managed grasslands; rural mosaic = $\sim 50\%:50\%$ intensive agricultural land and semi-natural habitats, with minor % settlements. Urban = $\geq 80\%$ urban land use, including buildings, transport infrastructure, gardens, parks and other green spaces.

To provide orthogonal axis scores differentiating land-cover gradients for use in statistical models, we used a PCA of the untransformed land cover data (Figure S1.1, Table S1.1). The principal axis (90% of variation) contrasted urban (built) area from cropland and was considered a measure of the gradient in 'urbanisation' among

FIGURE 1 (a) Overview map of all 12 study landscapes around Dijon, Côte d'Or, France, each with 1 km radius and separated by a minimum of 2 km. Inset examples are for (b) rural mosaic, (c) intensive agricultural and (d) urban landscapes. Scale bars in inset landscapes have a length on 1 km. Colour codes: Red—Built up urban areas, Orange—Fallow land, Yellow—Cropland, Dark green—Forest, Light green—Grassland, Purple—Shrubland, Blue—Open water. Base map from Open Street Map (www.openstreetmap.org).



the three landscape classes (Figure S1.1). The second axis (5%) contrasted intensive anthropogenic land uses (cropland, built urban area, but also parks and gardens) against semi-natural land cover categories (e.g., unmanaged meadows, mixed forests) and was therefore interpreted as a measure of 'land use intensity'.

2.3 | Plant-pollinator sampling

Pollinator sampling (2021) was performed within a 500m radius around the landscape centroid in early spring (mid-April), late spring (end May-early June) and summer (mid-July). Permission was granted by the land owners, but no specific licences or ethics approval were required. Sampling targeted habitats providing peak floral resources for pollinators at a given time period (e.g., forests were sampled in early spring, but not later in summer when flowers were reduced/absent; mass-flowering crops were sampled only during their flowering period). For each landscape and sampling round, flower visitors were captured on standardised 1-km \times 2m transects (120-min search effort) divided into sub-transects (minimum 25 \times 2m at 3min searching effort) spatially allocated in proportion to the area and distribution of each pollinator habitat type (EUNIS level 2). Pollinator samples were stored in cool boxes and euthanised at -80°C in the laboratory at the end of each day. Interacting plants and pollinators were identified to level of species or species-complex, genus or morphospecies for difficult species (Tables S1.2 and S1.3).

2.4 | Flowering plant composition, cover and nectar resources

Within each sub-transect, flowering plants were surveyed in between 1 and 5 quadrats (0.5 \times 2.0m²) depending on local plant heterogeneity to record the identity and count of floral units (e.g., umbels, capitules) per flowering plant species. Floral resource (nectar sugar) availability per m² was calculated by taking species (or closest relative) values of nectar sugar content per floral unit (mg) from existing data sets (Baude et al., 2015; Filipiak et al., 2022), multiplying that by the number of floral units per species, and summed for all the flowering plant species in the quadrat. Mean potential nectar sugar content (mgm⁻²) across sub-transects and weighted by their length (proportional to habitat coverage per landscape) was summed across all sub-transects (pollinator habitats) to derive the potential nectar sugar content (mgm⁻²) per landscape (1km \times 2m) and sampling round. Similarly, a sugar content-weighted average of the Shannon index of each vegetation plot was used as a measure for the potential diversity of nectar sources. While microclimate, soil biogeochemistry and nectar depletion may drive intraspecific differences in nectar content, our approach allowed estimation of the community-wide potential sugar content and diversity per landscape.

2.5 | Network structure

Plant-pollinator networks were constructed per sampling round to account for temporal turnover in species (Table S1.4) and avoid bias or creating forbidden links (Prendergast & Ollerton, 2022b). Using the R (v 4.1.2) bipartite package (Dormann et al., 2009), we calculated assemblage properties (Supporting Information S2) at the network-level (species richness and abundance, connectance, network asymmetry, nestedness (NODF), specialisation (H_2') and linkage density) and species-level (closeness, species strength, normalised degree and specialisation (d')). Many network-level metrics are correlated with network size (species number; Dormann et al., 2009). To correct this, we carried out z-score standardisation for nestedness, specialisation and linkage density, based on 10,000 random (null model) networks of the same size and connectance for each empirical network (vaznull function, bipartite; Vázquez & Aizen, 2003). A one-sample t-test was performed to assess the differences between the empirical networks and the null model networks.

2.6 | Species interaction dependence and network robustness

To account for the probability of extirpation from plant-pollinator interaction networks varying with the degree of life-history dependence on mutualism we assigned an intrinsic interaction dependence score to each insect and plant species (Tables S1.2 and S1.3). Plants were scored according to their dependency on insects for sexual reproduction (0—no insect pollinator dependence/vegetative propagation only/agricultural crop; 0.5—facultative dependence on insect pollination for sexual reproduction/vegetative propagation or selfing for seed production; 1—obligate dependence on insect pollination for seed production) (Fitter & Peat, 1994). Flower visitors were scored according to their known degree of dependency on flowers for nutrition (0—not or marginally dependent on nectar and pollen e.g. lacewings; 0.5—facultative flower visitors that include pollen as a minor part of diet e.g. most calyptate flies, Vespidae; 1—obligate flower visitors including bees and hoverflies). Mean interaction dependence was determined by separately calculating the abundance-weighted mean interaction dependence of the plant and the pollinator community and subsequently calculating the geometric mean of the mean plant and pollinator dependency scores.

Extinction risk was simulated (10,000 iterations) with a SCM (Vieira & Almeida-Neto, 2015) for each network with a single plant or pollinator species extirpated randomly at each iteration step. Subsequently, the basal extinction probability was calculated for each species of the other level (pollinator or plant, respectively) as the proportion of interactions with the extirpated species relative to its total number of interactions. The extinction chance of all remaining species was the product of the basal extinction chance

and the interaction dependency score. If this resulted in coextinctions, these iterative steps continued for the species dependent on the newly extirpated species, until no further species extinctions occurred.

These SCMs allowed estimation of network robustness against initial extinctions for each landscape network through (i) the proportional frequency of coextinctions, (ii) the mean degree of coextinction cascade (number of consecutive coextinction events) and (iii) the mean number of extinct species. Degree and number of extinct species were only calculated for iterations that led to a coextinction cascade (degree >1). All metrics were z-score standardised by running 10,000 SCM-iterations on each of 10,000 null models. Additionally, for each individual pollinator species in each network, the extinction rate (number of extinction events per 10,000 iterations) was calculated.

2.7 | Statistical analysis

To analyse how landscape structure and floral resources affect interaction networks and coextinction probabilities we used linear mixed models (LMM—Gaussian) or Generalised linear mixed models (GLMM—negative binomial for pollinator abundance, plant and pollinator species richness). Random effects fitted were 'site identity' in network level models and 'network identity' in species-level models. Model selection used AICc (network-level) or AIC (species-level) optimisation procedure to select the best model. To fulfil model assumptions, power or exponential variance structures were used for certain continuous fixed effects. Pairwise comparisons used Tukey's HSD tests. To avoid collinearity between predictors, we excluded models containing variables with a variance inflation factor (VIF) >3. Singletons (e.g., network at one time period of a single plant and pollinator) were always dropped from all analyses. One network created outliers in the SCM due to its small sample size (15 individuals, including 9 singletons) and was removed from the models containing SCM metrics.

2.7.1 | Landscape gradients and structure and robustness of plant–pollinator networks

To assess the relationship of network structure to gradients in landscape structure and floral resources, we modelled the response of network-level properties (see above) to urbanisation (PC1), land use intensity (PC2), local nectar availability (sugar mg/m²), nectar diversity (Shannon) and accounting for phenological turnover in species and interactions (categorical: sampling round).

To test how coextinctions related to network structure gradients in landscape structure and floral resources, we modelled the response of coextinction (proportional frequency of coextinctions, mean degree of coextinction cascade, the mean number of extinct species per coextinction cascade) to different network properties (total species number, network asymmetry, connectance, NODF, H_2' , linkage

density and mean interaction dependence) and in separate models landscape gradients (PC1–PC2, nectar availability and diversity).

2.7.2 | Species-level network position and extinction risks

Beyond the robustness of the entire network, species were hypothesised to differ in extinction risk according to their position within the network and dependence on floral resources. First, we modelled (GLM) how species-level network properties (closeness, species strength, specialisation- d' and normalised degree, see [Supporting Information S2](#)) differed among broad pollinator groups that reflect dietary specialisation/dependence on floral resources. Predictors were as follows: (i) bee genus (*Andrena*, *Apis*, *Bombus* and *Lasioglossum*) or (ii) pollinator group identity (bees, hoverflies, calyptrate flies, empid flies and sawflies) and their respective abundance (log). Then to assess which species-level metrics affected coextinction risk, we modelled (GLMM, negative binomial) the number of extinction events as a response variable and all species-level metrics, their pairwise interactions, and interaction dependence as fixed effects.

3 | RESULTS

We recorded 2946 unique flower visits carried out by 281 pollinator species on 175 plant species. In total, 2123 Hymenoptera (72% of total), 719 Diptera (24%), 49 Lepidoptera (2%) and 46 Coleoptera (2%) were found ([Table S1.2](#)). Of these, bees were the most important pollinator group, accounting for 2025 visits (68%) by 122 species, including the honeybee (*Apis mellifera* 1023 flower visits 35%). Ornamental plants were an important flower source in urban landscapes, accounting for 236 out of 978 visits (24%), but not in rural and agricultural landscapes. Agricultural crops received 592 visits (64%) and 213 visits (20%) in agricultural and rural landscapes, respectively ([Table S1.5](#)).

Observed plant–pollinator networks were less nested ($z\text{NODF} = -0.59$, $CI_{95} = -0.95$ to -0.23 , $t = -3.35$, $df = 34$, $p = 0.002$), had a lower linkage density ($z\text{LD} = -1.67$, $CI_{95} = -2.02$ to -1.32 , $t = -9.73$, $df = 34$, $p < 0.0001$) and were more specialised ($zH_2' = 2.06$, $CI_{95} = 1.35$ – 2.77 , $t = 5.87$, $df = 34$, $p < 0.0001$) than null model networks comprising randomly created networks of equivalent size and connectance.

The empirical networks differed in robustness from the simulated null model networks: extinction cascades were significantly more frequent than in null model networks ($z\text{P.Casc} = 1.27$, $CI_{95} = 0.92$ – 1.61 , $t = 7.44$, $p < 0.0001$), while the standardised degree of the cascades ($z\text{Degree}_{\text{casc}} = -1.25$, $CI_{95} = -1.72$ to -0.77 , $t = -5.30$, $p < 0.0001$) and the number of extinct species per cascade event ($z\text{Ext}_{\text{casc}} = -1.24$, $CI_{95} = -1.47$ to -1.02 , $t = -11.12$, $p < 0.0001$) were lower than in null model networks.

3.1 | Landscape gradients and structure and robustness of plant-pollinator networks

Plant-pollinator network structure varied between different landscape types (Table 1, Figure 2) and among seasons (Table 1; Figure S1.2). Urban networks had a lower connectance (Table 1; Figure 2a), a slightly higher linkage density and were less specialised (Table 1). Increasing urbanisation was also strongly positively correlated with increased plant species richness, contributing to more

symmetrical networks (Table 1, Figure 2d). Land use intensity decreased species richness both for plants and pollinators, leading to more tightly connected and nested networks (Figure 2b,c, Table 1). Nectar diversity increased with urbanisation ($F_{1,10} = 10.63$, $p = 0.01$, Figure S1.3). Local nectar sugar availability had a strong positive effect on pollinator abundance (Table 1; Figure S1.3).

Network structure strongly affected plant-pollinator network robustness to coextinction cascades. Linkage density was the principal network property that reduced the risk of initiating a coextinction

TABLE 1 Relationship between landscape-scale plant-pollinator network structure (network-level) and land-use gradients in landscape cover, nectar resources and time period.

Response var.	Expl. var.	Coef.	SE	z/t-value	p-value
Pollinator abundance	Intercept	4.068	0.136	30.0	<0.0001
	Land use intensity	-0.031	0.018	-1.72	0.0853
	Nectar availability	0.005	0.002	2.96	0.0031
Plant species richness	Intercept	1.798	0.136	13.23	<0.0001
	Urbanisation	0.075	0.012	6.43	<0.0001
	Land use intensity	-0.031	0.013	-2.44	0.0146
	Period (late spring)	0.560	0.174	3.22	0.0013
	Period (summer)	0.551	0.176	3.13	0.0018
Pollinator species richness	Intercept	3.036	0.084	36.05	<0.0001
	Urbanisation	0.028	0.014	1.95	0.0516
	Land use intensity	-0.038	0.015	-2.51	0.0119
Connectance ^a	Intercept	0.209	0.019	10.95	<0.0001
	Urbanisation	-0.011	0.003	-3.98	0.0032
	Land use intensity	0.009	0.003	2.64	0.0268
Asymmetry	Intercept	0.528	0.042	12.49	<0.0001
	Urbanisation	-0.016	0.004	-3.78	0.0036
	Period (late spring)	-0.100	0.060	-1.68	0.1083
	Period (summer)	-0.231	0.061	-3.78	0.0011
NODF (z)	Intercept	-0.577	0.160	-3.60	0.0010
	Land use intensity	0.077	0.028	2.79	0.0191
$H_2'(z)^b$	Intercept	1.308	0.377	3.47	0.0023
	Urbanisation	-0.078	0.032	-2.45	0.0342
	Period (late spring)	-0.113	0.509	-0.22	0.8260
	Period (summer)	2.335	0.520	4.49	0.0002
Linkage density (z)	Intercept	-1.445	0.254	-5.68	<0.0001
	Urbanisation	0.060	0.026	2.31	0.0460
	Land use intensity	0.047	0.026	1.82	0.1024
	Period (late spring)	0.054	0.360	0.15	0.8818
	Period (summer)	-0.784	0.368	-2.13	0.0452
Interaction dependence	Intercept	0.552	0.044	12.60	<0.0001
	Land use intensity	-0.014	0.007	-1.87	0.0906

Note: Final best models (AICc selection) are shown. Coefficients are from LMM (t-values) or GLMM (z-values of abundance, species richness). (z)=z-score standardised against null-model networks to control for network size and connectance.

^aFor urbanisation, an exponential variance structure was used (exponent = -0.052).

^bFor urbanisation, a power variance structure was used (power = -0.85).

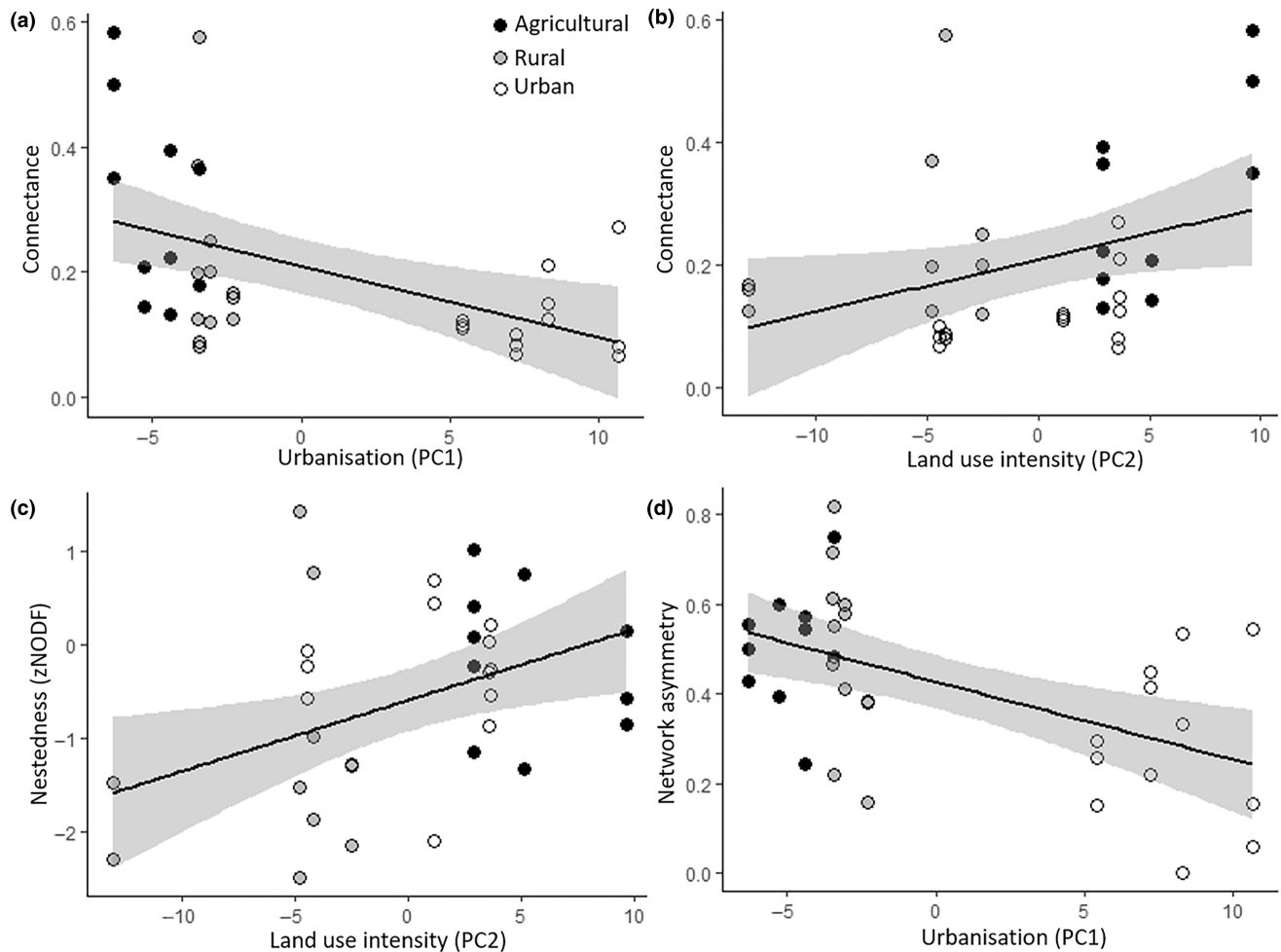


FIGURE 2 Land use gradients (urbanisation and land use intensity) affecting the network (a, b) connectance, (c) nestedness (NODF) and (d) network asymmetry. Each data point corresponds to a plant-pollinator network for intensive agricultural, rural mosaic and urban landscapes ($n=12$ 1-km radius) at three time period (early spring, late spring, summer). Fitted lines ($\pm 95\%$ CI grey shading) are derived from a LMM (Gaussian).

cascade, but if one did occur, it was a short but more intensive series of coextinctions (Figure 3a,c; Table 2). Asymmetrical networks reduced the risk of a coextinction cascade occurring, while nested networks had significantly longer degree of coextinction cascade (Table 2). Networks containing species with a high level of interaction dependence had a marginally lower risk of initiating a cascade, and tended to comprise a shorter extinction series (Table 2—lower mean cascade degree).

Gradients in landcover did not have a strong effect on network robustness against coextinction cascades. Urbanisation (PC1) was not selected in the best-subset of models. Networks in intensively used landscapes (PC2) had a lower risk of initiating a coextinction cascade (Figure 3b, Coef. = -0.074 ± 0.026 , $t = -2.82$, $p = 0.0183$), while the number of extinct species was marginally higher (Figure 3d, Coef. = 0.038 ± 0.018 , $t = 2.09$, $p = 0.0626$). Networks in landscapes with a high nectar diversity were prone to longer coextinction cascades (Coef. = 4.704 ± 1.496 , $t = 3.15$, $p = 0.0051$). Nectar sugar availability only marginally affected the proportional frequency of coextinctions (Coef. = 0.0042 ± 0.0022 , $t = 1.90$, $p = 0.07$).

3.2 | Species-level network position and extinction risks

There were marked differences in closeness, normalised degree, species strength and specialisation- d' among the principal bee genera (*Andrena*, *Apis*, *Bombus* and *Lasioglossum*). Honeybees played a central role in the structure of these plant-pollination networks, with higher closeness, species strength and normalised degree than the other genera (Figure 4). The genera *Bombus*, and to a lesser extent *Apis*, had the highest d' -values and hence specialisation on floral resources in the network, compared to the genera *Lasioglossum* and *Andrena* (Figure 4). Bees overall had higher species strength and specialisation- d' than calyptate flies, but otherwise there were few differences in species-level metrics among the broader pollinator groups (Figure S1.4).

The model containing interaction dependence and an interaction effect between species strength and normalised degree was selected as the optimal model (Figure 5). While interaction dependence was the main factor affecting extinction risk (Coef. = 0.626 ± 0.024 ,

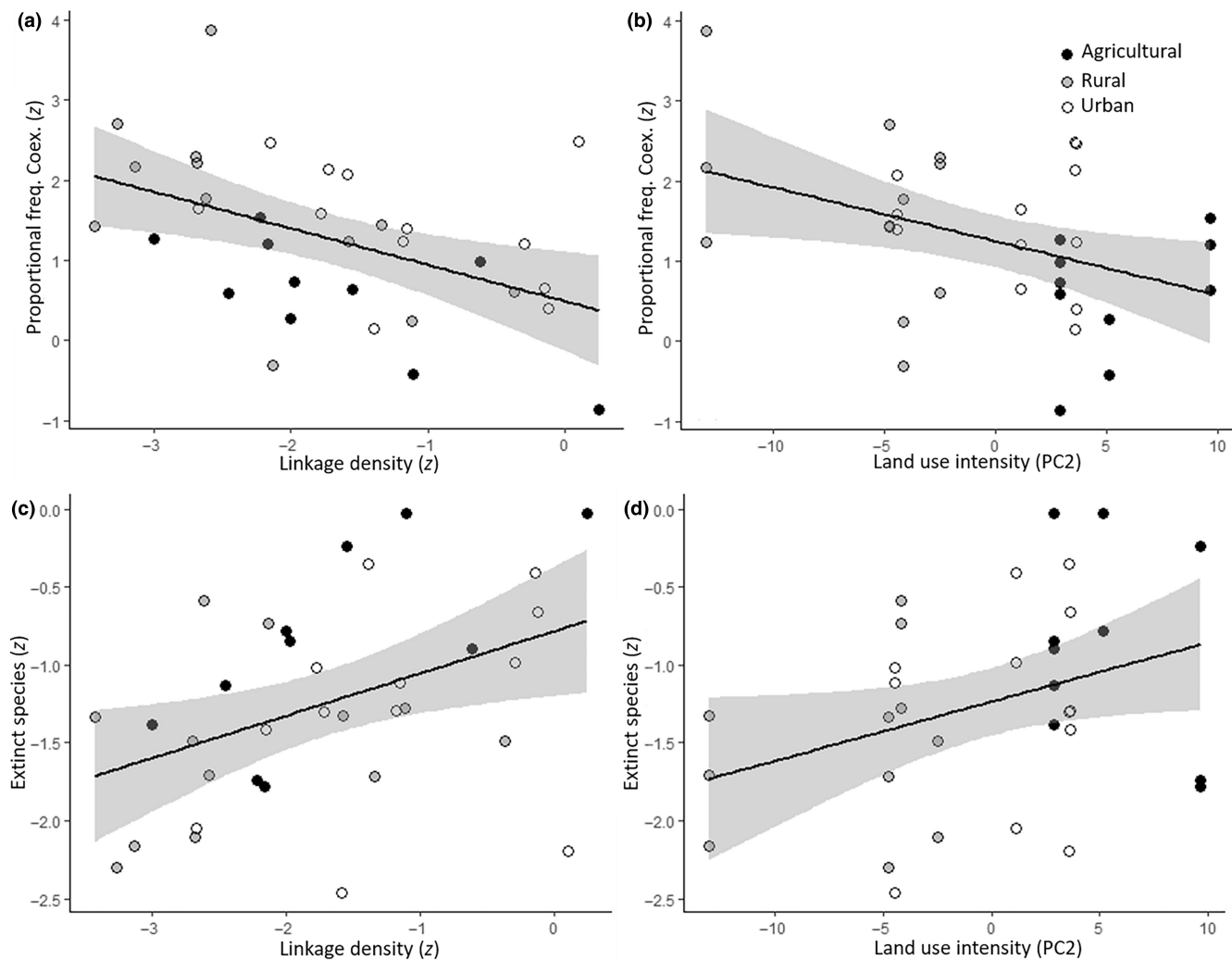


FIGURE 3 Response of the proportional frequency of coextinctions (a, b) and the number of extinct species (c, d) in landscape-scale plant-pollinator networks (12 × 3 time periods) to network linkage density (a–c) and land use intensity (b–d, PC2 of land cover). All network metrics were z-score standardised against 10,000 null models which each underwent 10,000 iterations in the SCM-model.

TABLE 2 Relationship between network robustness to coextinctions and landscape-scale plant-pollinator network structure (network-level).

Response var.	Expl. var.	Coef.	SE	t-value	p-value
Proportional frequency of coextinctions (z)	Intercept	2.146	0.609	3.52	0.0023
	Asymmetry	-2.772	0.807	-3.43	0.0028
	Int. dependence	-1.165	0.597	-1.95	0.0660
	Linkage density (z)	-0.541	0.128	-4.21	0.0005
Cascade degree (z)	Intercept	1.349	1.012	1.33	0.2002
	Connectance	-8.752	2.306	-3.80	0.0014
	Int. dependence	-2.563	1.147	-2.23	0.0392
	Linkage density (z)	-0.653	0.241	-2.70	0.0151
	NODF (z)	0.881	0.281	3.14	0.0060
#Extinct species (z)	Intercept	-0.783	0.204	-3.84	0.0009
	Linkage density (z)	0.271	0.103	2.62	0.0159

Note: NODF—Nestedness. Final best models (AICc selection) are shown. Coefficients are from LMM (t-values). (z) = z-score standardised against null-model networks to control for network size and connectance.

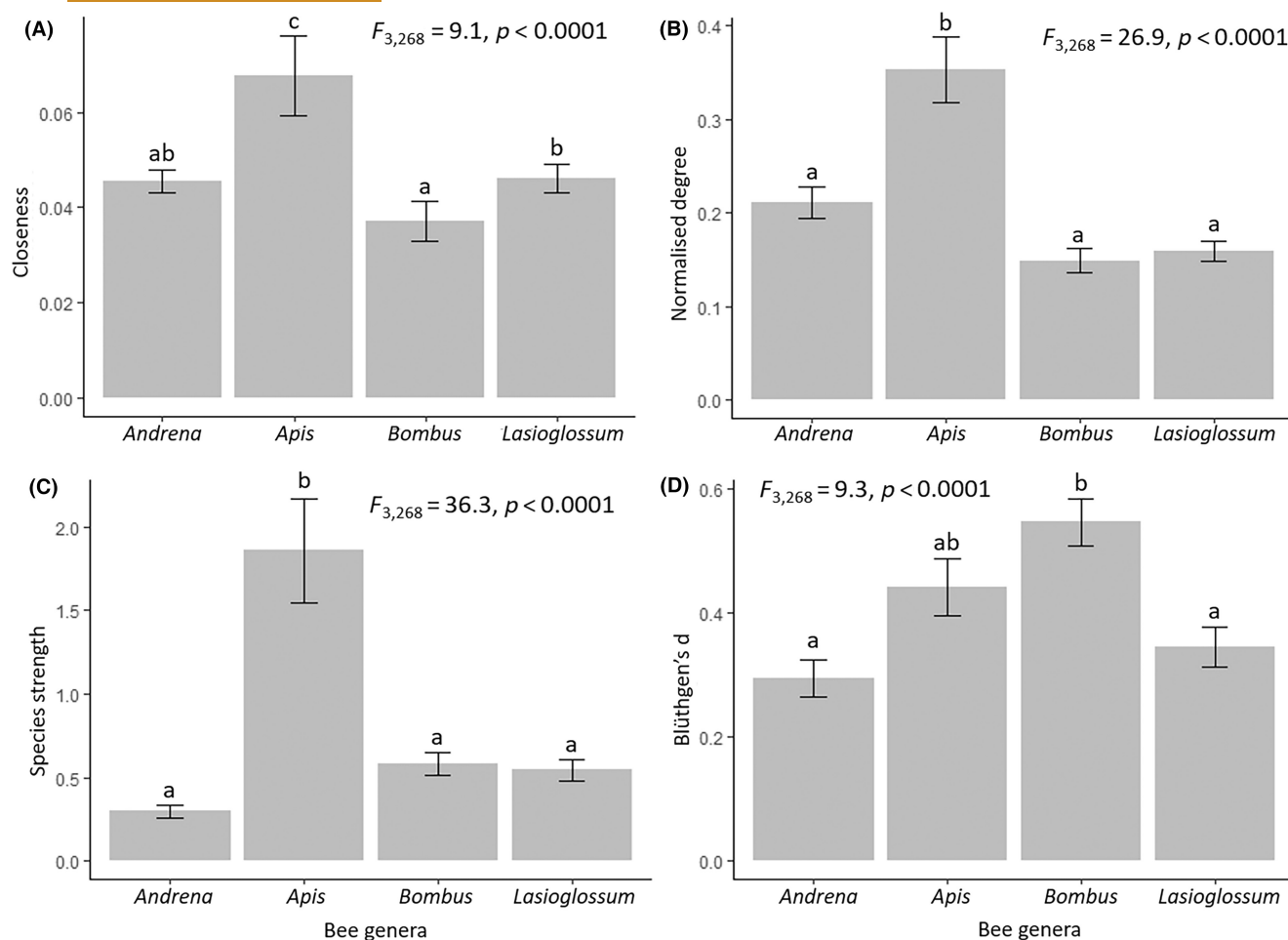


FIGURE 4 Differences in species-level network metrics between the four most abundant bee genera. Different letters indicate a significant difference at the $p < 0.05$ level. Differences are shown for (A) closeness, (B) normalised degree, (C) species strength and (D) Blüthgen's d .

$t = 26.63$, $p < 0.0001$), a higher species strength also led to a highly significant decrease in extinction risk (Coef. $= -0.115 \pm 0.023$, $t = -5.14$, $p < 0.0001$), although this effect weakened with increasing normalised degree (Coef. 0.124 ± 0.112 , $t = 1.10$, $p = 0.27$; Interaction coef. $= 0.152 \pm 0.065$, $t = 2.34$, $p = 0.019$; Figure 5).

4 | DISCUSSION

4.1 | Landscape gradients and structure and robustness of plant-pollinator networks

As predicted, the type and intensity of land-use at the landscape scale modified plant-pollinator network structure and, to a lesser extent, robustness. Landscape urbanisation led to species-rich networks with comparatively lower connectance and higher symmetry and linkage density (Baldock et al., 2015, 2019) that arose from relatively higher level of plant species richness, including ornamental and horticultural taxa. In contrast, networks in intensive agricultural landscapes were smaller (less speciose), more

connected and more nested than in urban and rural landscapes. Networks in intensively managed landscapes were less likely to undergo coextinction cascades, but when extinctions occurred, more species were lost.

Network structure affects the robustness of the assemblage to perturbations and extinctions (Thébault & Fontaine, 2010; Vanbergen et al., 2017; Vieira & Almeida-Neto, 2015). Although relatively weakly correlated with the landscape urbanisation gradient, linkage density was the principal network-level property that reduced the risk of initiating a coextinction cascade. The reduced proportion of networks that initiated a coextinction cascade and the lower cascade degree in strongly linked networks indicate that losing an interaction partner is less problematic for species strongly linked to many partners (Thébault & Fontaine, 2010). However, if a species loss occurred, despite the shorter extinction cascade, a high number of species were lost. This is possibly because the loss of a strongly linked species may lead to a greater number of coextinctions in networks with a high linkage density.

Nestedness can increase robustness of the network as long as the most linked species are retained (Memmott et al., 2004;

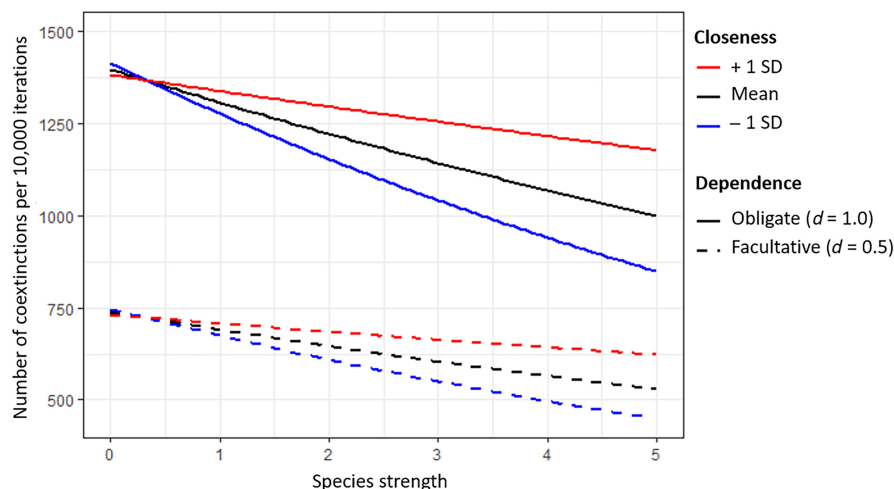


FIGURE 5 The effect of species strength on coextinction risk in stochastic coextinction models with 10,000 iterations. While extinction risk is much higher for obligate flower visitors (solid lines) than for facultative flower visitors (dashed lines), a high species strength always reduces extinction risk, although for species with a high normalised degree (red lines), this effect is reduced, compared to species with a low normalised degree (blue lines).

Thébault & Fontaine, 2010, but see James et al., 2012). Less bio-diverse, intensively used landscapes (predominantly intensive agriculture) had higher nestedness but were associated with a risk of prolonged (higher degree) coextinction cascades if an extinction happened. Conventional intensive agriculture produces structurally-simple landscapes providing few flowering plant resources for pollinators (Baude et al., 2016; Vanbergen & The Insect Pollinators Initiative, 2013). Such landscapes support simpler networks of generalist plant and pollinator species (Redhead et al., 2018) and increased nestedness can arise from concentration of foraging on mass-flowering crops that occupy a central, generalist position in the network (Russo et al., 2019). Specialist interactions are most vulnerable to extirpation, but specialists in mutualistic networks tend to interact with nested subsets of more robust generalist species, which contributes to robustness (Bascompte et al., 2003; Jordano et al., 2006). Although our species-level analysis of extinction risk showed generalists connected with specialists had the lowest extinction risk, when a generalist insect or plant was extirpated from a nested network, this precipitated the subsequent and severe loss of multiple linked specialist species (Traveset et al., 2017). In contrast, the rural mosaic of various semi-natural habitats may lead to more linked, functionally redundant networks (Sritongchuay et al., 2019) that are less susceptible to intense coextinction cascades.

Greater network connectance has also been linked to reduced robustness to coextinctions (Traveset et al., 2017; Vanbergen et al., 2017; Vieira & Almeida-Neto, 2015). We found, however, that more connected networks had shorter extinction cascades, in line with other studies (Thébault & Fontaine, 2010). We also found that greater network symmetry produced a higher risk of initiating a coextinction cascade (Pastor et al., 2012). In our landscape-scale networks, pollinator species always outnumbered plant species, and a subset of strongly linked plant species may have provided a buffer against coextinctions of weakly linked pollinators and conferred a degree of robustness (Bascompte et al., 2006). The role of local floral resources in influencing network structure and robustness remains to be determined, however. Although urbanisation affected

nectar diversity, we found no clear effect of variation in local nectar sources on network structure, implying that overall habitat heterogeneity was the main driver (Baldock et al., 2019).

4.2 | Species-level network position and extinction risks

Bees were slightly more specialised than flies in the observed networks (Weiner et al., 2011), but showed a strong variation in specialisation between genera. Honeybees focussed on the most abundant pollen and nectar sources (Geslin et al., 2017), thereby occupying a central network position (high closeness) and had a higher species strength than other bee taxa (Cruz et al., 2022). Because of their dominance, managed honeybees may compete with and reduce connectance among wild species (Aizen et al., 2008; Mallinger et al., 2017) and rewire or disrupt plant-pollinator networks (Magrach et al., 2017; Prendergast & Ollerton, 2022a). Conversely, the highly generalist honeybee may provide functional redundancy that increases network robustness (Aslan, 2019; Corcos et al., 2020). The overall outcome is likely highly context dependent and related to honeybee abundance and niche overlap with wild pollinators and local species assemblages. Bumblebees had an intermediate species strength between honeybees and other wild bee genera (*Andrena*, *Lasioglossum*) and occupied the least central position in the networks, possibly because of fidelity among *Bombus* species for different forage plants and so were relatively more specialised within the networks.

Although more connected species may have a higher risk of co-extinction (Traveset et al., 2017), we found that species strength was generally positively related to species robustness against extirpation. Species strength is increased more by interactions with specialist than generalist partners. The observed interaction between species strength and normalised degree suggests that for generalist species, interactions with specialists contribute more to robustness than interactions with generalists. Specialists therefore rarely drive coextinction cascades, and their extinction is

usually a consequence of extinction of a generalist partner, rather than the cause. Hence these specialist interactions may be 'low risk' compared with generalist-generalist interactions, possibly explaining the observed negative relationship between extinction risk and species strength.

4.3 | Assumptions and caveats

Our plant-pollinator networks departed from some fundamental predictions, being highly specialised with a low linkage density (but as seen in Souza et al., 2018; Vanbergen et al., 2017) and less nested compared with the null models (c.f. Bascompte et al., 2003; Bastolla et al., 2009; Santamaría & Rodríguez-Gironés, 2007). Lower nestedness in our case may be an artefact due to resource partitioning to avoid competition (Staniczenko et al., 2013) with the predominance of managed honeybees in the networks.

In contrast to null models, our empirical networks showed a higher risk of initiating a coextinction cascade, but cascades were shorter with fewer species lost. The distribution of coextinction degree was similar to Vanbergen et al. (2017) both in raw and z-transformed coextinction cascades (Figure S1.5). This higher stability compared with null models may be because of the non-random degree distribution, which in real-life mutualistic networks tends to follow a power-law or a truncated power-law distribution (Bascompte et al., 2003; Ramos-Jiliberto et al., 2012), and which is known to increase network stability (Albert et al., 2000).

A caveat to our model is that it does not incorporate flower visitor effectiveness dictated by trait matching among plants and pollinators (Garibaldi et al., 2015). However, life-history dependence on mutualism was integrated in our model, which provides an albeit coarse proxy measure of mutualism effectiveness at the community level. Contrary to expectation a higher level of mean interaction dependence marginally lowered the risk of initiating a coextinction cascade and its mean degree. Whilst the mechanism is unclear, it is possible that species that have an obligate dependence on mutualism occupy a more robust (e.g., central, generalist) position in the network.

5 | CONCLUSIONS

Urbanisation and land-use intensification gradients profoundly modified plant-pollinator network structure. Landscape intensification alone affected the frequency of extinctions by modifying the network structure and shifting the community towards species with lower interaction dependence. At the level of species, the strength of a species interaction with others in the network increased robustness against extirpation and so highly linked generalist organisms represent a stabilising influence on mutualistic networks. Our analysis highlights the complex interplay between land-use, network assembly and community robustness to species losses. Future research

should examine how land-use driven modification of nutritional and pollen landscapes for pollinators and plants leads to variable pollination effectiveness among species (pollen-transport networks) and plant reproduction outcomes (e.g., seed set and gene flow). Moreover, the consequences of these modified networks for other trophic (e.g., knock-on effects for herbivores) or host-parasite interactions (e.g., plant-pollinator-pathogen) remain to be established.

AUTHOR CONTRIBUTIONS

Data collection in the field was carried out by W. Proesmans, E. Felten, E. Laurent, N. Cyrille, A. Labonté and A. J. Vanbergen. Insect identification was carried out by W. Proesmans, A. J. Vanbergen, M. Albrecht, R. Paxton, O. Schweiger and H. Szentgyörgyi conceived and designed the experimental set-up. W. Proesmans carried out the analyses and led the writing effort. All authors provided critical input in writing and analyses. All authors approved of the final version to be published.

ACKNOWLEDGEMENTS

We are grateful to Cassandre Vidal, Eric Vieren, Augustin Chenut, Nicolas Henon and Chantal Ducourtieux for their help with the fieldwork. We thank the landowners for granting permission to carry out the research on their properties. This work was carried out within the Biodiversa project VOODOO (Viral eco-evolutionary dynamics of wild and domestic pollinators under global change www.voodoo-project.eu) and was funded by grant ANR-19-EBI3-0006 (France), NCN UMO-2019/32/Z/NZ8/00006 (Poland), NSF31BD30_186532/1 (Switzerland), DFGPA632/10-1,12/1 and BMBF16LC1905A (Germany) under the joint call BiodivERsA 2018-2019 CALL 'BIODIVERSITY AND ITS INFLUENCE ON ANIMAL, HUMAN, AND PLANT HEALTH'. Co-funding was provided to WP, MA, OS and AJV by the H2020 Safeguard (European Commission) project Grant/Award Number: GA 101003476. [Correction added on 3 February 2024, after first online publication: Details of H2020 Safeguard funding have been added.]

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

R-code and raw data are available in Dryad Digital Repository: <https://doi.org/10.5061/dryad.msbcc2g51> (Proesmans et al., 2023).

ORCID

Willem Proesmans  <https://orcid.org/0000-0003-0358-6732>

Matthias Albrecht  <https://orcid.org/0000-0001-5518-3455>

Audrey Labonté  <https://orcid.org/0000-0001-5092-1471>

Corina Maurer  <https://orcid.org/0000-0001-8103-4111>

Robert Paxton  <https://orcid.org/0000-0003-2517-1351>

Oliver Schweiger  <https://orcid.org/0000-0001-8779-2335>

Hajnalka Szentgyörgyi  <https://orcid.org/0000-0002-5753-800X>

Adam J. Vanbergen  <https://orcid.org/0000-0001-8320-5535>

REFERENCES

- Aizen, M. A., Morales, C. L., & Morales, J. M. (2008). Invasive mutualists erode native pollination webs. *PLoS Biology*, 6(2), e31. <https://doi.org/10.1371/journal.pbio.0060031>
- Albert, R., Jeong, H., & Barabási, A.-L. (2000). Error and attack tolerance of complex networks. *Nature*, 406, 378–382. <https://doi.org/10.1038/35019019>
- Aslan, C. E. (2019). Implications of non-native species for mutualistic network resistance and resilience. *PLoS One*, 14(6), e0217498. <https://doi.org/10.1371/journal.pone.0217498>
- Baldock, K. C. R., Goddard, M. A., Hicks, D. M., Kunin, W. E., Mitschunas, N., Morse, H., Osgathorpe, L. M., Potts, S. G., Robertson, K. M., Scott, A. V., Staniczenko, P. P. A., Stone, G. N., Vaughan, I. P., & Memmott, J. (2019). A systems approach reveals urban pollinator hotspots and conservation opportunities. *Nature Ecology & Evolution*, 3(3), 363–373. <https://doi.org/10.1038/s41559-018-0769-y>
- Baldock, K. C. R., Goddard, M. A., Hicks, D. M., Kunin, W. E., Mitschunas, N., Osgathorpe, L. M., Potts, S. G., Robertson, K. M., Scott, A. V., Stone, G. N., Vaughan, I. P., & Memmott, J. (2015). Where is the UK's pollinator biodiversity? The importance of urban areas for flower-visiting insects. *Proceedings of the Royal Society B: Biological Sciences*, 282, 20142849.
- Bascompte, J., Jordano, P., Melián, C. J., & Olesen, J. M. (2003). The nested assembly of plant-animal mutualistic networks. *Proceedings of the National Academy of Sciences of the United States of America*, 100(16), 9383–9387. <https://doi.org/10.1073/pnas.1633576100>
- Bascompte, J., Jordano, P., & Olesen, J. M. (2006). Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science*, 312, 431–433. <https://doi.org/10.1126/science.1123412>
- Bastolla, U., Fortuna, M. A., Pascual-García, A., Ferrera, A., Luque, B., & Bascompte, J. (2009). The architecture of mutualistic networks minimizes competition and increases biodiversity. *Nature*, 458, 1018–1020. <https://doi.org/10.1038/nature07950>
- Baude, M., Kunin, W. E., Boatman, N. D., Conyers, S., Davies, N., Gillespie, M. A. K., Morton, R. D., Smart, S. M., & Memmott, J. (2016). Historical nectar assessment reveals the fall and rise of Britain in bloom Europe PMC funders group. *Nature*, 530(7588), 85–88. <https://doi.org/10.1038/nature16532.Historical>
- Baude, M., Kunin, W. E., & Memmott, J. (2015). Nectar sugar values of common British plant species [AgriLand].
- Colwell, R. K., Dunn, R. R., & Harris, N. C. (2012). Coextinction and persistence of dependent species in a changing world. *Annual Review of Ecology, Evolution, and Systematics*, 43, 183–203. <https://doi.org/10.1146/annurev-ecolsys-110411-160304>
- Corcos, D., Cappellari, A., Mei, M., Paniccà, D., Cerretti, P., & Marini, L. (2020). Contrasting effects of exotic plant invasions and managed honeybees on plant-flower visitor interactions. *Diversity and Distributions*, 26, 1397–1408. <https://doi.org/10.1111/ddi.13132>
- Cruz, C. P., Luna, P., Guevara, R., Hinojosa-Díaz, I. A., Villalobos, F., & Dáttilo, W. (2022). Climate and human influence shape the interactive role of the honeybee in pollination networks beyond its native distributional range. *Basic and Applied Ecology*, 63, 186–195. <https://doi.org/10.1016/j.baae.2022.06.009>
- Cusser, S., Neff, J. L., & Jha, S. (2019). Landscape context differentially drives diet breadth for two key pollinator species. *Oecologia*, 191, 873–886. <https://doi.org/10.1007/s00442-019-04543-5>
- Dormann, C. F., Fründ, J., Blüthgen, N., & Gruber, B. (2009). Indices, graphs and null models: Analyzing bipartite ecological networks. *The Open Ecology Journal*, 2, 7–24. <https://doi.org/10.2174/1874213000902010007>
- Filipiak, M., Walczynska, A., Denisow, B., Petanidou, T., & Ziolkowska, E. (2022). Phenology and production of pollen, nectar, and sugar in 1612 plant species from various environments. *Ecology*, 103, e3705. <https://doi.org/10.1002/ecy.3705>
- Fitter, A. H., & Peat, H. J. (1994). The ecological flora database. *Journal of Ecology*, 82, 415–425.
- Garibaldi, L. A., Bartomeus, I., Bommarco, R., Klein, A. M., Cunningham, S. A., Aizen, M. A., Boreux, V., Garratt, M. P. D., Carvalheiro, L. G., Kremen, C., Morales, C. L., Schüepp, C., Chacoff, N. P., Freitas, B. M., Gagic, V., Holzschuh, A., Klatt, B. K., Krewenka, K. M., Krishnan, S., ... Woyciechowski, M. (2015). Trait matching of flower visitors and crops predicts fruit set better than trait diversity. *Journal of Applied Ecology*, 52, 1436–1444. <https://doi.org/10.1111/1365-2664.12530>
- Geslin, B., Gauzens, B., Baude, M., Dajoz, I., Henry, M., Ropars, L., Rollin, O., Thébault, E., Vereecken, J., Geslin, B., Gauzens, B., Baude, M., Dajoz, I., & Fontaine, C. (2017). Massively introduced managed species and their consequences for plant-pollinator interactions. *Advances in Ecological Research*, 57, 147–199. <https://doi.org/10.1016/bs.aecr.2016.10.007>
- James, A., Pitchford, J. W., & Plank, M. J. (2012). Disentangling nestedness from models of ecological complexity. *Nature*, 487, 227–230. <https://doi.org/10.1038/nature11214>
- Jha, S., & Kremen, C. (2013). Resource diversity and landscape-level homogeneity drive native bee foraging. *Proceedings of the National Academy of Sciences of the United States of America*, 110(2), 555–558. <https://doi.org/10.1073/pnas.1208682110>
- Jordano, P., Bascompte, J., & Olesen, J. M. (2006). The ecological consequences of complex topology and nested structure in pollination webs. In *Specialization and generalization in plant-pollinator interactions* (pp. 173–199). Chicago University Press.
- Kaiser-Bunbury, C. N., Muff, S., Memmott, J., Müller, C. B., & Caflisch, A. (2010). The robustness of pollination networks to the loss of species and interactions: A quantitative approach incorporating pollinator behaviour. *Ecology Letters*, 13, 442–452. <https://doi.org/10.1111/j.1461-0248.2009.01437.x>
- Le Féon, V., Schermann-Legionnet, A., Delettre, Y., Aviron, S., Billeter, R., Bugter, R., Hendrickx, F., & Burel, F. (2010). Intensification of agriculture, landscape composition and wild bee communities: A large scale study in four European countries. *Agriculture, Ecosystems & Environment*, 137, 143–150. <https://doi.org/10.1016/j.agee.2010.01.015>
- Magrach, A., González-Varo, J. P., Boiffier, M., Montserrat, V., & Bartomeus, I. (2017). Honeybee spillover reshuffles pollinator diets and affects plant reproductive success. *Nature Ecology & Evolution*, 1(9), 1299–1307. <https://doi.org/10.1038/s41559-017-0249-9>
- Mallinger, R. E., Gaines-Day, H. R., & Gratton, C. (2017). Do managed bees have negative effects on wild bees? A systematic review of the literature. *PLoS One*, 12(12), e0189268. <https://doi.org/10.1371/journal.pone.0189268>
- Martínez-Núñez, C., Manzaneda, A. J., Lendínez, S., Pérez, A. J., Ruiz-Valenzuela, L., & Rey, P. J. (2019). Interacting effects of landscape and management on plant-solitary bee networks in olive orchards. *Functional Ecology*, 33, 2316–2326. <https://doi.org/10.1111/1365-2435.13465>
- 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, 2604–2615. <https://doi.org/10.1111/1365-2664.14260>
- Memmott, J., Waser, N. M., & Price, M. V. (2004). Tolerance of pollination networks to species extinctions. *Proceedings of the Royal Society B: Biological Sciences*, 271, 2605–2611. <https://doi.org/10.1098/rspb.2004.2909>
- Morrison, B. M. L., & Dirzo, R. (2020). Distinct responses of antagonistic and mutualistic networks to agricultural intensification. *Ecology*, 101(10), e03116. <https://doi.org/10.1002/ecy.3116>
- Pastor, J. M., Santamaría, S., Méndez, M., & Galeano, J. (2012). Effects of topology on robustness in ecological bipartite networks. *Networks and Heterogeneous Media*, 7(3), 429–440. <https://doi.org/10.3934/nhm.2012.7.429>

- Prendergast, K. S., & Ollerton, J. (2021). Plant-pollinator networks in Australian urban bushland remnants are not structurally equivalent to those in residential gardens. *Urban Ecosystems*, 24, 973–987. <https://doi.org/10.1007/s11252-020-01089-w>
- Prendergast, K. S., & Ollerton, J. (2022a). Impacts of the introduced European honeybee on Australian bee-flower network properties in urban bushland remnants and residential gardens. *Austral Ecology*, 47(1), 35–53. <https://doi.org/10.1111/aec.13040>
- Prendergast, K. S., & Ollerton, J. (2022b). Spatial and temporal scale of analysis alter conclusions about the effects of urbanisation on plant-pollinator networks. *Arthropod-Plant Interactions*, 16, 553–565. <https://doi.org/10.1007/s11829-022-09925-w>
- Proesmans, W., Felten, E., Laurent, E., Albrecht, M., Cyrille, N., Labonté, A., Maurer, C., Paxton, R., Schweiger, O., Szentgyörgyi, H., & Vanbergen, A. J. (2023). Data from: Urbanisation and agricultural intensification modulate plant-pollinator network structure and robustness. *Dryad Digital Repository*. <https://doi.org/10.5061/dryad.msbcc2g51>
- Ramos-Jiliberto, R., Valdovinos, F. S., Moisset de Espanés, P., & Flores, J. D. (2012). Topological plasticity increases robustness of mutualistic networks. *Journal of Animal Ecology*, 81(4), 896–904. <https://doi.org/10.1111/j.1365-2656.2012.01960.x>
- Redhead, J. W., Woodcock, B. A., Pocock, M. J. O., Pywell, R. F., Vanbergen, A. J., & Oliver, T. H. (2018). Potential landscape-scale pollinator networks across Great Britain: Structure, stability and influence of agricultural land cover. *Ecology Letters*, 21, 1821–1832. <https://doi.org/10.1111/ele.13157>
- Renner, S. S., Graf, M. S., Hentschel, Z., Krause, H., & Fleischmann, A. (2021). High honeybee abundances reduce wild bee abundances on flowers in the city of Munich. *Oecologia*, 195, 825–831. <https://doi.org/10.1007/s00442-021-04862-6>
- Riedinger, V., Renner, M., Rundlöf, M., Steffan-Dewenter, I., & Holzschuh, A. (2014). Early mass-flowering crops mitigate pollinator dilution in late-flowering crops. *Landscape Ecology*, 29, 425–435. <https://doi.org/10.1007/s10980-013-9973-y>
- Russo, L., Albert, R., Campbell, C., & Shea, K. (2019). Experimental species introduction shapes network interactions in a plant-pollinator community. *Biological Invasions*, 21(12), 3505–3519. <https://doi.org/10.1007/s10530-019-02064-z>
- Santamaría, L., & Rodríguez-Gironés, M. Á. (2007). Linkage rules for plant-pollinator networks: Trait complementarity or exploitation barriers. *PLoS Biology*, 5(2), e31. <https://doi.org/10.1371/journal.pbio.0050031.t001>
- Schleuning, M., Fründ, J., Schweiger, O., Welk, E., Albrecht, J., Albrecht, M., Beil, M., Benadi, G., Blüthgen, N., Brühlheide, H., Böhning-Gaese, K., Dehling, D. M., Dormann, C. F., Exeler, N., Farwig, N., Harpke, A., Hickler, T., Kratochwil, A., Kuhlmann, M., ... Hof, C. (2016). Ecological networks are more sensitive to plant than to animal extinction under climate change. *Nature Communications*, 7, 13965. <https://doi.org/10.1038/ncomms13965>
- 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, 2409–2420. <https://doi.org/10.1111/1365-2745.12978>
- Sritongchuy, T., Hughes, A. C., Memmott, J., & Bumrungsri, S. (2019). Forest proximity and lowland mosaic increase robustness of tropical pollination networks in mixed fruit orchards. *Landscape and Urban Planning*, 192, 103646. <https://doi.org/10.1016/j.landurbplan.2019.103646>
- Staniczenko, P. P. A., Kopp, J. C., & Allesina, S. (2013). The ghost of nestedness in ecological networks. *Nature Communications*, 4, 1391. <https://doi.org/10.1038/ncomms2422>
- Thébault, E., & Fontaine, C. (2010). Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science*, 329(5993), 853–856. <https://doi.org/10.1126/science.1188321>
- Theodorou, P., Albigh, K., Radzevičiūtė, R., Settele, J., Schweiger, O., Murray, T. E., & Paxton, R. J. (2017). The structure of flower visitor networks in relation to pollination across an agricultural to urban gradient. *Functional Ecology*, 31, 838–847. <https://doi.org/10.1111/1365-2435.12803>
- Traveset, A., Tur, C., & Eguíluz, V. M. (2017). Plant survival and keystone pollinator species in stochastic coextinction models: Role of intrinsic dependence on animal-pollination. *Scientific Reports*, 7, 6915. <https://doi.org/10.1038/s41598-017-07037-7>
- Valido, A., Rodríguez-Rodríguez, M. C., & Jordano, P. (2019). Honeybees disrupt the structure and functionality of plant-pollinator networks. *Scientific Reports*, 9, 4711. <https://doi.org/10.1038/s41598-019-41271-5>
- Vanbergen, A. J., & The Insect Pollinators Initiative. (2013). Threats to an ecosystem service: Pressures on pollinators. *Frontiers in Ecology and the Environment*, 11(5), 251–259. <https://doi.org/10.1890/120126>
- Vanbergen, A. J., Woodcock, B. A., Heard, M. S., & Chapman, D. S. (2017). Network size, structure and mutualism dependence affect the propensity for plant-pollinator extinction cascades. *Functional Ecology*, 31(6), 1285–1293. <https://doi.org/10.1111/1365-2435.12823>
- Vázquez, D. P., & Aizen, M. A. (2003). Null model analyses of specialization in plant-pollinator interactions. *Ecology*, 84(9), 2493–2501. <https://doi.org/10.1890/02-0587>
- Vieira, M. C., & Almeida-Neto, M. (2015). A simple stochastic model for complex coextinctions in mutualistic networks: Robustness decreases with connectance. *Ecology Letters*, 18, 144–152. <https://doi.org/10.1111/ele.12394>
- Weiner, C. N., Werner, M., Linsenmair, K. E., & Blüthgen, N. (2011). Land use intensity in grasslands: Changes in biodiversity, species composition and specialisation in flower visitor networks. *Basic and Applied Ecology*, 12, 292–299. <https://doi.org/10.1016/j.baae.2010.08.006>
- Weiner, C. N., Werner, M., Linsenmair, K. E., & Blüthgen, N. (2014). Land-use impacts on plant-pollinator networks: Interaction strength and specialization predict pollinator declines. *Ecology*, 95(2), 466–474. <https://doi.org/10.1890/13-0436.1>

SUPPORTING INFORMATION

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

Supporting Information S1. Figure S1.1. Separation of the 12 study sites according to a PCA of surrounding land use.

Figure S1.2. Effect of phenology on network structure: (a) network asymmetry, (b) specialization and (c) linkage density.

Figure S1.3. (a) Nectar (sugar) availability throughout the season. Late-season landscapes are richer in nectar than early and mid-season networks. (b) Effect of nectar availability on pollinator abundance. Landscapes with higher nectar availability have a higher pollinator abundance. An outlier with very high nectar availability (381 mg/m²) has been removed from the graph. (c) Mean Shannon diversity of nectar (weighted by sugar content) is highest in urban areas.

Figure S1.4. Differences in species-level network metrics between the five main pollinator functional groups.

Figure S1.5. (a) Proportion of coextinction cascades that reach at least degree N. (b) Z-scores of the proportions of extinction cascades reaching at least the amount of degrees indicated in the X-axis.

Table S1.1. scores for the first two PCA-axes based on EUNIS land use categories.

Table S1.2. All flower visitors that were encountered in this study with their respective abundances and interaction dependence (0=no flower visitors, 0.5=partly dependent on floral resources, 1=completely dependent on floral resources).

Table S1.3. Plant species visited by pollinators in this study, including their dependence on pollination (0 = (almost) completely reproducing vegetatively or agricultural crops*/perennial ornamental/garden plants**, 0.5 = both sexually and asexually reproducing, 1 = only reproducing sexually).

Table S1.4. Temporal turnover in pollinator and plant communities between the three sampling periods. Distance is expressed as mean Bray–Curtis dissimilarity \pm SD among all study sites.

Table S1.5. Total number of visits to ornamental plants, agricultural crops and wild plant species in each of the three landscape categories.

Supporting Information S2. Explanation of all network- and species-level metrics used in the analyses.

How to cite this article: Proesmans, W., Felten, E., Laurent, E., Albrecht, M., Cyrille, N., Labonté, A., Maurer, C., Paxton, R., Schweiger, O., Szentgyörgyi, H., & Vanbergen, A. J. (2024). Urbanisation and agricultural intensification modulate plant–pollinator network structure and robustness. *Functional Ecology*, 38, 628–641. <https://doi.org/10.1111/1365-2435.14503>