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RESEARCH PAPER

Predator – prey interactions are less specialised in urban parks compared to peri-urban forests

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ABSTRACT

Species diversity is positively associated with specialisation and complexity of interaction networks and the delivery of related ecosystem functions. However, anthropogenic environments, such as urban areas, can have altered species diversity which may affect species interaction networks. For example, urban parks can be important for supporting bird diversity in cities, but their predatory interactions with arthropods may be weaker, along with reduced delivery of ecosystem functions such as insect control or pest removal. Here, in a case study of four sites, we compared networks of insectivorous birds and their prey from urban parks and peri-urban forests, using high-throughput DNA metabarcoding of bird faecal samples. We compared prey taxonomical diversity and composition, and network properties between the two habitats. We built predator – prey networks with 50 individual birds of eleven species whose faecal samples returned >100 million sequence reads of 1363 arthropod zOTUs assigned to 489 species. We found that the diversity of prey was lower in urban parks than in forests, and prey composition between urban sites overlapped more and had a lower turnover, indicating a more homogeneous prey community, than forest sites. Urban bird – arthropod networks were less specialised, more nested and more functionally redundant than their forest counterparts. Our results show a loss of specialisation in predator – prey interactions in urban areas as a consequence of increased overlap in prey species among predators. However, given the limited sample size, our reconstructed networks cannot fully characterise the local bird assemblages, even though the main species were sampled. Despite the limited scope of inference, the observed loss of specialisation could have broader implications for urban ecosystem services, such as insect control, but extensive further replication is needed to test these potential consequences.

Introduction

Species interactions are critical determinants of ecosystem functions, such as decomposition, nutrient uptake, carbon sequestration or insect pest control (Norris, 2012; Oliver et al., 2015). The underlying mechanisms are mediated by species traits and roles in ecological networks, for example predators and prey in trophic networks (Balvanera et al., 2006; Cardinale et al., 2009; Thompson et al., 2012). Not all species contribute equally and, in some ecosystems, rare or common species can contribute disproportionately to functions (Basile, 2022; Winfree et al., 2015). Therefore, understanding the property of species interaction networks can inform about the provision of ecosystem functions.

Network properties such as interaction diversity, specialisation and complexity are influenced by species diversity, but the consequences of changes in species diversity on network properties are not easily understood (Hooper et al., 2005; Landi et al., 2018; Larsen et al., 2005). For example, the loss of functions in an ecosystem not only correlates with the degree of specialisation and number of interactions within the network but also with changes in the number of species (Baiser et al., 2011; Dunne et al., 2002). Changes in species diversity can influence interaction networks not only through local differences (at the level of alpha diversity), but also through differences in diversity between sites (beta diversity), and through differences in the landscape species pool (gamma diversity). Such changes can depend on the different environmental conditions, especially for anthropogenic environments (Aguilar-Trigueros et al., 2017; Cadotte & Tucker, 2017). However, it remains unclear how differences in species diversity between natural and anthropogenic environments affect species interactions and overall network properties.

Anthropogenic alteration of the environment causes homogenisation

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of biological communities, and in urban areas this process largely depends on the degree of habitat heterogeneity that is preserved throughout the landscape including peri-urban habitats (McKinney, 2006; McKinney & Lockwood, 1999; Sexton & Egerer, 2026). For some taxa, such as birds and arthropods, urban conditions often reduce the occurrence of specialist species. Consequently, urban assemblages tend to be dominated by fewer common, highly adaptable generalist species, resulting in less diverse and more homogeneous assemblages compared to those in natural, peri-urban habitats (Hahs et al., 2023; Knop, 2016; Morelli et al., 2016). Because of the erosion of urban diversity, species networks and their specialised interactions can also be eroded. At the same time, urban habitats can have higher species richness of certain taxonomic groups, such as trees, than natural habitats (Augustinus et al., 2024). In some cases, predator – prey networks, such as insectivorous bats and their prey, can even include more species and interactions in urban green areas than in the surrounding natural areas (Scholz et al., 2025). Hence, the linkages between species diversity and network properties are not easily predicted.

Understanding interactions in urban networks is important for preserving key functions emerging from predator - prey interactions, which consist of insect and pest control, and tree biosecurity. Among the main predators of arthropods are birds, which in urban habitats can include many insectivorous species (Basile et al., 2025a; Ibáñez-Álamo et al., 2020, 2024). The diversity and predation rate of birds on arthropods tends to increase with urban tree canopy cover, eventually approaching that of forests (Basile et al., 2025b; Schillé et al., 2025). However, it is not clear whether those interactions are influenced by prey species diversity and composition, and to what extent predator – prey network properties differ between urban and peri-urban habitats. Studies from agricultural habitats, such as orchards, highlighted the role of neutral processes, i.e., random encounters of predators and prey that were independent of prey diversity (García et al., 2024). In such cases, the overall interaction properties, such as specialisation or number of interactions, were driven by the most common bird species (Jiménez-Albarral et al., 2025). However, studies in different type of networks, such as bird pollinators, suggest that habitat conditions also play a role in determining the degree of interaction specialisation (Morrison & Mendenhall, 2020). Ultimately, understanding how bird – arthropod interactions differ between urban and peri-urban habitats is highly relevant for tree biosecurity, due to the potential role of birds in decreasing herbivory rates and disrupting the spill-over of insect pests from cities to the surrounding natural areas (Branco et al., 2019; Mills, 2001; Paap et al., 2017; Theodorou, 2022; Vidal & Murphy, 2018).

Here, we conducted an exploratory case study comparing bird – arthropod interactions in paired urban parks and forests with similar levels of bird diversity and abundance. We built predator – prey networks by using high throughput DNA metabarcoding to identify birds' prey from faecal samples. Our objectives were to compare: (1) the richness and diversity of the prey communities between habitats, (2) the heterogeneity of prey community composition in each habitat, and (3) the predator – prey network properties. As we did not measure arthropod availability in the two habitats, our case study focused on the realised diet of the bird assemblages, which is only a fraction of the available arthropod diversity. Thus, we assumed that, although urbanisation can alter arthropod communities, urban parks, with their heterogeneity of habitats, can still support a wide variety of prey and diverse bird assemblages. Therefore, we hypothesised that richness and diversity of prey in the realised diet of birds would be similar between habitats, but that prey species composition would be different. Furthermore, due to the homogenisation of both predator and prey assemblages, we hypothesised that network properties would differ between habitats, with a loss of interaction specialisation in urban areas. Ultimately, while our case study does not allow broader generalisations, we aim to provide insights into what differentiates urban predator – prey networks from their forest counterparts.

Methods

Bird sampling

We collected faecal samples from birds in urban parks and peri-urban forests in the cities of Zurich and Lugano (Switzerland) from June to August 2024. In each city, we selected one urban and one forest site separated by ~3 km with comparable elevation and climate. Forests were managed for recreation with no influence of timber removal in the surrounding of the sampling sites, except for occasional maintenance operations. Urban parks were characterized by large trees and dense bushes alternated with open areas covered in grass. Habitat differences resulted in bird species composition only partly overlapping between urban and forest sites, although overall bird abundance and diversity were similar, according to previous findings from the same study areas (Basile et al., 2025a). We used 30 m of mist-nets and generic forest bird soundscape playbacks to lure and capture birds during the first and last 3 – 4 h of daylight for a total of nine days at urban sites and fifteen days at forest sites (Bibby et al., 2000). We identified the species of each captured individual and ringed it with an alphanumeric aluminium ring to distinguish individuals, alongside taking several biometric variables such as sex, age, wing chord length, tarsus length, fat, muscle and weight. We then placed each bird in a single-use paper bag placed inside a cotton bag for a maximum of ten minutes to allow for defecation, before releasing it (Hoenig et al., 2022). We used sterile cotton buds and sterile toothpicks to collect the faecal samples and stored them in 2 mL screw-capped tubes filled with 1 mL of ethanol puriss. (Sigma-Aldrich). We collected one faecal sample from each individual of tree- and shrub-dwelling insectivorous and omnivorous bird species, including also those species that may occasionally include insects in their diet, such as house sparrows (Brzek et al., 2009). To assess the potential bias in species composition arising from species-specific behavioural differences in capture probability, we compared the species composition of captured birds with the species composition measured at each site with point count surveys (Basile et al., 2025a). The comparison indicated that captured bird species overlapped with ~ 35% and 50% of the observed bird species at the forest sites of Lugano and Zurich, respectively, and with 60% and 80% of the observed bird species at the urban sites of Lugano and Zurich, respectively.

Sample preparation, DNA extraction and library preparation

We stored the faecal samples in a refrigerator at −20 °C until DNA extraction. We dried faecal samples and then ground them with a swing mill (Retsch 400: Qiagen) using two 3-mm metal beads. We isolated DNA in four runs using the QIAamp Fast DNA Stool Mini Kit instructions for pathogen detection (Qiagen) in a sterile bank. We selected the minibarcode CFMRb, which was developed to study the arthropod diet of animals and amplifies a 180-basepair (bp) region of the mitochondrial cytochrome c oxidase gene (COI) (Jusino et al., 2019). We performed a polymerase chain reaction (PCR) using the forward primer LCO1490 (Folmer et al., 1994) and the reverse primer CO1-CFMRb (Jusino et al., 2019). We tested each sample in triplicates to account for biases of individual PCR reactions (Huggett et al., 2008). The primers included the Illumina adapter overhang sequences, 0–3 'N' spacer regions (Naik et al., 2023) and the CFMRb target primers (synthesized at Integrated DNA Technologies). Afterwards, we pooled the triplicates of each sample and verified by gel electrophoresis on a 1.5% agarose gel prior to purification using the Agencourt AMPure XP system (Beckman Coulter) with 0.8x concentration. The index PCR reactions included eight negative control samples of the DNA extraction and the first PCR. We sent the library to the Lausanne Genomic Technologies Facility (University of Lausanne; https://wp.unil.ch/gtf/) for sequencing on an AVITI benchtop sequencing system (Element Biosciences), where it ran on two lanes.

Bioinformatics

Bioinformatic analysis was performed at the Genetic Diversity Center of the ETH Zurich using a custom pipeline. The base call files were reformatted into FASTQ files using the short-read aligner BBmap v39.01 (Bushnell, 2014). The sequence analysis tool USEARCH v11.0.667 (Edgar, 2010) was used to perform data cleaning steps. Filtered sequences were then de-replicated with the algorithm UPARSE (Edgar, 2013) to obtain unique amplicons and denoised using the UNOISE algorithm implemented in USEARCH (Edgar, 2016). Thus, we obtained zero-radius Operational Taxonomic Units (zOTUs, also called Amplicon Sequence Variant, ASV) discarding singletons and chimeras in the process. As zOTUs identify all correct amplicon sequences in the dataset with differences down to the single nucleotide (Callahan et al., 2017), one species might have more than one zOTU assigned. All zOTUs were then compared against the reference sequences in the MIDORI2 database (Leray et al., 2022), predicting taxonomies with the SINTAX command implemented in USEARCH. SINTAX predicts taxonomy by using k-mer* similarity to identify the top hit in a reference database and provides bootstrap confidence for all ranks in the prediction (Edgar, 2016). We set a minimum threshold of 0.85, against the commonly used 0.8, but the real assignments were higher and scored 0.972 for the phylum Arthropoda. After analysing the differences in zOTU composition between the two lanes using a permutational analysis of variance (PERMANOVA), which showed fully overlapping results ($F = 0.04$, d.f. $= 1$, $p = 1$), we merged the samples from the two lanes.

Statistical analysis

Prey taxa filtering and preliminary composition assessment

After the taxonomic classification, we filtered out all zOTUs that could not be assigned to at least the taxonomic rank of family, all zOTUs

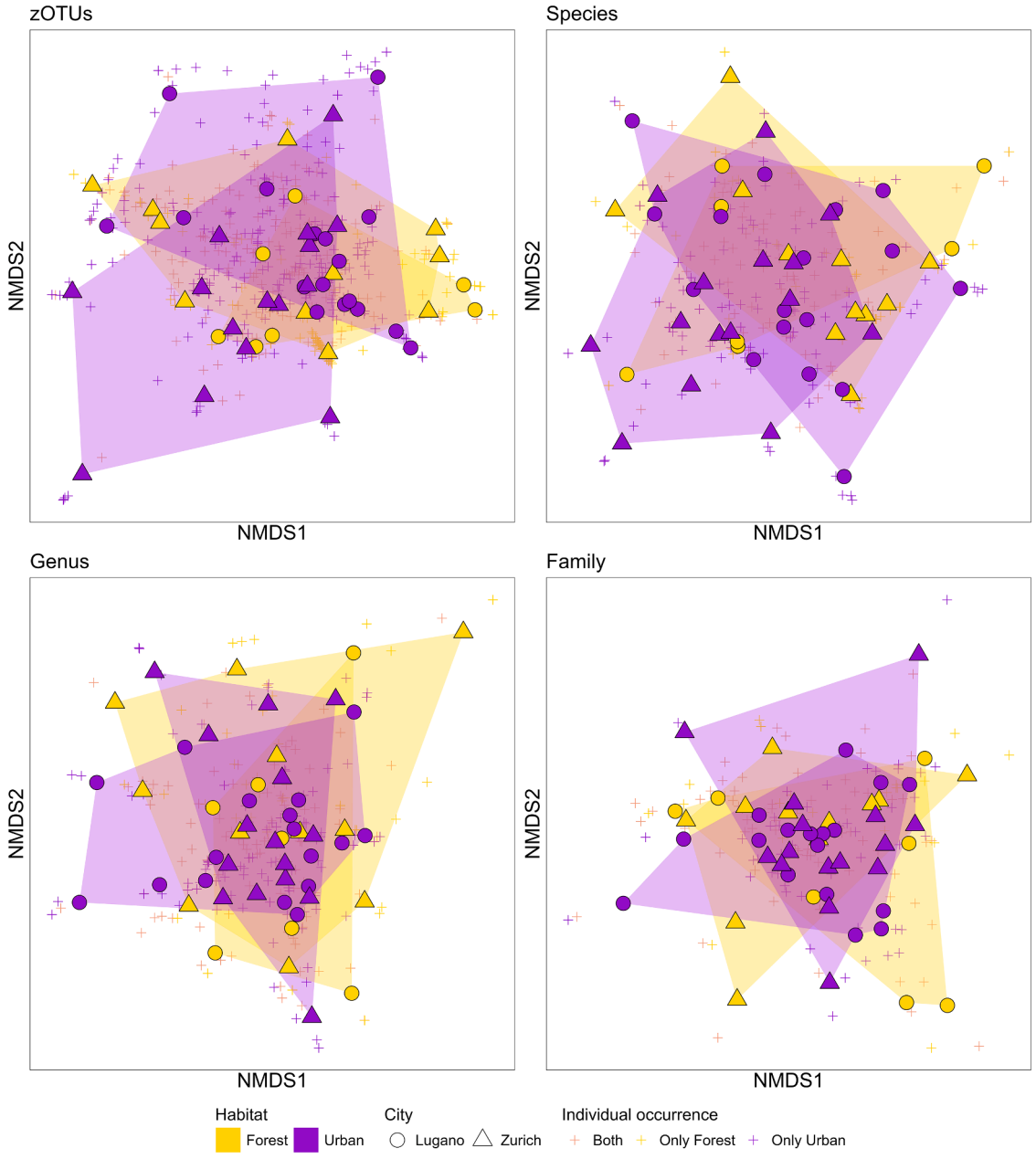


Fig. 1. NMDS of bird – arthropod networks for each sampling site in forest (yellow) and urban (purple) habitats of the cities of Lugano (circles) and Zurich (triangles). Circles and triangles show individual bird samples while crosses show individual prey. Shaded polygons delineate the convex hull occupied by each network in the NMDS space.

with a read count smaller than that of the negative controls, all singletons, and all non-arthropods taxa (Deagle et al., 2019; Drake et al., 2022). We also excluded the taxa Sarcoptiformes, Mesostigmata, Ixodida and Collembola that could occur in the samples from non-dietary inclusion such as minute-sized arthropods that can be prey of other arthropods or can occur on the external body part of birds (Sheppard et al., 2005).

Before testing for differences between urban parks and forests, we evaluated whether the samples from the same habitat were comparable between the cities. Thus, we performed a permutational multivariate analyses of variance (PERMANOVA) on the prey communities to assess differences between cities nested within habitats. We compared predator – prey networks using bird individuals and prey, at the four taxonomic ranks of zOTU, species, genera and families. We weighted prey occurrence by sequence read counts and scaled them using Aitchison distances that are based on centered log-ratio transformation adapted to sparse matrices including many zeros, typical of metabarcoding data (Aitchison et al., 2000; Martino et al., 2019). We performed PERMANOVAs with 1000 permutations with the R package 'vegan' and visualised the bird – arthropod networks with non-metric multidimensional scaling (NMDS) (Mcardle & Anderson, 2001). As we did not find significant differences in prey composition at all taxonomic ranks ($F_{zOTUs} = 1.13, p = 0.36$; $F_{species} = 0.91, p = 0.46$; $F_{genus} = 1.89, p = 0.06$; $F_{family} = 1.14, p = 0.33$), we assumed that samples of prey assemblages were comparable and could be further analysed (Fig. 1).

Prey diversity and composition analysis

We estimated species richness and diversity of prey in urban parks and peri-urban forests with rarefaction and extrapolation techniques to standardise by sample coverage. We assessed the alpha and gamma diversity of prey at four taxonomic ranks (zOTU, species, genus and family) employing a diversity decomposition approach based on Hill numbers of order $q = 0$, 1 and 2, which correspond to species richness, Shannon diversity and Simpson diversity, respectively (Chao, Chiu et al., 2014; Chao et al., 2023). To assess the heterogeneity of prey composition in each habitat, we used the same rarefaction and extrapolation approach to calculate beta diversity and its decomposed components of non-overlap and turnover metrics using Jaccard-type dissimilarities (Chao & Ricotta, 2019). We considered that bird assemblages could differ in prey species composition and number of individuals, although they included the same number of predator species (8) for each habitat. To overcome those differences, we weighted prey taxon occurrence by the number of zOTUs, as a proxy of abundance that is independent of PCR amplification bias, and compared estimates at sample coverage of 0.9, for all diversity metrics. The overall diversity analysis was performed with the R package 'iNEXT.beta3D' (Chao et al., 2023).

Predator - prey network analysis

To compare predator – prey network attributes between habitats, we measured functional complementarity (FC), interaction specialization (H2'), niche overlap (NO), and weighted nestedness (wNODF) (Almeida-Neto et al., 2008; Blüthgen et al., 2006; Burgos et al., 2007; Devoto et al., 2012; Memmott et al., 2004). We used these indices to measure the network properties considering the entire bird assemblages and the four taxonomic ranks of prey. We measured the distribution of interactions across prey (FC), the selectivity of interactions between bird assemblages and prey (H2'), the overlap in the resource use among bird assemblages within habitats (NO), and the number of shared interactions between bird assemblages and prey (wNODF). We weighted data by interaction frequency to account for potential sampling bias (Blüthgen et al., 2006; Dormann et al., 2009). We used both sequence read counts or the simple frequency of zOTUs for each prey taxon for the analysis, but the two metrics returned almost identical results (Figure S1), hence we adopted only the first one.

To assess how much the observed network were specific to each habitat, we tested them against null models that assumed an equal probability of interactions for all species (Vázquez et al., 2009). We considered that our empirical measures could be significantly larger or smaller than the null models, which would indicate that some properties were different than expectations. For instance, an observed H2' higher than the null model would indicate that some prey were selected by some predators more often that the expectations. In addition, we also looked at differences in predictions between habitats. We used *z*-scores for testing the network indices against 1000 simulated null networks and used a two-tailed *z*-test ($p < \alpha$; $\alpha = 0.05$).

Due to the larger size of the urban samples, we performed a sensitivity analysis to determine whether differences in network properties were driven by sample size. We downsampled urban networks randomly ten times and analysed them in the same way. Null models were also recalculated for the downsampled networks. The sensitivity analysis is reported in the supporting information (Figure S1) and indicated that sample size only marginally influenced one network index, with no influence on all others. Network analyses were performed with the R package 'bipartite' (Dormann et al., 2009).

Results

We collected 18 faecal samples in forests and 32 in cities (Table 1). Among the most abundant bird species, we caught 18 blackcaps (*Sylvia atricapilla*), ten great tits (*Parus major*), and seven European robins (*Erithacus rubecula*). The initial list of prey taxa was derived from 131,102,554 sequencing reads and included 1363 zOTUs, of which 803 were assigned to 489 species (Fig. 2). Of those prey species, 229 were found in forest and 341 in urban habitats, with 81 species found in both habitats (Fig. 2). The predator – prey network of urban habitats included more prey species than its forest counterpart, though both included the same number of predator bird species (Fig. 3).

Rarefaction and extrapolation analysis of prey assemblages indicated that sample coverage differed between the two habitats - with 0.66 (range 0.3 – 0.93) in forests and 0.81 (range 0.6 – 0.95) in urban habitats. Standardised estimates of alpha and gamma richness ($q = 0$) at 90% of the sample coverage showed overlap between habitats for the taxonomic ranks of family, genus and species. In contrast, Shannon and Simpson diversity were significantly higher in forests (Fig. 4). Particularly for the species rank, the decrease with Hill numbers in alpha and gamma diversity of prey was more pronounced in urban habitats than in forests (forest: $\alpha_{q=0} = 236.5 \pm 22$ SE, $\alpha_{q=1} = 116.4 \pm 8.7$ SE, $\alpha_{q=2} = 37.1 \pm 4.5$ SE; urban: $\alpha_{q=0} = 272.9 \pm 16.6$ SE, $\alpha_{q=1} = 68.8 \pm 4.1$ SE, $\alpha_{q=2} = 12.7 \pm 1.1$ SE; forest: $\gamma_{q=0} = 399 \pm 36.9$ SE, $\gamma_{q=1} = 181.5 \pm 13.9$ SE, $\gamma_{q=2} = 57 \pm 6.6$ SE; urban: $\gamma_{q=0} = 414.6 \pm 22.6$ SE, $\gamma_{q=1} = 94.5 \pm 5.7$ SE, $\gamma_{q=2} = 15.2 \pm 1.3$ SE). The estimates at the zOTU rank showed only a higher alpha Simpson diversity in forests, whereas gamma richness of zOTUs was significantly higher for urban habitats. Beta diversity, including non-overlap and turnover, showed mostly overlapping results across Hill

Table 1
Bird species and number of individuals captured at each site.

Species		Lugano		Zurich	
Common name	Scientific name	Forest	Urban	Forest	Urban
Short-toed treecreeper	*Certhia brachydactyla*		1		
European robin	*Erithacus rubecula*	2	1	4	
Eurasian jay	*Garrulus glandarius*	2	1		
Great tit	*Parus major*	1	7		2
House sparrow	*Passer domesticus*				2
Common chiffchaff	*Phylloscopus collybita*				1
Marsh tit	*Poecile palustris*			1	
Eurasian blackcap	*Sylvia atricapilla*		7	2	9
Euraisan wren	*Troglodytes troglodytes*			2	
Common blackbird	*Turdus merula*	2		1	1
Song thrush	*Turdus philomelos*			1	

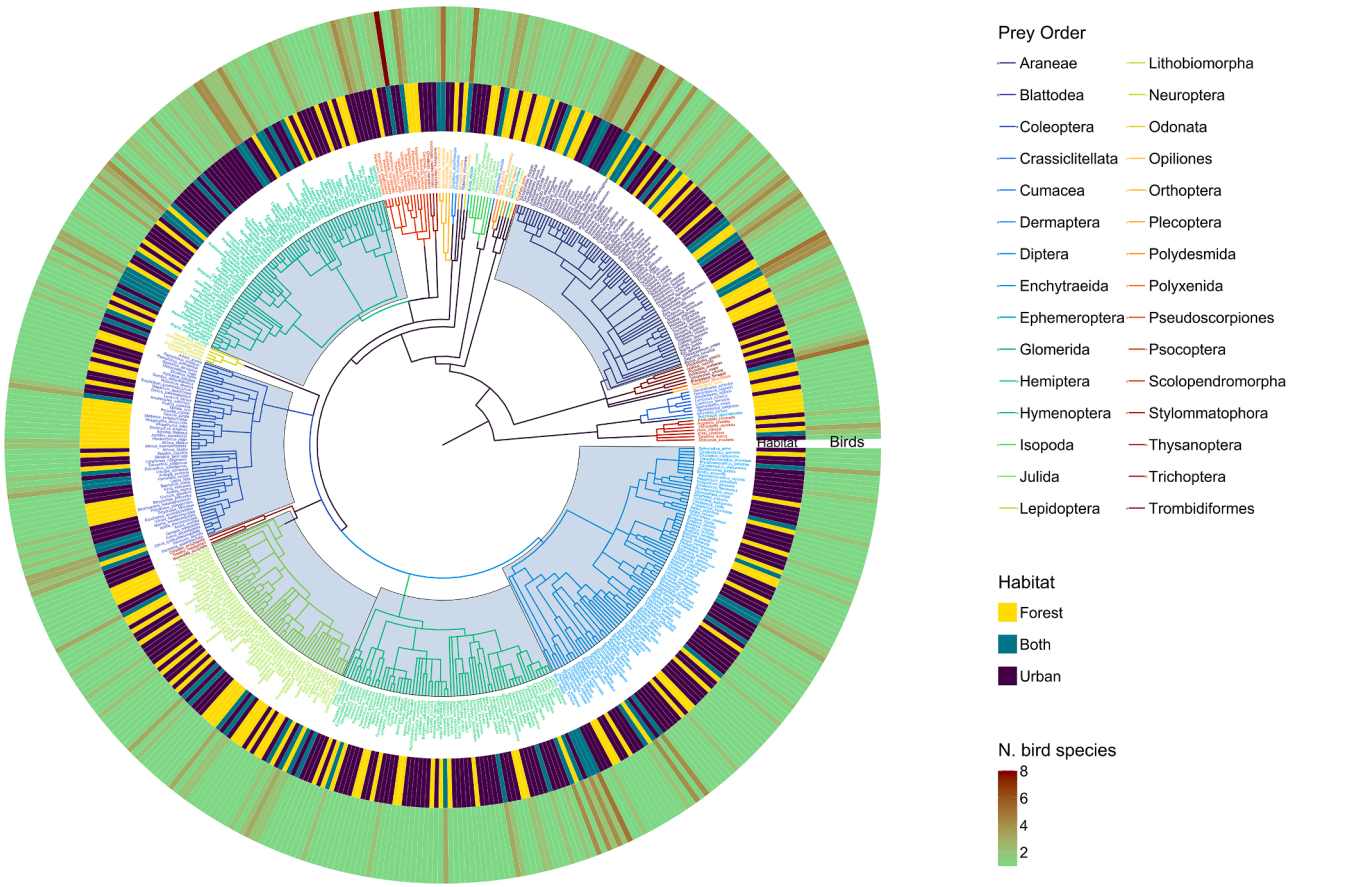


Fig. 2. Equidistant phylogenetic tree of prey species, with the most diverse orders in blue-shaded highlight (anticlockwise from the tree root): Araneae, Hemiptera, Coleoptera, Lepidoptera, Hymenoptera, Diptera. The tree was generated using NCBI taxonomy. The colours of 'Habitat' indicate whether the prey species was identified from faecal samples of birds from forest, urban or both habitats. The colours for 'N. bird species' indicate how many species of birds included the given prey in their faecal samples.

numbers and between habitats (Fig. 4). Shannon beta diversity of family and Simpson beta diversity of species were higher in forests, while beta richness and Shannon beta diversity of zOTUs were higher in urban habitats.

Urban networks were more redundant (FC) than forest networks for all taxonomic ranks (Fig. 5) and both urban and forest network were more redundant than the null model expectations (FC_{urban}: $z_{species} = 6.11$, $p < 0.001$; FC_{forest}: $z_{species} = 6.32$, $p < 0.001$; similar p values for zOTU, genus and family ranks). Urban networks were also less specialised (H2') than forest networks (Fig. 5). However, urban networks were significantly more specialised than null model expectations for family, genus and species ranks ($H2'_{urban}$: $z_{species} = 4.18$, $p < 0.001$; similar p values for genus and family ranks), while they were significantly less specialised for zOTUs ($H2'_{urban}$: $z_{zOTU} = -6.2, p < 0.001$). For forest networks, the H2' index for family was more specialised than expectation, whereas genus, species and zOTUs were within the null model expectations. Niche overlap (NO) was higher in urban than in forest networks for all taxonomic ranks (Fig. 5). In both urban and forest networks, niche overlap of prey species, genera and families was lower than null model expectations (NO_{urban}: $z_{species} = -8.41$, $p < 0.001$; similar p values for genus and family ranks), while the niche overlap in prey zOTUs was within null model expectations. Niche overlap of urban networks was also higher than forest null networks at all taxonomic ranks except family. Urban networks were more nested (wNODF) than forest networks (Fig. 5). The comparison with null models indicated that urban prey families, genera and species were less nested than expectations ($wNODF_{urban}$: $z_{species} = -2.55$, $p < 0.01$; $p < 0.05$ for genus and family ranks), but prey zOTUs were more nested than expectations ($wNODF_{urban}$: $z_{zOTU} = 3.67$, $p < 0.01$). Only for the family rank, urban networks were similar in wNODF to forest null networks. The sensitivity analysis confirmed all comparisons except for functional complementarity. FC was lower for the downsampled urban network, but still significantly higher than forest networks (Figure S1).

Discussion

In this case study, we compared predator – prey networks from urban parks and peri-urban forests. Our findings indicated that the diversity of prey in urban parks was lower for all taxonomic ranks, despite the species richness was similar. Contrary to our hypothesis, the prey community of urban parks showed particularly lower Simpson diversity, which assigns more weight to highly abundant species (Chao, Gotelli et al., 2014). We also found that the beta diversity of prey species was lower in urban birds, in agreement with our hypothesis, indicating that their diet was more homogeneous than that of forest birds. The lower diversity of urban prey was also reflected by a decline in network properties with higher functional complementarity, niche overlap and number of shared interactions, and lower interaction specialisation, which aligned with our hypothesis. Altogether, our findings indicated that, within our case study, urban predator – prey network are less selective and more homogeneous than forest networks.

Our findings are partly expected as urbanisation decreases the diversity of arthropods (Fenoglio et al., 2020). Thus, urban bird diets were more similar among individuals and sites than forest diets, in spite of potential geographic differences. The presence of non-native plants and non-native insects in urban habitats may have affected the results, as

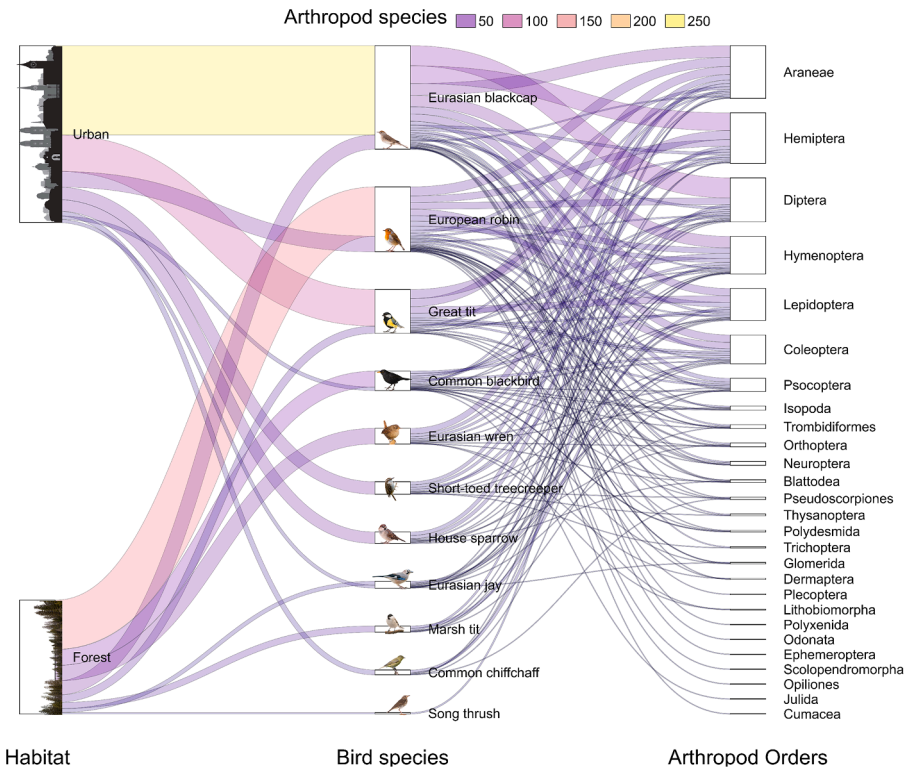


Fig. 3. Predator – prey networks of forest and urban habitats. Bar size and edge colours indicate the number of arthropod species included in each habitat, species of bird faecal sample or arthropod order.

those are known to negatively affect bird predation rates, due to sub-optimal habitat condition for both predators and prey (Basile et al., 2025a; Jarrett et al., 2020; Narango et al., 2018). This may result in birds narrowing their choices to the most abundant prey. As birds can have different degrees of prey selectivity, the diversity of their prey is not necessarily related to the diversity of available arthropods. We acknowledge that some differences could have been driven by different availability of arthropod species between habitats, yet the standardised diversity estimates indicated that the diversity of prey was lower for urban birds. We note that we restricted the sampling to tree-dwelling, insectivorous species to enhance comparability between habitats.

In line with that, we found urban predator – prey networks to be less specialised and with more redundant interactions than forest ones. Higher generalisation in urban habitats has been observed for plant-hummingbird pollinator and plant-frugivore bird networks before (Maruyama et al., 2019; Schneiberg et al., 2020). However, a decrease in specialisation is usually driven by a loss of specialist predators, while in this study we found a loss of selectivity associated with lower prey diversity even if the predator assemblage did not include true specialists and partly overlapped between habitats. Studies on interspecific competition usually found higher niche segregation among co-existing insectivorous birds in natural and semi-natural conditions with high diversity of prey (Bumelis et al., 2022; Mansor et al., 2022). That is, more overlap and redundancy with less prey diversity. Accordingly, when going from peri-urban forests to urban areas, we found higher overlap and redundancy with a decline in prey diversity.

These findings suggest that in the urban habitats there was an increase in random prey encounters, which were likely driven by very abundant prey. Similar patterns have been observed in other habitats, where different insectivorous bird species shared a wide range of prey (Orłowski & Karg, 2013; Zurdo et al., 2023). Although not in urban conditions, similar homogenisation of predator – prey interactions have been observed with increasing agricultural cover for both bird and arthropod predators (da Silva et al., 2024; Riggi et al., 2017). However, some network properties were different than null model expectations, suggesting that the homogenisation of predator – prey interactions in urban habitats was milder than expected.

We acknowledge several limitations inherent to the design and sample size of this case study. First, our inferences are based on four sites and a relatively small number of faecal samples, which represents a low sampling effort compared to broader ecological network studies. Second, because a faecal sample represents a snapshot of an individual bird's diet, we could only partly characterize their entire diet and interactions with prey. Third, comparisons with point counts revealed an incomplete representation of the local bird assemblages in our mist-netting data, with some true specialists (such as woodpeckers) going entirely unsampled (Basile et al., 2025a). Consequently, we cannot exclude the possibility that the reconstructed networks in this study do not fully characterize the complexity of the underlying complete predator – prey networks. While our sensitivity analysis suggests we may have only slightly overestimated the functional complementarity of urban networks due to uneven sampling between habitats, the low number of sites dictates that our findings cannot be generalised beyond this specific study system without further replication.

Neutral processes are known to drive the delivery of functions in several species networks. For example, pest control services in experimental settings tend to be driven by the most abundant predators (Mei et al., 2024). Similarly, crop pollination is driven by the most abundant pollinators under agricultural intensification (Kleijn et al., 2015). Therefore, the decline in specialisation that we observed in urban networks may have broader implications for ecosystem functioning, though testing these outcomes was beyond the scope of this case study.

Conclusions

In conclusion, this case study provides preliminary evidence that urban predator – prey networks may be more homogeneous and less specialised than those in peri-urban forests. However, these results must

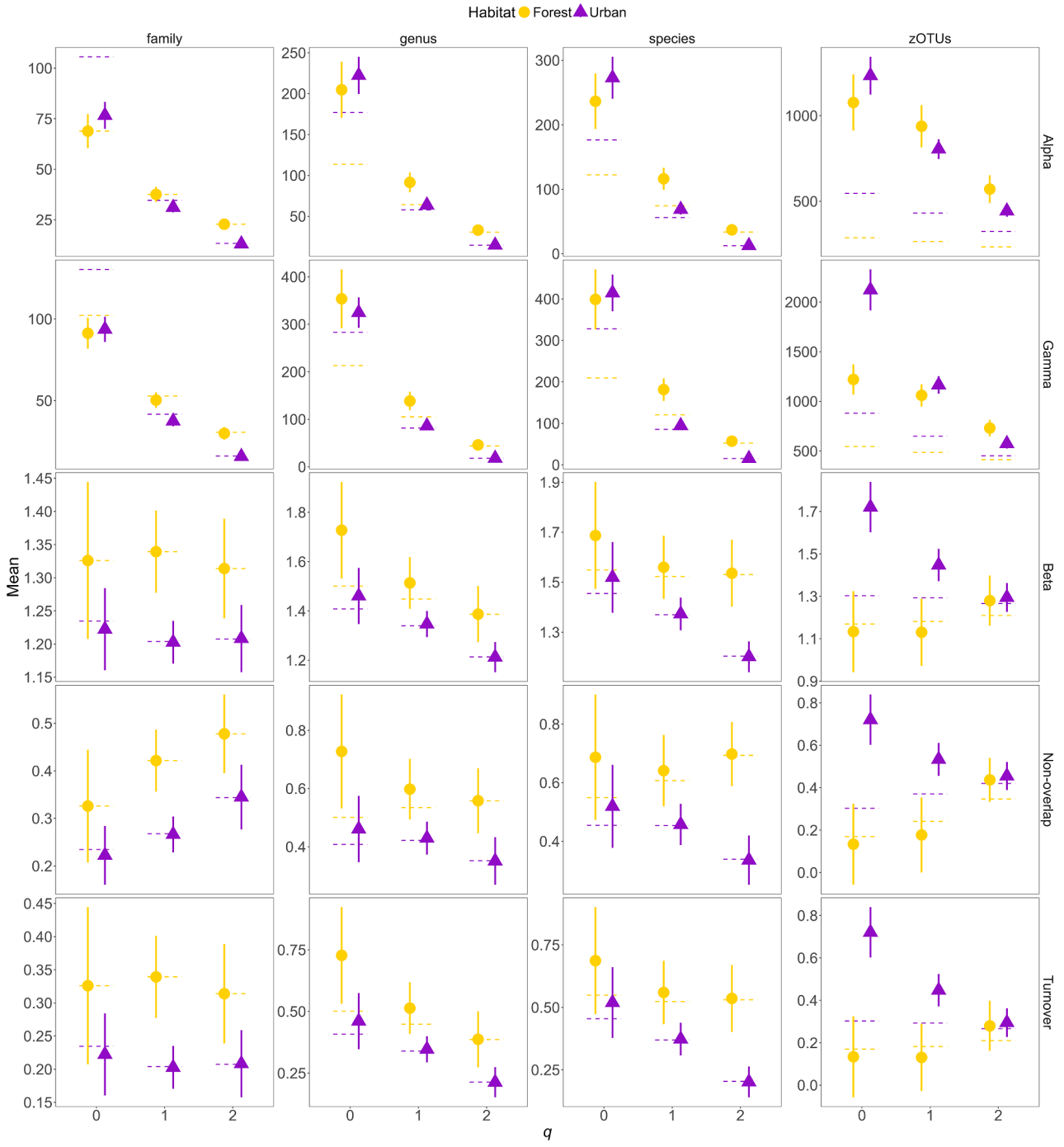


Fig. 4. Alpha, beta and gamma diversity of prey assemblages of forest (yellow circles) and urban (purple triangles) birds. Beta diversity is shown also with its Jaccard-type non-overlap and turnover metrics. Circles and triangles show mean diversity estimates and solid lines 95% confidence intervals for a standardised sample coverage of 90%. Horizontal dashed lines show the observed diversity values, for which the sample coverage was above 90% in some cases. Estimates are shown for four taxonomic ranks of prey and for different Hill numbers $q = 0$, 1, 2, which represent different weights that species abundances have in the diversity calculation and correspond to species richness ($q = 0$), Shannon diversity ($q = 1$), and Simpson diversity ($q = 2$).

be interpreted with caution. To determine whether the patterns observed here extend beyond this specific system, future research should undertake greater replication across multiple urban – forest paired sites and include more extensive within-site dietary sampling. Changes in network properties may also depend on individual shift in dietary preferences between habitats. Although our study was not designed for testing this, future research could aim at collecting more samples from the same species in both habitats to better understand potential causes of shifts.

Furthermore, to disentangle the mechanisms driving these network shifts, future studies should directly quantify prey availability and incorporate measurements of habitat structure, such as canopy cover and microhabitat availability. Urbanisation is often studied as a gradient of increasing disturbance and habitat change (Sol et al., 2014), while our findings are from a country with a fairly nuanced urbanisation pressure. Therefore, future studies could expand the scope of research beyond comparison between habitats and to other variables describing habitat structure.

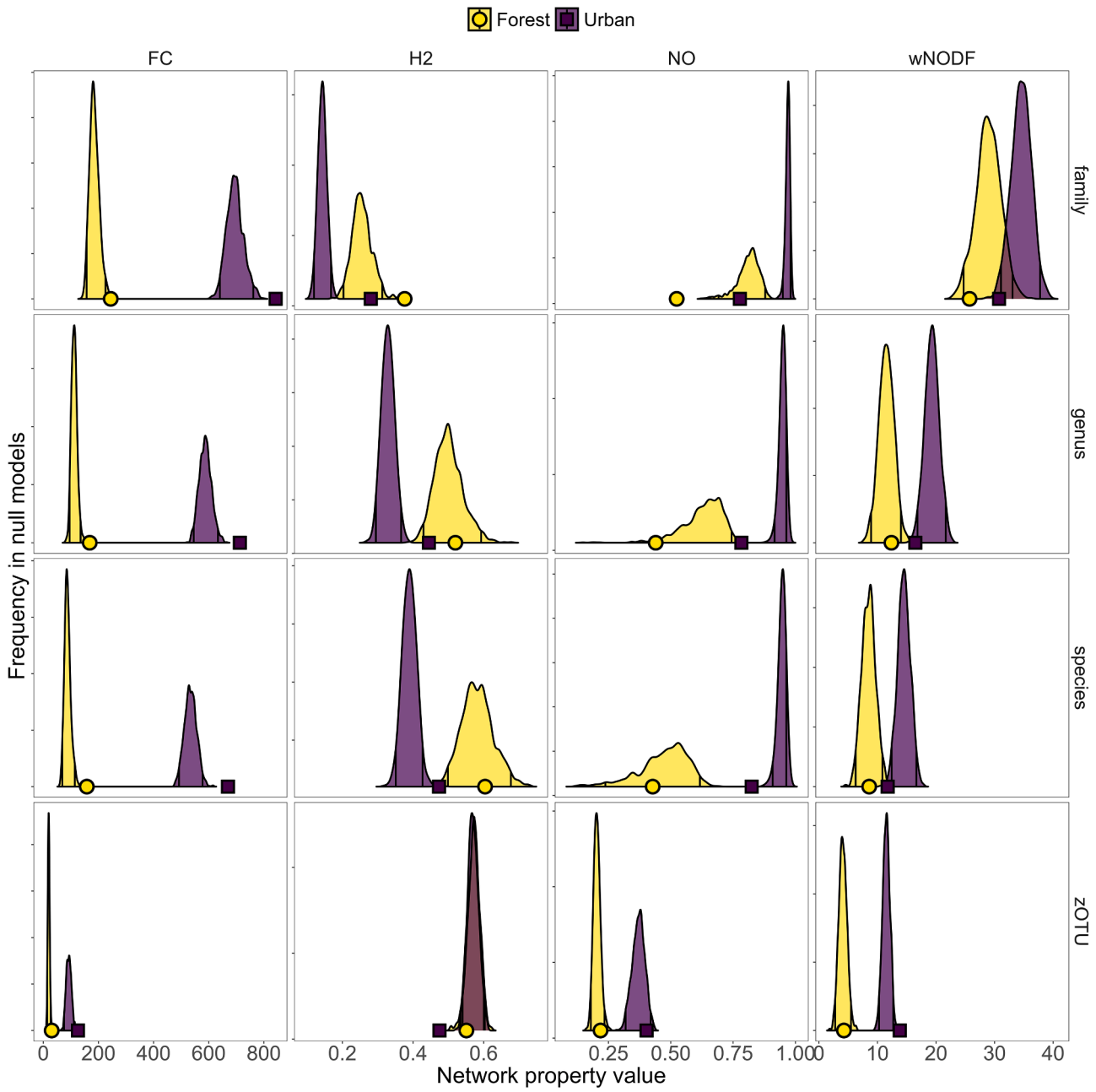


Fig. 5. Urban (purple) and forest (yellow) network indices measured for predator – prey interactions and simulated with 1000 null models. Dots and squares indicate the observed values for forest and urban habitats, respectively. The density curves indicate the distribution of the expected values from the null models. The black lines show the 95% density distribution. FC = functional complementarity; H2 = specialisation index; NO = niche overlap; wNODF = nestedness.

If the findings of this case study hold true more broadly, they support hypotheses from previous studies suggesting that preserving forest-like characteristics in urban green spaces could promote species interaction heterogeneity (Basile et al., 2025b; Schillé et al., 2025). Maintaining complex, specialised predator – prey interactions in cities might ultimately be important for supporting ecosystem functions such as tree biosecurity and insect pest control, but verifying the direct delivery of these functions remains a critical endeavour for future research.

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Data availability

Data are available from EnviDat.

Basile, M., Brockerhoff, E. (2025). Urban bird capture data with prey species and fungal community. *EnviDat.*https://www.doi.org/10.16904/envidat.639.

The genetic data is available on NCBI, Bioproject PRJNA1277191 https://dataview.ncbi.nlm.nih.gov/object/PRJNA1277191?reviewer=trcsiag925tl2a9ma64cuofr1i

The genetic data is available also from EnviDat.

Basile, M., Brockerhoff, E., Cornejo, C. (2025). Metabarcoding of urban and forest bird faecal samples. EnviDat. https://www.doi.org/10.16904/envidat.662.

Ethic statement

Bird captures were performed under the authorization from the Swiss Federal Office of the Environment, n. BAFU-417.525–06–3/16/1. Samples from live birds were collected under the authorization from the Cantonal Veterinary Offices of Ticino and Zurich, N -36665-TI/2024/2024.

CRediT authorship contribution statement

Marco Basile: Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Carolina Cornejo:** Writing – review & editing, Supervision, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Matthias Tschumi:** Writing – review & editing, Investigation, Funding acquisition, Conceptualization. **Eckehard G. Brockerhoff:** Writing – review & editing, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.baae.2026.09.001.

References

Aguilar-Trigueros, C. A., Rillig, M. C., & Ballhausen, M. B. (2017). Environmental filtering is a relic. A response to Cadotte and Tucker. *Trends in Ecology and Evolution, 32*(12), 882–884. https://doi.org/10.1016/j.tree.2017.09.013

Aitchison, J., Barceló-Vidal, C., Martín-Fernández, J. A., & Pawlowsky-Glahn, V. (2000). Logratio analysis and compositional distance. *Mathematical Geology, 32*(3), 271–275. https://doi.org/10.1023/A:1007529726302

Almeida-Neto, M., Guimarães, P., Guimarães, P. R., Loyola, R. D., & Ulrich, W. (2008). A consistent metric for nestedness analysis in ecological systems: Reconciling concept and measurement. *Oikos (Copenhagen, Denmark), 117*(8), 1227–1239. https://doi.org/10.1111/j.0030-1299.2008.16644.x

Augustinus, B. A., Abegg, M., Queloz, V., & Brockerhoff, E. G. (2024). Higher tree species richness and diversity in urban areas than in forests: Implications for host availability for invasive tree pests and pathogens. *Landscape and Urban Planning, 250*, Article 105144. https://doi.org/10.1016/j.landurbplan.2024.105144

Baiser, B., Ardeshiri, R. S., & Ellison, A. M. (2011). Species richness and trophic diversity increase decomposition in a Co-evolved food web. *PLoS ONE, 6*(5), Article e20672. https://doi.org/10.1371/journal.pone.0020672

Balvanera, P., Pfisterer, A. B., Buchmann, N., He, J., Nakashizuka, T., Raffaelli, D., & Schmid, B. (2006). Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters, 9*(10), 1146–1156. https://doi.org/10.1111/j.1461-0248.2006.00963.x

Basile, M. (2022). Rare species disproportionally contribute to functional diversity in managed forests. *Scientific Reports, 12*(1), 5897. https://doi.org/10.1038/s41598-022-09624-9

Basile, M., Augustinus, B. A., & Brockerhoff, E. G. (2025a). Tree cover and geographic origin of tree species drive bird functional groups in urban environments. *Wildlife Biology*. , Article e01446. https://doi.org/10.1002/wlb3.01446

Basile, M., Augustinus, B. A., & Brockerhoff, E. G. (2025b). Urban tree canopy cover over 30 % and native trees enhance bird insectivory and tree biosecurity. *Biological Conservation, 310*, Article 111387. https://doi.org/10.1016/j.biocon.2025.111387

Bibby, C. J., Burgess, N. B., Hill, D. A., & Mustoe, S. (2000). *Bird census techniques* (2nd ed.). Academic Press.

Blüthgen, N., Menzel, F., & Blüthgen, N. (2006). Measuring specialization in species interaction networks. *BMC Ecology, 6*(1), 1–12, 10.1186/1472-6785-6-9/TABLES/2.

Branco, M., Nunes, P., Roques, A., Fernandes, M. R., Orazio, C., & Jacte, H. (2019). Urban trees facilitate the establishment of non-native forest insects. *NeoBiota, 52*, 25–46. https://doi.org/10.3897/neobiota.52.36358

Brzek, P., Kohl, K., Caviedes-Vidal, E., & Karasov, W. H. (2009). Developmental adjustments of house sparrow (*Passer domesticus*) nestlings to diet composition. *Journal of Experimental Biology, 212*(9), 1284–1293. https://doi.org/10.1242/JEB.023911

Bumelis, K. H., Cadman, M. D., & Hobson, K. A. (2022). Endogenous biomarkers reveal diet partitioning among three sympatric species of swallows. *Ornithology, 139*(1), 1–13. https://doi.org/10.1093/ornithology/ukab078

Burgos, E., Ceva, H., Perazzo, R. P. J., Devoto, M., Medan, D., Zimmermann, M., & María Delbue, A. (2007). Why nestedness in mutualistic networks? *Journal of Theoretical Biology, 249*(2), 307–313. https://doi.org/10.1016/j.jtbi.2007.07.030

Bushnell, B. (2014). BBMap: A fast, accurate, splice-aware aligner. *BMC Bioinformatics, 13*(1). Number https://escholarship.org/uc/item/1h3515gn.

Cadotte, M. W., & Tucker, C. M. (2017). Should environmental filtering be abandoned? *Trends in Ecology & Evolution, 32*(6), 429–437. https://doi.org/10.1016/j.tree.2017.03.004

Callahan, B. J., McMurdie, P. J., & Holmes, S. P. (2017). Exact sequence variants should replace operational taxonomic units in marker-gene data analysis. *The ISME Journal, 11*(12), 2639–2643. https://doi.org/10.1038/ismej.2017.119

Cardinale, B. J., Srivastava, D. S., Duffy, J. E., Wright, J. P., Downing, A. L., Sankaran, M., Jouseau, C., Cadotte, M. W., Carroll, I. T., Weis, J. J., Hector, A., & Loreau, M. (2009). Effects of biodiversity on the functioning of ecosystems: A summary of 164 experimental manipulations of species richness. *Ecology, 90*(3), 854. https://doi.org/10.1890/08-1584.1. –854.

Chao, A., Chiu, C.-H., & Jost, L. (2014a). Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through hill numbers. *Annual Review of Ecology, Evolution, and Systematics, 45*(1), 297–324. https://doi.org/10.1146/annurev-ecolsys-120213-091540

Chao, A., Gotelli, N. J., Hsieh, T. C., Sander, E. L., Ma, K. H., Colwell, R. K., & Ellison, A. M. (2014b). Rarefaction and extrapolation with Hill numbers: A framework for sampling and estimation in species diversity studies. *Ecological Monographs, 84*(1), 45–67. https://doi.org/10.1890/13-0133.1

Chao, A., & Ricotta, C. (2019). Quantifying evenness and linking it to diversity, beta diversity, and similarity. *Ecology, 100*(12), Article e02852. https://doi.org/10.1002/ECY.2852

Chao, A., Thorn, S., Chiu, C. H., Moyes, F., Hu, K. H., Chazdon, R. L., Wu, J., Magnago, L. F. S., Dornelas, M., Zelený, D., Colwell, R. K., & Magurran, A. E. (2023). Rarefaction and extrapolation with beta diversity under a framework of Hill numbers: The iNEXT.Beta3D standardization. *Ecological Monographs, 93*(4). https://doi.org/10.1002/ecm.1588

da Silva, L. P., Mata, V. A., Lopes, P. B., Pinho, C. J., Chaves, C., Correia, E., Pinto, J., Heleno, R. H., Timoteo, S., & Beja, P. (2024). Dietary metabarcoding reveals the simplification of bird–pest interaction networks across a gradient of agricultural cover. *Molecular Ecology, 33*(8), Article e17324. https://doi.org/10.1111/MEC.17324

Deagle, B. E., Thomas, A. C., McInnes, J. C., Clarke, L. J., Vesterinen, E. J., Clare, E. L., Kartzinel, T. R., & Eveson, J. P. (2019). Counting with DNA in metabarcoding studies: How should we convert sequence reads to dietary data? *Molecular Ecology, 28*(2), 391–406. https://doi.org/10.1111/mec.14734

Devoto, M., Bailey, S., Craze, P., & Memmott, J. (2012). Understanding and planning ecological restoration of plant–pollinator networks. *Ecology Letters, 15*(4), 319–328. https://doi.org/10.1111/j.1461-0248.2012.01740.x

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.

Drake, L. E., Cuff, J. P., Young, R. E., Marchbank, A., Chadwick, E. A., & Symondson, W. O. C. (2022). An assessment of minimum sequence copy thresholds for identifying and reducing the prevalence of artefacts in dietary metabarcoding data. *Methods in Ecology and Evolution, 13*(3), 694–710. https://doi.org/10.1111/2041-210X.13780

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

Edgar, R. C. (2010). Search and clustering orders of magnitude faster than BLAST. *Bioinformatics (Oxford, England), 26*(19), 2460–2461. https://doi.org/10.1093/bioinformatics/btq461

Edgar, R. C. (2013). UPARSE: Highly accurate OTU sequences from microbial amplicon reads. *Nature Methods, 10*(10), 996–998. https://doi.org/10.1038/nmeth.2604

Edgar, R. C. (2016). UNOISE2: Improved error-correction for Illumina 16S and ITS amplicon sequencing. *BioRxiv*. , Article 081257. https://doi.org/10.1101/081257

Fenoglio, M. S., Rossetti, M. R., & Videla, M. (2020). Negative effects of urbanization on terrestrial arthropod communities: A meta-analysis. *Global Ecology and Biogeography, 29*(8), 1412–1429. https://doi.org/10.1111/geb.13107

Folmer, O., Black, M., Hoeh, W., Lutz, R., & Vrijenhoek, R. (1994). DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology, 3*(5), 294–299.

García, D., Rumeu, B., Illera, J. C., Miñarro, M., Palomar, G., & González-Varo, J. P. (2024). Common birds combine pest control and seed dispersal in apple orchards through a hybrid interaction network. *Agriculture, Ecosystems & Environment, 365*, Article 108927. https://doi.org/10.1016/j.agee.2024.108927

Hahs, A. K., Fournier, B., Aronson, M. F. J., Nilon, C. H., Herrera-Montes, A., Salisbury, A. B., Threlfall, C. G., Rega-Brodsky, C. C., Lepczyk, C. A., La Sorte, F. A., MacGregor-Fors, I., Scott MacIvor, J., Jung, K., Piana, M. R., Williams, N. S. G., Knapp, S., Vergnes, A., Acevedo, A. A., Gainsbury, A. M., … Moretti, M. (2023). Urbanisation generates multiple trait syndromes for terrestrial animal taxa worldwide. *Nature Communications, 14*(1), 1–14. https://doi.org/10.1038/s41467-023-39746-1. *2023 141*.

Hoenig, B. D., Snider, A. M., Forsman, A. M., Hobson, K. A., Latta, S. C., Miller, E. T., Polito, M. J., Powell, L. L., Rogers, S. L., Sherry, T. W., Toews, D. P. L., Welch, A. J., Taylor, S. S., & Porter, B. A. (2022). Current methods and future directions in avian diet analysis. *Ornithology, 139*(1), 139. https://doi.org/10.1093/ORNITHOLOGY/UKAB077

Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., Lodge, D. M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A. J., Vandermeer, J., & Wardle, D. A. (2005). Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs, 75*(1), 3–35. https://doi.org/10.1890/04-0922

Huggett, J. F., Novak, T., Garson, J. A., Green, C., Morris-Jones, S. D., Miller, R. F., & Zumla, A. (2008). Differential susceptibility of PCR reactions to inhibitors: An important and unrecognised phenomenon. *BMC Research Notes, 1*(1), 70. https://doi.org/10.1186/1756-0500-1-70

Ibáñez-Álamo, J. D., Izquierdo, L., Mourocq, E., Benedetti, Y., Kaisanlahti-Jokimäki, M.-L., Jokimäki, J., Morelli, F., Rubio, E., Pérez-Contreras, T., Sprau, P., Suhonen, J., Tryjanowski, P., & Díaz, M. (2024). Urban landscape organization is associated with species-specific traits in European birds. *Science of The Total Environment, 908*, Article 167937. https://doi.org/10.1016/j.scitotenv.2023.167937

Ibáñez-Álamo, J. D., Morelli, F., Benedetti, Y., Rubio, E., Jokimäki, J., Pérez-Contreras, T., Sprau, P., Suhonen, J., Tryjanowski, P., Kaisanlahti-Jokimäki, M. L., Møller, A. P., & Díaz, M. (2020). Biodiversity within the city: Effects of land sharing and land sparing urban development on avian diversity. *Science of The Total Environment, 707*, Article 135477. https://doi.org/10.1016/J.SCITOTENV.2019.135477

Jarrett, C., Powell, L. L., McDevitt, H., Helm, B., & Welch, A. J. (2020). Bitter fruits of hard labour: Diet metabarcoding and telemetry reveal that urban songbirds travel further for lower-quality food. *Oecologia, 193*(2), 377–388. https://doi.org/10.1007/S00442-020-04678-W/FIGURES/3

Jiménez-Albarral, J. J., Morán-López, T., Illera, J. C., Miñarro, M., & García, D. (2025). Insectivore diet and abundance determine the contribution of bird species to services and disservices in an agricultural ecosystem. *Ornithological Applications, 127*(2). https://doi.org/10.1093/ornithapp/duaf006

Jusino, M. A., Banik, M. T., Palmer, J. M., Wray, A. K., Xiao, L., Pelton, E., Barber, J. R., Kawahara, A. Y., Gratton, C., Peery, M. Z., & Lindner, D. L. (2019). An improved method for utilizing high-throughput amplicon sequencing to determine the diets of insectivorous animals. *Molecular Ecology Resources, 19*(1), 176–190. https://doi.org/10.1111/1755-0998.12951

Kleijn, D., Winfree, R., Bartomeus, I., Carvalheiro, L. G., Henry, M., Isaacs, R., Klein, A.-M., Kremen, C., M'Gonigle, L. K., Rader, R., Ricketts, T. H., Williams, N. M., Lee Adamson, N., Ascher, J. S., Báldi, A., Batáry, P., Benjamin, F., Biesmeijer, J. C., Blitzer, E. J., … Potts, S. G. (2015). Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. *Nature Communications, 6*(1), 7414. https://doi.org/10.1038/ncomms8414

Knop, E. (2016). Biotic homogenization of three insect groups due to urbanization. *Global Change Biology, 22*(1), 228–236. https://doi.org/10.1111/gcb.13091

Landi, P., Minoarivelo, H. O., Brännström, Å., Hui, C., & Dieckmann, U. (2018). Complexity and stability of ecological networks: A review of the theory. *Population Ecology, 60*(4), 319–345. https://doi.org/10.1007/s10144-018-0628-3

Larsen, T. H., Williams, N. M., & Kremen, C. (2005). Extinction order and altered community structure rapidly disrupt ecosystem functioning. *Ecology Letters, 8*(5), 538–547. https://doi.org/10.1111/J.1461-0248.2005.00749.X

Leray, M., Knowlton, N., & Machida, R. J. (2022). MIDORI2: A collection of quality controlled, preformatted, and regularly updated reference databases for taxonomic assignment of eukaryotic mitochondrial sequences. *Environmental DNA, 4*(4), 894–907. https://doi.org/10.1002/edn3.303

Mansor, M. S., Rozali, F. Z., Davies, S., Nor, S. M., & Ramli, R. (2022). High-throughput sequencing reveals dietary segregation in Malaysian babblers. *Current Zoology, 68*(4), 381–389. https://doi.org/10.1093/cz/zoab074

Martino, C., Morton, J. T., Marotz, C. A., Thompson, L. R., Tripathi, A., Knight, R., & Zengler, K. (2019). A novel sparse compositional technique reveals microbial perturbations. *MSystems, 4*(1). https://doi.org/10.1128/msystems.00016-19

Maruyama, P. K., Bonizário, C., Marcon, A. P., D'Angelo, G., da Silva, M. M., da Silva Neto, E. N., Oliveira, P. E., Sazima, I., Sazima, M., Vizentin-Bugoni, J., dos Anjos, L., Rui, A. M., & Marçal Júnior, O. (2019). Plant-hummingbird interaction networks in urban areas: Generalization and the importance of trees with specialized flowers as a nectar resource for pollinator conservation. *Biological Conservation, 230*, 187–194. https://doi.org/10.1016/j.biocon.2018.12.012

Mcardle, B. H., & Anderson, M. J. (2001). Fitting multivariate models to community data:A comment on distance-based redundancy analysis. *Ecology, 82*(1), 290–297. https://doi.org/10.1890/0012-9658(2001)082[0290:FMMTCD]2.0.CO;2

McKinney, M. L. (2006). Urbanization as a major cause of biotic homogenization. *Biological Conservation, 127*(3), 247–260. https://doi.org/10.1016/j.biocon.2005.09.005

McKinney, M. L., & Lockwood, J. L. (1999). Biotic homogenization: A few winners replacing many losers in the next mass extinction. *Trends in Ecology and Evolution, 14*(Table 1), 450–453. https://doi.org/10.1016/S0169-5347(99)01679-1

Mei, Z., Scheper, J., & Kleijn, D. (2024). Arthropod predator identity and evenness jointly shape the delivery of pest control services. *Pest Management Science, 80*(2), 569–576. https://doi.org/10.1002/ps.7779

Memmott, J., Waser, N. M., & Price, M. V. (2004). Tolerance of pollination networks to species extinctions. *Proceedings of the Royal Society of London. Series B: Biological Sciences, 271*(1557), 2605–2611. https://doi.org/10.1098/rspb.2004.2909

Mills, N. J. (2001). Factors influencing top-down control of insect pest populationsin biological control systems. *Basic and Applied Ecology, 2*(4), 323–332. https://doi.org/10.1078/1439-1791-00070

Morelli, F., Benedetti, Y., Ibáñez-Álamo, J. D., Jokimäki, J., Mänd, R., Tryjanowski, P., & Møller, A. P. (2016). Evidence of evolutionary homogenization of bird communities in urban environments across Europe. *Global Ecology and Biogeography, 25*(11), 1284–1293. https://doi.org/10.1111/geb.12486

Morrison, B. M. L., & Mendenhall, C. D. (2020). Hummingbird–Plant interactions are more specialized in forest compared to coffee plantations. *Diversity, 12*(4), 126. https://doi.org/10.3390/d12040126

Naik, T., Sharda, M., C P, L., Virbhadra, K., & Pandit, A. (2023). High-quality single amplicon sequencing method for illumina MiSeq platform using pool of 'N' (0–10) spacer-linked target specific primers without PhiX spike-in. *BMC Genomics, 24*(1), 141. https://doi.org/10.1186/s12864-023-09233-4

Narango, D. L., Tallamy, D. W., & Marra, P. P. (2018). Nonnative plants reduce population growth of an insectivorous bird. *Proceedings of the National Academy of Sciences of the United States of America, 115*(45), 11549–11554. https://doi.org/10.1073/PNAS.1809259115/SUPPL_FILE/PNAS.1809259115.SAPP.PDF

Norris, K. (2012). Biodiversity in the context of ecosystem services: The applied need for systems approaches. *Philosophical Transactions of the Royal Society B: Biological Sciences, 367*(1586), 191–199. https://doi.org/10.1098/rstb.2011.0176

Oliver, T. H., Heard, M. S., Isaac, N. J. B., Roy, D. B., Procter, D., Eigenbrod, F., Freckleton, R., Hector, A., Orme, C. D. L., Petchey, O. L., Proença, V., Raffaelli, D., Suttle, K. B., Mace, G. M., Martín-López, B., Woodcock, B. A., & Bullock, J. M. (2015). Biodiversity and resilience of ecosystem functions. *Trends in Ecology & Evolution, 30*(11), 673–684. https://doi.org/10.1016/j.tree.2015.08.009

Orłowski, G., & Karg, J. (2013). Diet breadth and overlap in three sympatric aerial insectivorous birds at the same location. *Bird study : The journal of the British Trust for Ornithology, 60*(4), 475–483. https://doi.org/10.1080/00063657.2013.839622

Paap, T., Burgess, T. I., & Wingfield, M. J. (2017). Urban trees: Bridge-heads for forest pest invasions and sentinels for early detection. *Biological Invasions, 19*(12), 3515–3526. https://doi.org/10.1007/s10530-017-1595-x

Riggi, L. G., Gagic, V., Rusch, A., Malsher, G., Ekbom, B., & Bommarco, R. (2017). Pollen beetle mortality is increased by ground-dwelling generalist predators but not landscape complexity. *Agriculture, Ecosystems & Environment, 250*, 133–142. https://doi.org/10.1016/j.agee.2017.06.039

Schillé, L., Paquette, A., Marcotte, G., Ouellet, H., Cobus, S., Barbaro, L., & Castagneyrol, B. (2025). Urban tree diversity fosters bird insectivory despite a loss in bird diversity with urbanization. *Landscape and Urban Planning, 256*, Article 105274. https://doi.org/10.1016/j.landurbplan.2024.105274

Schneiberg, I., Boscolo, D., Devoto, M., Marcilio-Silva, V., Dalmaso, C. A., Ribeiro, J. W., Ribeiro, M. C., de Camargo Guaraldo, A., Niebuhr, B. B., & Varassin, I. G. (2020). Urbanization homogenizes the interactions of plant-frugivore bird networks. *Urban Ecosystems, 23*(3), 457–470. https://doi.org/10.1007/s11252-020-00927-1

Scholz, C., Teige, T., Ngoufack Djoumessi, K. P., Buchholz, S., Pritsch, F., Planillo, A., & Voigt, C. C. (2025). Dietary diversification of an insect predator along an urban-rural gradient. *Landscape and Urban Planning, 256*, Article 105273. https://doi.org/10.1016/j.landurbplan.2024.105273

Sexton, A. N., & Egerer, M. (2026). Re-thinking the urban biotic homogenization hypothesis. *Ecology Letters, 29*(2), Article e70342. https://doi.org/10.1111/ele.70342

Sheppard, S. K., Bell, J., Sunderland, K. D., Fenlon, J., Skervin, D., & Symondson, W. O. C. (2005). Detection of secondary predation by PCR analyses of the gut contents of invertebrate generalist predators. *Molecular Ecology, 14*(14), 4461–4468. https://doi.org/10.1111/j.1365-294X.2005.02742.x

Sol, D., González-Lagos, C., Moreira, D., Maspons, J., & Lapiedra, O. (2014). Urbanisation tolerance and the loss of avian diversity. *Ecology Letters, 17*(8), 942–950. https://doi.org/10.1111/ele.12297

Theodorou, P. (2022). The effects of urbanisation on ecological interactions. *Current Opinion in Insect Science, 52*, Article 100922. https://doi.org/10.1016/j.cois.2022.100922

Thompson, R. M., Brose, U., Dunne, J. A., Hall, R. O., Hladyz, S., Kitching, R. L., Martinez, N. D., Rantala, H., Romanuk, T. N., Stouffer, D. B., & Tylianakis, J. M. (2012). Food webs: Reconciling the structure and function of biodiversity. *Trends in Ecology & Evolution, 27*(12), 689–697. https://doi.org/10.1016/j.tree.2012.08.005

Vázquez, D. P., Chacoff, N. P., & Cagnolo, L. (2009). Evaluating multiple determinants of the structure of plant–animal mutualistic networks. *Ecology, 90*(8), 2039–2046. https://doi.org/10.1890/08-1837.1

Vidal, M. C., & Murphy, S. M. (2018). Bottom-up vs. top-down effects on terrestrial insect herbivores: A meta-analysis. *Ecology Letters, 21*(1), 138–150. https://doi.org/10.1111/ELE.12874

J. Winfree, R., Fox, W., Williams, N. M., Reilly, J. R., & Cariveau, D. P (2015). Abundance of common species, not species richness, drives delivery of a real-world ecosystem service *Ecology Letters, 18*(7), 626–635. https://doi.org/10.1111/ele.12424

Zurdo, J., Barrero, A., da Silva, L. P., Bustillo-de la Rosa, D., Gómez-Catasús, J., Morales, M. B., Traba, J., & Mata, V. A. (2023). Dietary niche overlap and resource partitioning among six steppe passerines of Central Spain using DNA metabarcoding. *Ibis, 165*(3), 905–923. https://doi.org/10.1111/IBI.13188