



Original article

Anthropogenic disturbance and plant drivers shape multitrophic arthropod dynamics in urban ecotones: Evidence from urban edge

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ABSTRACT

Arthropods maintain key ecosystem functions, and yet, remarkable reductions have been documented among various arthropod groups. Urban edges refer to dynamic ecosystems that serve as refuges for huge numbers of arthropods while being strongly influenced by anthropogenic disturbance. However, understanding how different facets of habitat heterogeneity, especially anthropogenic disturbance, affect various arthropod groups in urban edges remains limited. To tackle this problem, we monitored arthropod abundance, density, and diversity of four trophic levels and two ecosystem services groups of 288 sampling points distributed alongside the urban edges of Dexing city, China. First, we observed that anthropogenic disturbance negatively affected order- and trophic-level arthropod diversity but did not explain the loss of arthropod abundance and density, except those of predators and herbivores. Second, we revealed that plant abundance produced trophic-specific abundance changes in arthropods except omnivores, but only herbivore abundance increased with plant diversity. Finally, our results suggest that the top-down control that predators exert on herbivores was not significant in urban edges, but the anthropogenic drivers of habitat fragmentation in urban edges explained the decrease in pollinator diversity. We revealed the group-specific trends of arthropods living in urban edges to anthropogenic disturbance and explained the importance of plants in shaping multitrophic diversity and ecosystem multifunctionality. Thus, group-specific heterogeneity must be considered in the investigation of arthropod communities in urban edges.

1. Introduction

Arthropod populations are declining drastically worldwide (Sánchez-Bayo & Wyckhuys, 2019; Liang et al., 2025). The underlying factors are multifaceted and presumably interdependent. They include human pressures, such as land-use change, climate change, resource exploitation and pollution (Keck et al., 2025). However, arthropods are of extraordinary ecological and socioeconomic significance as they provide humans with multiple essential ecosystem services (Soliveres et al., 2016). Pollinators mediate 82% of angiosperm pollination worldwide (Ollerton et al., 2011). Meanwhile, arthropod predators alleviate plant pressure from insect herbivores through top-down trophic cascades and further influence vegetation carbon sequestration processes (Li et al., 2024). Concern over arthropod loss has aroused attention from policy-makers, media and scientists (van Klink et al., 2024). Factors affecting arthropod abundance and diversity in natural and urban ecosystems per se are well-documented (Chase et al., 2020;

Fairbairn et al., 2024; Cooke et al., 2025). However, the extent to which this ecological knowledge can be extrapolated to urban edges remains uncertain.

Urban edges represent ecotones where human-built environments interface with peripheral natural habitats (Grimm et al., 2008). This ecotone experiences anthropogenic disturbance, characterised by gradual changes in fragmentation and increased exposure to disturbances (e.g., pollution, artificial light, and noise), from urban edges to the interior (Yang et al., 2025). Compared with urban environments, urban edges experience reduced anthropogenic disturbance while maintaining higher arthropod abundance and diversity through habitat retention (Uhler et al., 2021; Ewers et al., 2024). On the other hand, relative to intact natural habitats of low vulnerability, urban edges exhibit greater environmental dynamism and habitat heterogeneity (Haddad et al., 2015), sustain higher numbers of multiple taxa and serve as refugia to a wide diversity of species (Harrison & Banks-Leite, 2020; Theodorou et al., 2020). As urban expansion increases the landscape

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proportion of these interface areas, their conservation should be prioritised to prevent further arthropod decline.

Road development constitutes one of the predominant anthropogenic disturbances in urban edges, and it inevitably leads not only to landscape fragmentation but also more edges (Forman & Alexander, 1998; Trombulak & Frissell, 2000). These edges can generate pronounced edge effects—shifts in abiotic conditions (e.g., light, pollution, and temperature) and biotic interactions near edges—that alter community structure (Murcia, 1995; Ries & Sisk, 2004; Harper et al., 2005). How edge effects associated with road-included fragmentation influence ecosystems and arthropod group remains highly debated. Some studies hold the view that habitat fragmentation can lead to habitat heterogeneity, reduced competition, and positive edge effects, which benefit arthropod diversity (Fahrig, 2017; Fahrig et al., 2019), whereas others highlighted that the positive edge effects relate to species are often generalists and even invasive, which can be detrimental to ecotones (Pfeifer et al., 2017; R. J. Fletcher et al., 2018). Moreover, fragmented landscapes can undermine a suite of ecosystem functions that plants exert on arthropods, such as regulation of arthropod diversity at higher trophic levels (Laforest-Lapointe et al., 2017) and trophic interaction among arthropod species (Penone et al., 2019; Vázquez-González et al., 2024), which consequently facilitate further arthropod loss. Given that ecological trait varies greatly among arthropod communities (Wong & Didham, 2024), this heterogeneity further complicates the debate around the conservation of arthropod groups in urban edges.

Arthropod conservation requires quantification of its responses to anthropogenic disturbances, such as road infrastructure expansion and related plant loss within habitats (Ewers et al., 2024; Marsh et al., 2025), which seems deceptively simple. Numerous empirical investigations have addressed this research question; however, they are commonly confined to one or a few taxonomic groups such as bees (Fiordaliso et al., 2025), butterflies (Priyadarshana et al., 2025), beetles (Ewers et al., 2007) or spiders (Butz et al., 2023), which introduce three challenges. First, arthropod responses to anthropogenic disturbance are often trophic specific (Schuldt et al., 2019), although some landscape-level responses show noticeable congruence (Banks-Leite et al., 2014). Second, taxon-specific investigations can easily overestimate functional consequences of anthropogenic disturbance, as they are unable to account for compensation by functionally similar taxa within the same trophic level (Harrison & Banks-Leite, 2020). Finally, complex interactions among arthropod communities, such as the top-down control that predators exert on herbivores, can also lead to diverse responses to anthropogenic disturbance (Albert et al., 2022). Consequently, findings from these taxonomically constrained studies may predominantly reflect investigator-selected indicator taxa rather than the community-wide effects of anthropogenic disturbance on multitrophic arthropods and associated ecosystem functions. This conflation of trophic-specific responses and cross-taxon functional compensation results in a limited comprehensive understanding of how arthropod taxa at different trophic levels respond to anthropogenic disturbance along urban edges.

Here, we addressed these challenges by investigating how different facets of habitat heterogeneity, especially anthropogenic disturbance, affect arthropod abundance, density, and diversity in urban edges. Recognizing that various processes influence arthropods near urban edges, we defined anthropogenic disturbance as the net outcome of all factors shaping arthropod variation along the edge–interior gradient. Specifically, we used a dataset that includes 31901 terrestrial arthropods (Insecta, Arachnida, Crustacea, and Chilopoda, hereafter described collectively as ‘arthropods’, for brevity) obtained from 288 sticky traps. We then aggregated taxa into trophic-level functional groups and ecosystem service groups to examine group-specific trends. We aimed to achieve the following: (1) quantify the influence of anthropogenic disturbance on arthropods of different trophic levels; (2) unravel the effects of plant abundance and diversity on arthropod groups; (3) decipher the trends of various ecosystem services groups.

2. Methods

2.1. Study site

This study was conducted in the Fenghuang Mountain (Fig. 1), which is located at the urban edge of Dexing city, Jiangxi Province, China (28° 55′56.6″ N, 117° 35′20.9″ E). The urban area of Dexing is inhabited by approximately 80,000 people and covers an area of around 10 km². The region receives 1632 h of annual sunshine, with an average annual temperature of 19.3 °C and an average annual precipitation of 2049 mm (Shangrao Bureau of Statistics, 2022). The environment is heterogeneous, and the core urban area and the rural area are separated by mountains covered by subtropical mixed evergreen broadleaved forest, which represent the typical hills landscape of Southeast China. Such small-to-medium cities constitute a substantial share of urban land in China (National Bureau of Statistics of China, 2024), which serve as critical frontiers where biodiversity coexists with ongoing development pressures. Moreover, given that the enforcement of a one-way traffic restriction within the study area, anthropogenic disturbance along the roadway is spatially uniform; the primary variation arises from the distance between sampling points and the road. These conditions provide a suitable setting for a natural experiment.

2.2. Arthropod sampling

Arthropod data were collected from April 2024 to March 2025, using 288 sticky traps randomly distributed along the road within the urban edges. To efficiently collect active individuals and provide suitable comparisons of community properties, we used sticky traps but not methods that can potentially lead to the collection of inactive individuals (e.g., beating and sweep-netting) (Wong & Didham, 2024) or whose attractiveness and efficiency are influenced by environmental changes across the diel cycle (e.g., light traps) (Hausmann et al., 2020). As for any other arthropod sampling method that intercepts moving arthropods, sticky traps suffer from disadvantages, such as potential taxonomic bias and under-sampling of large insects. Sticky traps were deployed in April 2024 and laid out on the pine trunks at breast height; the size of the traps was associated with the perimeter of the pine trees (Supplementary Method S1). The collection process continued until March 2025, and the arthropods caught were recorded. As our records comprehensively represented arthropod populations from the preceding year (2024), especially covering two peak seasons of arthropod abundance (May and September) (Schuldt et al., 2019). We therefore, considered it valid to use the arthropod data on pine-based sticky trap as a good proxy for the overall terrestrial arthropod groups.

2.3. Taxonomic and functional groups

We used the local arthropod list of the Dexing Forestry Bureau (http://www.dxs.gov.cn/dxslyj/xxgk_index.shtml) to identify all arthropod samples and characterise arthropod communities within the sampling site. For arthropods that were difficult to identify on site, photographs were captured, and subsequent identification was conducted by an expert entomologist (Dr. Zhong Peng). We counted the individuals per order, as our research focused on the trends of arthropods from the perspective of trophic levels and ecosystem services, and order-level resolution can reliably distinguish functional groups and capture biodiversity changes relevant to ecosystem services (pest control and pollination) (Penone et al., 2019; Buzhdygan et al., 2020; Fenoglio et al., 2020; Theodorou et al., 2020). The result included 4 classes and 22 orders (Supplementary Table S1). Very few arthropods in these sticky traps could not be identified at the order level (0.02%) and were excluded from the study. Specifically, we did not include Homoptera into Hemiptera because members of the former are mainly herbivores, and the Hemiptera sample in our study contained predators, such as the assassin bug *Sphedanolestes impressicollis* (Reduviidae). We included

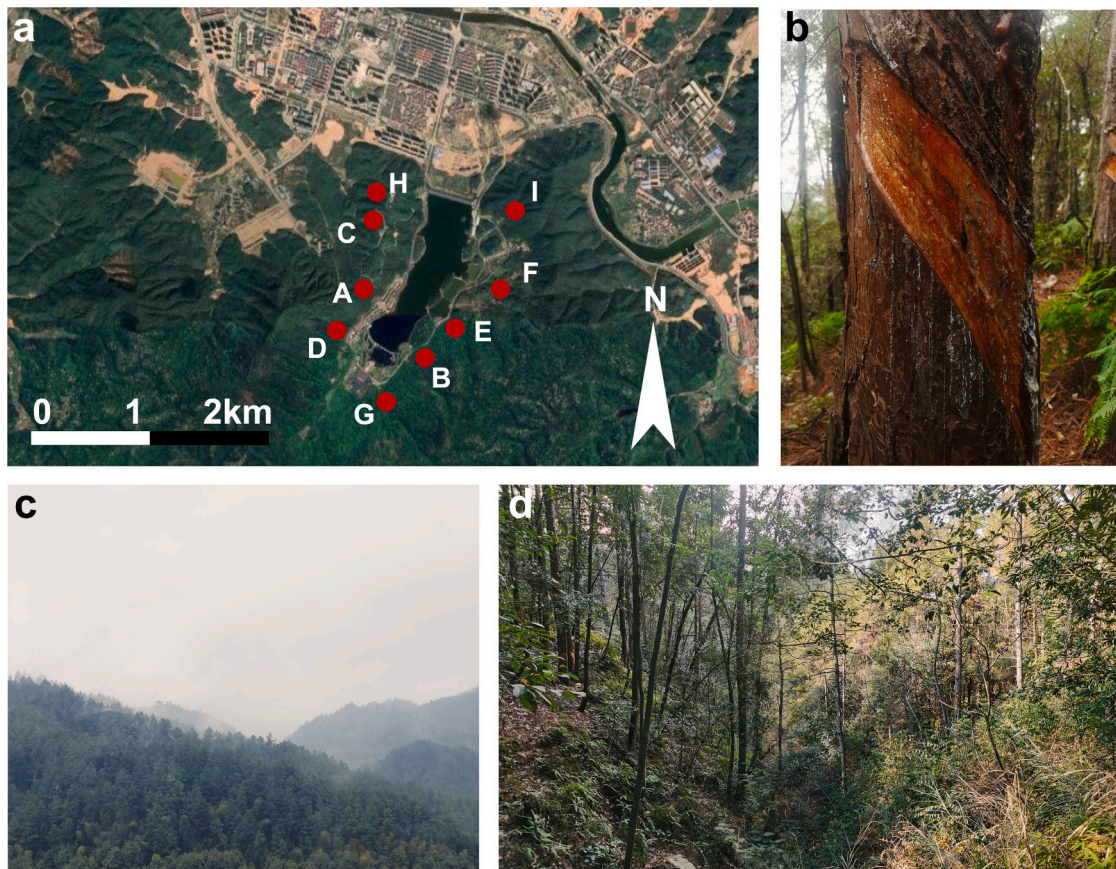


Fig. 1. a. Study area and sampling sites. b. Sticky trap. c. Study sites. d. Outlook of the plant communities in sampling area.

Lithobomorpha into Scolopendromorpha given their similar morphological characteristics and identical trophic levels.

We aggregated arthropod samples into trophic-level functional groups and ecosystem service groups to examine group-specific trends. We initially categorised arthropods into four trophic-level functional groups for separate analysis (herbivores, predators, omnivores, and detritivores; [Supplementary Table S2](#)). Second, we defined two ecosystem service groups—predators (pest regulators) and pollinators (flower-visiting taxa from Hymenoptera, Coleoptera, Diptera, and Lepidoptera; [Supplementary Table S2](#))—and treated these groups as proxies of arthropod-related regulating services (pest regulation and pollination). However, we failed to determine whether the arthropods collected in the study region are threatened due to the lack of arthropod data on the International Union for Conservation of Nature Red List in Jiangxi Province and the List of Key Protected Wildlife in Jiangxi Province. Specifically, Lepidoptera behave as herbivores during juvenile stages and as pollinators during the adult stage. As the sticky traps in our analysis had a sampling duration spanning a whole year, which encompasses the complete life cycle of Lepidoptera, we assigned them to the trophic-level functional group (herbivores) and ecosystem services group (pollinators). In doing so, we relied heavily on published studies, literature reviews, and expert knowledge ([Novotny et al., 2010](#); [Soliveres et al., 2016](#); [Schuldt et al., 2019](#); [Seibold et al., 2019](#); [Theodorou et al., 2020](#); [Li et al., 2023, 2024](#)). Finally, we measured the abundance (individuals), density (number per unit area), and alpha diversity (Shannon index, $H = -\sum p_i \ln(p_i)$, where p_i is the proportion of the entire arthropod community made up of species/trophic groups i) of each group at each sampling point ([Shannon, 1948](#)).

2.4. Facets of habitat heterogeneity

Our study targeted the habitat heterogeneity of subtropical mixed evergreen broadleaved forest at the urban edge, which represents the typical hills landscape of Southeast China, rather than the landscape-level heterogeneity of the entire ecotone. To holistically account for heterogeneity in urban edges, we employed the classification framework proposed by [Stein and Kreft \(2015\)](#). This system categorises heterogeneity across five subject areas, with four applicable to small scale in our analysis: vegetation, microscale topography, soil, and climate. In our study, the soil and climate were excluded due to the unavailability of their respective measures for all sampling points. Nevertheless, at the sampling point level, these excluded factors may exhibit significant correlation with vegetation and microscale topographic heterogeneity ([Heidrich et al., 2020](#)).

For vegetation, we first included the age of 288 focal pine trees (measured as perimeter at breast height (PBH) given that all focal trees are of the same species) in our analysis to account for variation in arthropod heterogeneity resulting from age-related differences in canopy structure ([Penone et al., 2019](#); [Shingley et al., 2023](#)). Then, we selected two sampling sites (sites H (sampling points number = 20) and I (sampling points number = 19), [Fig. 1](#)) to further investigate the effects of the plants on arthropods. In the selection of quadrat size for plant surveys, given the unknown typical dispersal distances of most arthropod species ([Seibold et al., 2019](#)), we adopted a heterogeneity-maximizing approach when selecting the size of the plant sample plot: the diameter selection process simultaneously achieved maximal vegetation coverage while maintaining nonoverlapping between plots. We measured the average distance between sampling points (3.20 m) and set the plot radius to 1.6 m. Each plot had a size of

approximately 8 m², which can capture the local vegetation and floral resources most likely to influence the insects intercepted by the sticky traps (Kennedy et al., 2013; Woodcock et al., 2014; Bihaly et al., 2024). All observed plants were identified at the species level (trees, shrubs, and herbs; Supplementary Table S3). We then calculated the plot-level plant abundance (individuals) and diversity (species-based Shannon index, $H = -\sum p_i \ln(p_i)$, where p_i is the proportion of the entire plant community consisting of species i) of each plant sample plot. Finally, considering the ecosystem services group of pollinators, we included entomophilous flowers as an ecosystem-specific variable relevant to pollinators (Supplementary Table S3). We calculated the above-mentioned abundance and diversity of entomophilous flowers per plot (hereafter referred to as flower abundance and flower diversity, respectively).

As for microscale topography, we recorded the aspect of each sampling point, as arthropods respond not only to macroclimate and large-scale land-use changes but also to ecological conditions within regions (Uhler et al., 2021), particularly in mountainous landscapes (Marder et al., 2025). Moreover, we measured the linear distance from sampling points to road edge, hereafter described as ‘distance to road edge’ for briefly, which we used as a generalised indicator of anthropogenic disturbance. This indicator implicitly integrates the impact of human activities on arthropods at urban edges and the arthropods’ adaptation to heterogeneous environments under such disturbances. Therefore, our measure of anthropogenic disturbance reflects the current balance between these opposing forces, and arthropods’ responses to anthropogenic disturbance have been demonstrated to vary with distance (Marsh et al., 2025).

2.5. Statistical analyses

We focused our analyses on the response patterns of the total arthropod group and individual trophic groups, rather than simply counting the taxa with positive or negative responses. As the turnover in the identity of trophic groups and functions is a more sensitive measure of changes in arthropod groups and related ecosystem functions (Li et al., 2024).

We used generalised linear mixed models (GLMMs) (Brooks et al., 2017) to determine the responses of arthropod abundance, density, and diversity to anthropogenic disturbance, vegetation, and microscale topography in urban edge landscape. Distance to road edge, the aspect of sampling points, and PBH of the trees were treated as fixed variables and the sampling site as a random effect to accommodate site-level environmental heterogeneity. We first built three different models for the total arthropod and four trophic levels:

model1 : *glmmTMB* (*arthropod abundance*
~ *Distance* + *Aspect* + *PBH* + (1|*Site*))

model2 : *glmmTMB* (*arthropod density*
~ *Distance* + *Aspect* + *PBH* + (1|*Site*))

model3 : *glmmTMB* (*arthropod diversity*
~ *Distance* + *Aspect* + *PBH* + (1|*Site*))

In the second step, we included plant abundance and diversity as variables. Given that vegetation was investigated in only two sampling sites, we used generalised linear models (GLMs). Specifically, based on the results of the first step (Supplementary Tables S4–S6), PBH was set as *offset(log(PBH))* in model 4 (except predators), which allowed proper comparison of sticky traps with different sizes, given that the number of caught arthropods is proportionally related to the size of the sticky traps:

model4 : *glmmTMB* (*arthropod abundance* ~ *Distance*
+ *Aspect* + *offset(log(PBH))* + *plant_abundance*
+ *plant_diversity*)

model5 : *glmmTMB* (*arthropod density* ~ *Distance* + *Aspect*
+ *PBH* + *plant_abundance* + *plant_diversity*)

model6 : *glmmTMB* (*arthropod diversity* ~ *Distance* + *Aspect*
+ *PBH* + *plant_abundance* + *plant_diversity*)

Moreover, for the specific ecosystem function related to arthropods (i.e., pest regulation and pollination in this study), we built separate models to analyse the top-down trophic cascade of herbivorous pest regulation and arthropod-related pollination. Specifically, we considered herbivore abundance, density, and diversity as fixed variables for model 7 and entomophilous flower abundance and diversity as fixed variables for model 8. For model pollination, we tested whether the number of caught pollinators and the size of sticky traps followed a proportional pattern before the analysis (Supplementary Table S11) and set variable PBH as *offset(log(PBH))* in model8, which allowed proper comparison of sticky traps of various sizes:

model7 : *glmmTMB* (*predator* ~ *Distance* + *Aspect*
+ *PBH* + *Herbivore* + (1|*Site*))

model8 : *glmmTMB* (*pollinator* ~ *Distance* + *Aspect*
+ *offset(log(PBH))* + *flower_abundance*
+ *flower_diversity*)

For model testing, we evaluated arthropod abundance by model assuming Poisson-, Negative Binomial-, or Tweedie-distribution to better suit count data and modelled log_e-transformed density and diversity assuming Gaussian distribution. We then tested the assumptions of variance homogeneity, residual normality, and under- or overdispersion using the R package DHARMA (Hartig et al., 2024).

3. Results

3.1. Sampling results

We identified 31901 arthropods from 288 sticky traps, representing four classes (Insecta 92.64%, Arachnida 6.93%, Crustacea 0.15%, and Chilopoda 0.29%, Fig. 2) and 22 orders (Supplementary Table S1). Some orders, such as Hymenoptera (recorded at 100% of all sampling points), Diptera (94.10% of sampling points) and Coleoptera (90.63% of sampling points), occurred on all or almost all sampling points, and others were restricted to points with specific slope orientations. For example, a total of 90% of the Opiliones samples (n = 50) occurred on south-facing slopes, although they accounted for only 37.15% of the total sampling points.

Next, we reclassified arthropods based on their trophic level (herbivores, predators, omnivores, and detritivores) and two ecosystem service categories, predators (pest regulation) and pollinators (pollination, see Supplementary Table S2), and quantified the abundance, density, and diversity of these groups. Sampling points varied greatly in terms of arthropod density and biodiversity. The average density of omnivorous arthropods was approximately 8 times that of non-omnivorous arthropods, and the trophic-level diversity of the most diverse point was almost 15 times that of the least diverse point (Table 1). The observed variations in order- and trophic-level distributions across the sampled points suggest distinct ecological preferences.

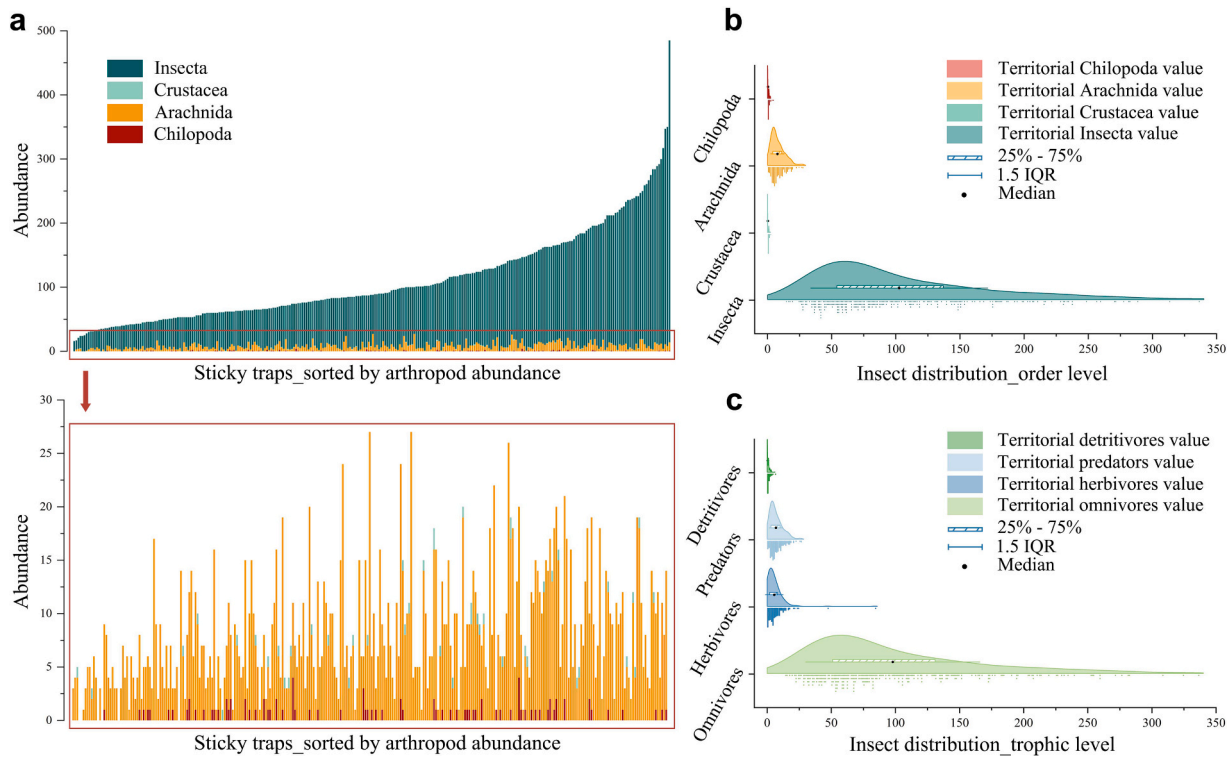


Fig. 2. Arthropod abundance and distribution of sampling points in urban edges. a. Each stacked bar represents 1 of 288 sampling points. Points are sorted by their arthropod abundance composed of four taxa (Insecta, Crustacea, Arachnida, and Chilopoda). b. Arthropod distribution at the class level. c. Arthropod distribution at the trophic level.

Table 1
Summary of habitat features and arthropod abundance, density, and diversity of 288 sampling points.

Variable	Mean ± s.d.	Min	Max
Facets of habitat heterogeneity			
Distance to road edge (m)	16.60 ± 12.32	1.30	59.80
PBH (cm)	99.01 ± 18.18	62	156
Plant abundance	14.74 ± 4.66	5	28
Plant diversity	1.93 ± 0.28	1.39	2.48
Flower abundance	9.38 ± 3.60	3	19
Flower diversity	1.55 ± 0.28	0.97	2.20
Arthropod groups			
Total arthropod abundance	110.8 ± 70.35	16	485
Total arthropod density	111.70 ± 67.70	17.35	461.90
Order-level arthropod diversity	1.14 ± 0.35	0.16	2.26
Trophic-level arthropod diversity	0.45 ± 0.21	0.00	1.06
Herbivore abundance	5.51 ± 6.90	0	84
Herbivore density	5.62 ± 6.60	0.00	76.36
Omnivore abundance	97.93 ± 67.86	14	465
Omnivore density	98.78 ± 65.98	14.29	442.86
Detritivore abundance	0.53 ± 0.89	0	6
Detritivore density	0.53 ± 0.88	0.00	5.26
Predator abundance	6.80 ± 5.06	0	26
Predator density	6.77 ± 4.70	0.00	25.24
Predator diversity	0.59 ± 0.38	0.00	1.57
Pollinator abundance	96.51 ± 67.52	14	465
Pollinator density	97.38 ± 65.69	14.29	442.86
Pollinator diversity	0.68 ± 0.24	0.00	1.17

Note: Facets of habitat heterogeneity were assessed by fieldwork. Abundance is expressed as the number of individuals, density as the number of individuals per unit trap area, and diversity as the Shannon index (Shannon, 1948). The diversity of different arthropod groups was assessed using taxa/trophic specific methods, and those of plants and flowers were assessed at each plant sample plot.

3.2. Diverging effects of anthropogenic disturbance

Across the order and trophic levels, we observed that the distance to road edge negatively affected order- ($P < 0.001$) and trophic-level arthropod diversities ($P < 0.001$) but did not explain the loss of total arthropod abundance ($P = 0.727$) and density ($P = 0.251$) (Fig. 3, Supplementary Table S4). However, this pattern contradicts differences among trophic levels. Specifically, when we concentrated on a specific trophic level, predator abundance ($P < 0.001$), density of herbivores ($P = 0.003$), and density of predators ($P < 0.001$) were all significantly positively related to the distance to road edge, even after considering variability across the trees' PBH (Supplementary Tables S5 and S6), whereas the effects of distance-to-road edge on the abundance and density of omnivores (abundance: $P = 0.370$, density: $P = 0.772$) and detritivores (abundance: $P = 0.668$, density: $P = 0.606$) were not significant (Supplementary Tables S5 and S6). In addition, the west and north slopes supported higher abundance and density of herbivores and predators (Supplementary Tables S5 and S6), although overall arthropod abundance and density did not differ significantly between slopes. Moreover, the trees' PBH was not significantly related to arthropod diversity (order-level: $P = 0.512$, trophic-level: $P = 0.737$) and density of all trophic levels, except for the density of predators ($P = 0.020$) (Supplementary Tables S4–S6).

3.3. Effects of plants vary across trophic levels

Given that plant species composition and forest structure can also affect local arthropod communities, we fitted separate fixed models for the abundance of arthropods at each trophic level (Fig. 4). Plant abundance positively affected the abundance of predators and detritivores (predators $P = 0.048$, detritivores $P = 0.041$, Supplementary Table S8) but had a negative effect on herbivore abundance ($P = 0.026$). However, the influence of plant diversity on arthropod abundance across trophic levels differed from that of plant abundance on herbivores, predators,

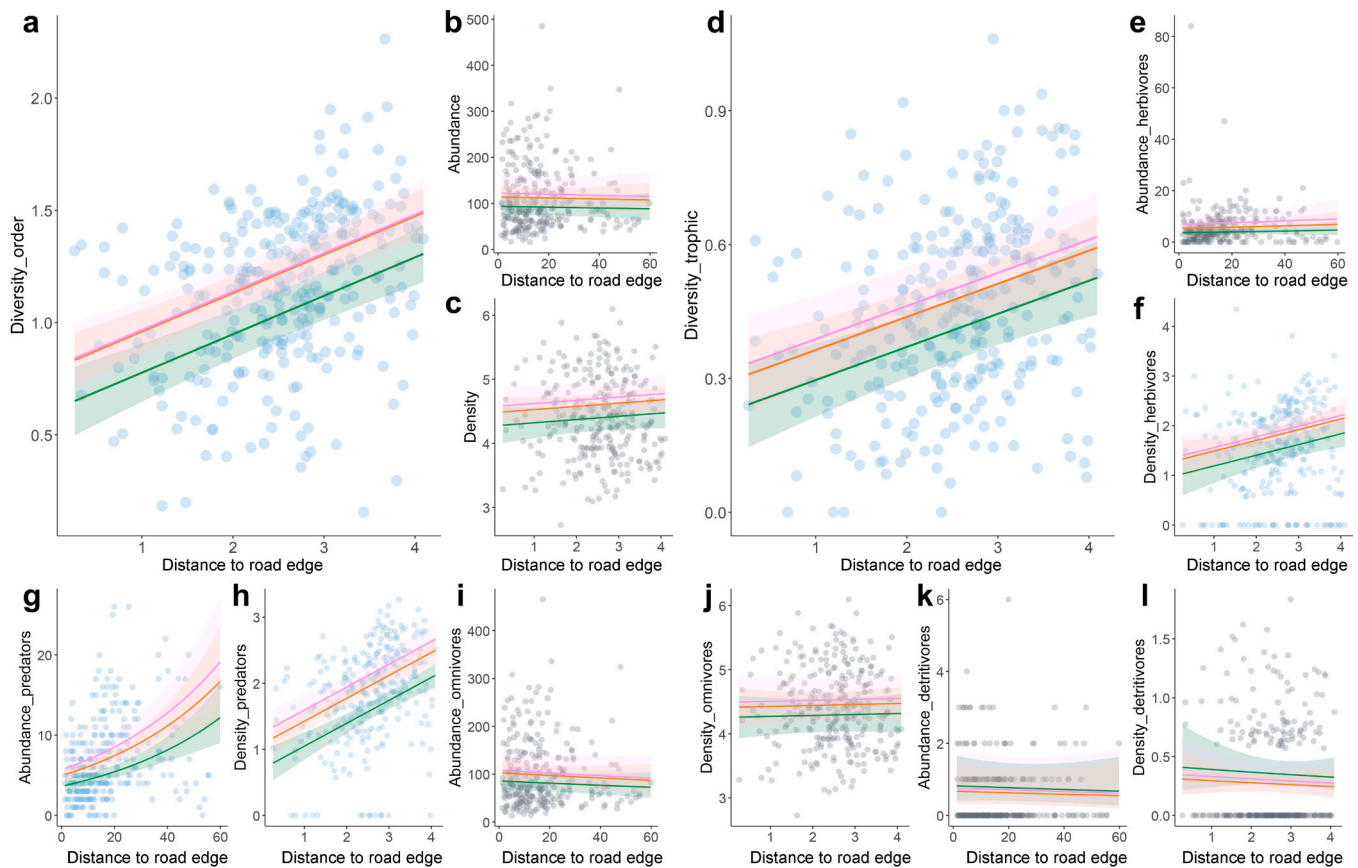


Fig. 3. Effect of anthropogenic disturbance on all arthropods and four trophic levels on urban edges in Dexing city. Each dot represents 1 of 288 sampling points sampled between April 2024 and March 2025. The blue graphs indicate a significant ($P \leq 0.05$) relationship between the distance-to-road edge and the arthropod abundance, density, and diversity measures. The gray graphs show the nonsignificant relationships. The lines represent the predicted values from the GLMMs, and the shaded areas are 95% confidence intervals (Supplementary Tables S4–S6). The line colours refer to the aspect of sampling points (Green: west, orange: north, pink: south). The ‘distance to road edge’ were \log_e -transformed for model density and diversity assuming Gaussian distribution. For effects of not-shown covariates, refer to Supplementary Table S4–S6.

and detritivores. That is, only the herbivore abundance increased with plant diversity ($P = 0.019$, Supplementary Table S9). The other trophic levels showed no significant relationship with plant diversity. A nonsignificant pattern was also observed for the overall arthropod abundance ($P = 0.494$) and diversity ($P = 0.406$), likely due to the small proportion of herbivores (Supplementary Table S7).

3.4. Top-down pest regulation and pollination services

Distance-to-road edge was positively related to abundance ($P < 0.001$), density ($P < 0.001$), and diversity ($P < 0.001$, Fig. 5, Supplementary Table S10) of predators but only explained pollinator diversity ($P = 0.022$, Supplementary Table S11 and S12). Tree PBH showed a positive association with the density ($P = 0.024$) and diversity ($P = 0.026$, Supplementary Table S10) of predators but negatively influenced the diversity of pollinators ($P = 0.012$, Supplementary Table S11 and S12). Moreover, regarding herbivorous pest regulation, herbivore abundance was not significantly related to the abundance, density, or diversity of predators (Supplementary Table S10), and herbivore diversity can only explain the increase in predator abundance. As for pollination service, flower diversity was not significantly related to the abundance, density, or diversity of pollinators (Supplementary Table S12), and flower abundance could only explain the loss of pollinator diversity ($P = 0.037$, Supplementary Table S12).

4. Discussion

4.1. Anthropogenic disturbance impaired arthropod diversity, but no consistency was found in abundance and density across trophic levels

First, our research indicated that anthropogenic disturbance in urban edges can affect the diversity of arthropod communities in various manners, including order- and trophic-level diversity and diversity within specific trophic groups. These findings are consistent with previous empirical evidence showing that anthropogenic disturbance, as represented by widespread roads in landscapes, is associated with negative effects on arthropod diversity (Forman & Alexander, 1998; Trombulak & Frissell, 2000; Marsh et al., 2025; Hahs et al., 2023); they provide further evidence regarding arthropod-related ecosystem functions, such as predation and pollination (Koh et al., 2016; Vázquez-González et al., 2024). A critical implication of these findings is the consistent decline in arthropod diversity caused by anthropogenic disturbance at urban edges across trophic levels. Although our dataset prevented us from determining rare species; prior work indicates that anthropogenic disturbance often disproportionately affects rare species and can reduce multiple ecosystem functions (Godoy et al., 2020).

Second, declines in arthropod abundance and density due to anthropogenic disturbance were not observed for the overall arthropod community but were evident for herbivores (abundance and density) and predators (density). This phenomenon is consistent with the buffering effect of the insurance hypothesis (Yachi & Loreau, 1999).

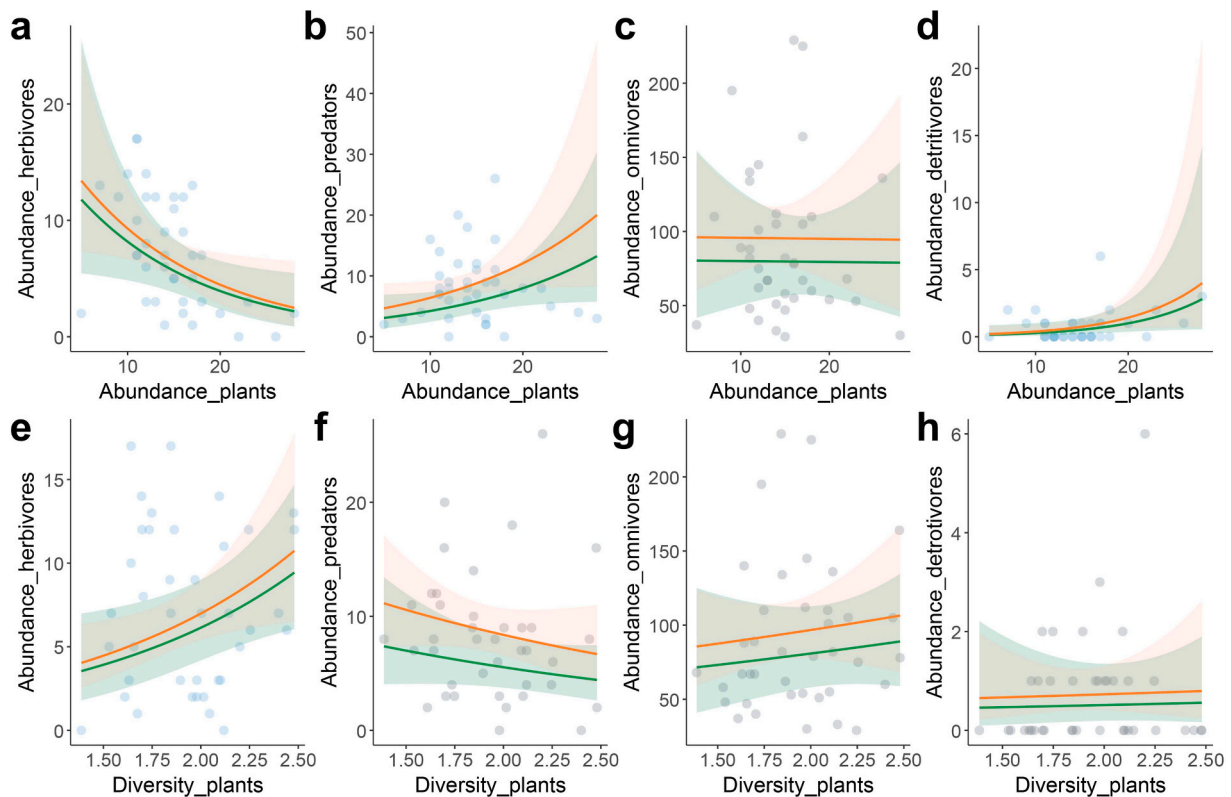


Fig. 4. Effects of plant abundance (a–d) and diversity (e–h) on four trophic levels on urban edges in Dexing city. Each dot represents 1 of 39 sampling points sampled between April 2024 and March 2025. The blue graphs indicate a significant ($P \leq 0.05$) relationship between the plant abundance/diversity and the arthropod abundance at four trophic levels (we did not show the results of arthropod density in this section because the number of caught arthropods (except predators, see below 3.4) is proportionally related to the size of the sticky traps, [Supplementary Tables S5 and S6](#)). The grey graphs reveal the nonsignificant relationships. The lines represent the predicted values from the GLMs, and the shaded areas are 95% confidence intervals ([Supplementary Table S8](#)). The line colours refer to the aspect of sampling points (Green: west, orange: north). For effects of not-shown covariates, refer to [Supplementary Table S8](#).

According to that theory, generalist omnivores, such as ants (Hymenoptera) and beetles (Coleoptera), can compensate for declines in abundance and density. Such functional compensation can confer great resilience of ecosystem functions to anthropogenic disturbance ([Dolezal et al., 2024](#); [van Klink et al., 2024](#)). Certain taxonomic groups that dominated pest regulation and litter decomposition declined with the increased anthropogenic disturbance, whereas other species increased in abundance and compensated for ecosystem functions ([Ewers et al., 2015](#); [Seibold et al., 2019](#)). Moreover, herbivores and predators with specialist diets are more sensitive to changes in abiotic conditions than generalists ([Ali & Agrawal, 2012](#)). This potentially explains the more pronounced effects of microhabitats on specialists and align with the observed effects of anthropogenic disturbance on abundance and density of herbivores and predators across different slope aspects. In addition, this difference can be attributed to the species with more specialised diets, which are less able to exploit available resources created by humans ([Hahs et al., 2023](#)), providing further evidence for the diverging response to anthropogenic disturbance across trophic levels.

4.2. Plant abundance produced trophic-specific changes in arthropod abundance, but plant diversity showed minimal influence at the scale of our analysis

We have shown that plant abundance induces trophic-specific abundance changes in arthropods except omnivores. The findings on predators and detritivores are consistent with previous empirical evidence, which indicates that plant abundance is a pivotal mechanism preventing the loss of arthropod abundance ([Fairbairn et al., 2024](#)). In contrast to predators and detritivores, the negative effect of plant

abundance on herbivores may have heterogeneous causes. Roadsides serve as hotspots for pioneer plants, but 60% of tropical herbivorous insects feed on plants within one family ([Novotny & Basset, 2005](#); [Cooke et al., 2025](#)), which means the pioneer plants cannot provide essential food resources for most herbivores. This condition provides further evidence on the effects of habitat fragmentation on biodiversity ([Ewers et al., 2024](#); [Fahrig et al., 2019](#); [R. J. Fletcher et al., 2018](#); [Haddad et al., 2015](#)). Moreover, empirical studies revealed frequent correlation of plant diversity and arthropod abundance ([Schuldt et al., 2019](#); [Li et al., 2024](#)), as multitrophic abundance can benefit from elevated structural and functional diversity of plant communities. However, our results show that plant diversity was not a pivotal variable for arthropod abundance, possibly because tree-related microhabitats depend more on horizontal heterogeneity ([Heidrich et al., 2020](#)), highlighting the importance of functional composition and spatial configuration of plant for insect associations ([Skaldina et al., 2024](#)), rather than species-based plant diversity. This phenomenon lends further evidence to the concept of scale variation in biodiversity.

Interestingly, the stem PBH of trees was not an important variable for most trophic levels, except for predators, despite large-perimeter trees being disproportionately important for ecosystem services and biodiversity worldwide ([Lindenmayer & Laurance, 2017](#)). This difference is possibly due to the more complex structure of large-perimeter trees, which provides more habitats and food resources for higher trophic levels, thereby enhancing predation. This phenomenon further proves the nonindependence of trophic cascades and has at least two studies supporting it, one involving spiders ([Butz et al., 2023](#)) and the other birds ([Buron et al., 2022](#)). However, the underlying mechanism for other trophic groups remains unclear and therefore requires further study.

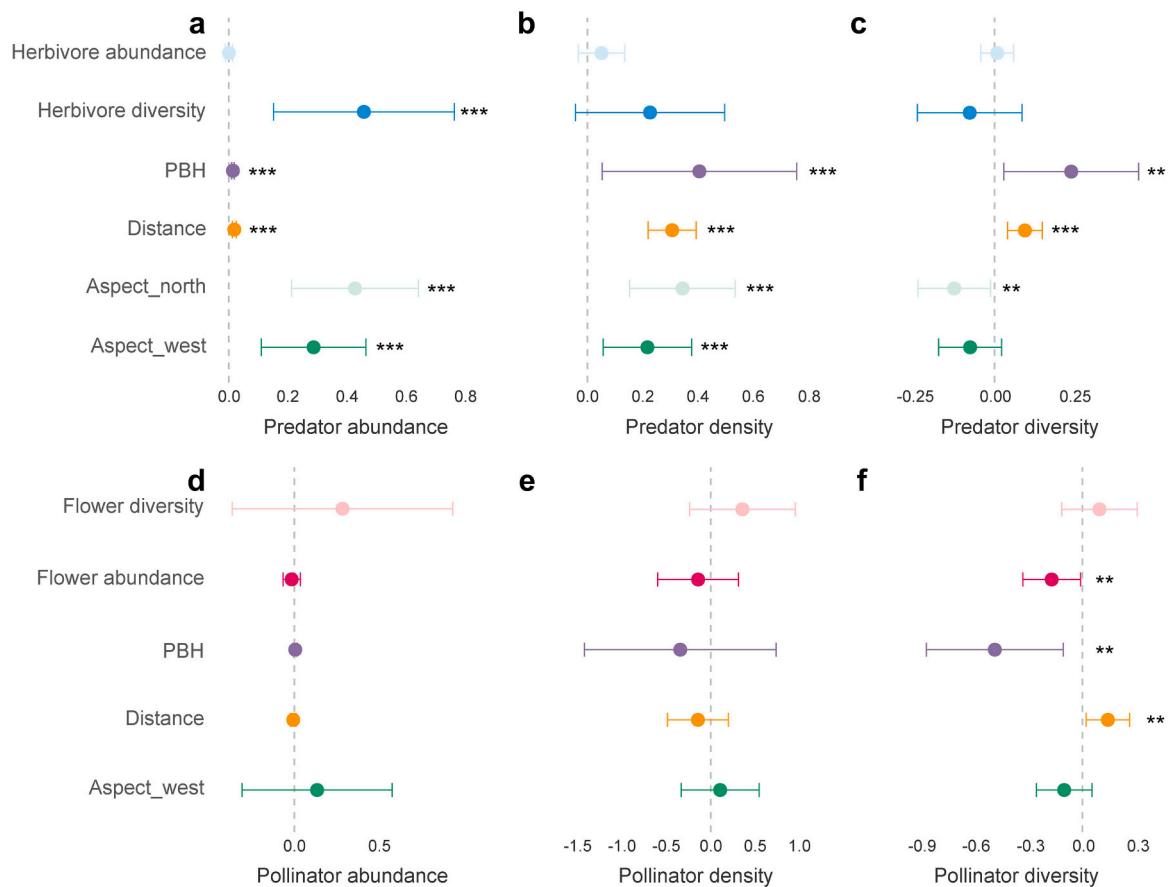


Fig. 5. Effects of variables on ecosystem services. a–c. Effects of habitat heterogeneity and herbivore on pest regulation on urban edges in Dexing city. **d–f.** Influence of habitat heterogeneity and entomophilous flowers on pollination on urban edges in Dexing city. For each category, the dot represents the marginal mean computed from the model. The bar shows the 95% confidence interval. ** $P < 0.05$, *** $P < 0.01$.

4.3. Habitat heterogeneity and variables associated with specific ecosystem services interactively influenced the corresponding arthropod groups

The top-down control that predators exert on herbivores was insignificant in urban edges. Ecosystem services, such as pest regulation, are thought to decrease with fragmentation, mediated by species richness due to facilitation, niche complementarity, or sampling effects (Cardinale et al., 2012; R. Fletcher, 2025). A possible rationale for the lack of this relationship in our research might be the more dynamic environments of urban edges than nature reserves like forests (Tschardt et al., 2016; Ewers et al., 2024); the elevated habitat heterogeneity can provide pest herbivores with more refuge from natural enemies. On the other hand, the compensation of alternative bird and mammal predators, which have greater mobility and generalist diets, are less sensitive to anthropogenic disturbance in urban edges than arthropod predators (Scholz et al., 2025). The relationships among predator communities, particularly through mechanisms such as intra-guild predation (Vázquez-González et al., 2024), may yield diverse outcomes in response to variations in fragmentation of urban edges, which expand previous findings on trophic cascades in different landscapes.

As for pollination, we observed that anthropogenic disturbance explained the decrease in pollinator diversity in urban edges but showed no significant correlation with either pollinator abundance or density. These findings are inconsistent with previous empirical evidence that focused on specific taxonomic groups, such as butterflies (Priyadarshana et al., 2025). A rationale for this phenomenon is that anthropogenic disturbance in urban edges creates ecotones, which offer resource

advantages to a limited group of adaptable species capable of thriving soil imperviousness and fragmentation (Koh et al., 2016; Pereira et al., 2021). The other side of the coin is rare species, outcome reversal and the success of dominant species overshadowing the decline of rare ones, providing a mechanism for the aforementioned paradox. This situation also explains why our results suggest a strong negative influence of anthropogenic disturbance on pollinator diversity. Moreover, our assessment of entomophilous flowers showed that their abundance was negatively associated with pollinator diversity. The possible reason for this phenomenon is that pollinators, especially bees, are more diverse in dry environments (Orr et al., 2021), whereas forest like habitats typically harbour fewer pollinators than open habitats (Fiordaliso et al., 2025). The high proportion (87%) of tree growth forms among entomophilous flowers in our study indicates a humid microclimate, which is consistent with previous research on forests (Li et al., 2024). Moreover, entomophilous flower diversity was not an essential factor for pollinators, as most pollinator arthropods are generalists that do not rely on specific floral resources but rather on the overall abundance of entomophilous flowering plants. Further investigations are needed to gain insights into the heterogeneity among different orders of pollinator arthropods and the occurrence and strength of specific interactions.

4.4. Limitations and future work

We must acknowledge that this work had inherent constraints that might have restricted the detection of stronger effects. First, our analysis focused on terrestrial arthropods. However, wildlife from other taxa, such as birds, can also provide pest regulation services. In addition, intra-guild predation (interactions between predator groups) (Staab &

Schuldt, 2020) means that our results may be biased by overlooking groups of species. Second, our findings should be interpreted as being most directly applicable to the current regional subtropical evergreen broad-leaved forest vegetation, and may not be fully generalizable to all subtropical forest types with different floristic compositions. Moreover, in addition to the vertical heterogeneity of plants considered in our study, horizontal heterogeneity can contribute to micro-ecological patterns across arthropod groups and influence the results. We thus encourage further empirical research to include a wider range of wildlife and forest types to examine and separate the entangled trends of arthropod groups in urban edges. Ideally, our inferences are most directly applicable to subtropical forest matrices experiencing low to moderate urbanisation and should not be generalised to non-forest habitats (e.g., grasslands, shrublands, deserts) or high-density megacities without further testing. Future studies should address habitat heterogeneity comprehensively and incorporate cross-ecoregional, medium- to long-term arthropod measurements across diverse landscape backgrounds to enhance the robustness and generality of inferences. This combination of strategies will lead to a more comprehensive understanding of how habitat heterogeneity influences arthropod groups and the resulting ecosystem services.

5. Conclusion

Landscape planning for biodiversity protection relies on the accurate estimation of how species respond to habitat heterogeneity. In this study, we revealed how different facets of habitat heterogeneity, especially anthropogenic disturbance, affect various arthropod groups in urban edges. The arthropod abundance of some specific trophic levels was not significantly affected, and the resulting compensatory effect may increase the risk of regional ecological imbalance in urban edges. We also revealed that plant abundance can promote arthropod diversity across trophic levels, whereas plant diversity had a limited effect at the scale of our analysis. Finally, the responses of ecosystem services groups to anthropogenic disturbance showed partial consistency. However, we did not find support for the top-down control predators exert on herbivores, and flower abundance surprisingly showed no positive effect on the diversity of pollinators.

Our research contributes to the increased amount of evidence indicating that anthropogenic disturbance undermines multitrophic arthropod diversity and arthropod-related ecosystem multifunctionality. This finding highlights the consistent effects of anthropogenic disturbance on distinct components of biodiversity and further underlines the importance of proactive conservation actions targeting areas of low vulnerability for rare species. Moreover, our findings have several implications for future basic and practical studies on the preservation of arthropod habitat in urban edges. We demonstrated the need for group-specific tendencies to heterogeneity in urban edges to gain full understanding of the multitrophic diversity and ecosystem multifunctionality supported in ecotones. Therefore, to better account for and separate the entangled trends of biodiversity in response to anthropogenic disturbance, we urge conducting urban ecology research in the future to classify species groups not only via taxonomical methods but also based on functional groups. This group-specific heterogeneity requires a more comprehensive approach to conservation planning, recognizing that ecotones, such as urban edges, are not inherently beneficial for all species groups, and that effective solutions must also consider the requirements of typically disregarded species groups.

CRedit authorship contribution statement

Zhechen Zhou: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Siqiang Wang:** Writing – review & editing, Writing – original draft, Validation, Software, Methodology, Formal analysis, Data curation,

Conceptualization. **Chun Yin Chung:** Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Formal analysis. **Yi Sun:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Funding acquisition, 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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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.ufug.2026.129397](https://doi.org/10.1016/j.ufug.2026.129397).

References

- Albert, G., Gauzens, B., Loreau, M., Wang, S., Brose, U., 2022. The hidden role of multi-trophic interactions in driving diversity–productivity relationships. *Ecol. Lett.* 25 (2), 405–415. <https://doi.org/10.1111/ele.13935>.
- Ali, J.G., Agrawal, A.A., 2012. Specialist versus generalist insect herbivores and plant defense. *Trends Plant Sci.* 17 (5), 293–302. <https://doi.org/10.1016/j.tplants.2012.02.006>.
- Banks-Leite, C., Pardini, R., Tambosi, L.R., Pearse, W.D., Bueno, A.A., Bruscagin, R.T., Condez, T.H., Dixo, M., Igari, A.T., Martensen, A.C., Metzger, J.P., 2014. Using ecological thresholds to evaluate the costs and benefits of set-asides in a biodiversity hotspot. *Science* 345 (6200), 1041–1045. <https://doi.org/10.1126/science.1255768>.
- Bihaly, Á.D., Piross, I.S., Pellaton, R., Szigeti, V., Somay, L., Vajna, F., Soltész, Z., Báldi, A., Sárosipataki, M., Kovács-Hostyánszki, A., 2024. Landscape-wide floral resource deficit enhances the importance of diverse wildflower plantings for pollinators in farmlands. *Agric. Ecosyst. & Environ.* 367, 108984. <https://doi.org/10.1016/j.agee.2024.108984>.
- Brooks, M.E., Kristensen, K., Benthem, K.J., van, Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Mächler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R. J.* 9 (2), 378–400.
- Buron, R., Hostetler, M.E., Andreu, M., 2022. Urban forest fragments vs residential neighborhoods: urban habitat preference of migratory birds. *Landscape Urban Plan.* 227, 104538. <https://doi.org/10.1016/j.landurbplan.2022.104538>.
- Butz, E.M., Schmitt, L.M., Parker, J.D., Burghardt, K.T., 2023. Positive tree diversity effects on arboreal spider abundance are tied to canopy cover in a forest experiment. *Ecology* 104 (8), e4116. <https://doi.org/10.1002/ecy.4116>.
- Buzhdygan, O.Y., Meyer, S.T., Weisser, W.W., Eisenhauer, N., Ebeling, A., Borreter, S.R., Buchmann, N., Cortois, R., De Deyn, G.B., de Kroon, H., Gleixner, G., Hertzog, L.R., Hines, J., Lange, M., Mommer, L., Ravenek, J., Scherber, C., Scherer-Lorenzen, M., Scheu, S., Petermann, J.S., 2020. Biodiversity increases multitrophic energy use efficiency, flow and storage in grasslands. *Nat. Ecol. & Evol.* 4 (3), 393–405. <https://doi.org/10.1038/s41559-020-1123-8>.
- Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S., Naeem, S., 2012. Biodiversity loss and its impact on humanity. *Nature* 486 (7401), 59–67. <https://doi.org/10.1038/nature11148>.
- Chase, J.M., Blowes, S.A., Knight, T.M., Gerstner, K., May, F., 2020. Ecosystem decay exacerbates biodiversity loss with habitat loss. *Nature* 584 (7820), 238–243. <https://doi.org/10.1038/s41586-020-2531-2>.
- Cooke, R., Outhwaite, C.L., Bladon, A.J., Millard, J., Rodger, J.G., Dong, Z., Dyer, E.E., Edney, S., Murphy, J.F., Dicks, L.V., Hui, C., Jones, J.L., Newbold, T., Purvis, A., Roy, H.E., Woodcock, B.A., Isaac, N.J.B., 2025. Integrating multiple evidence streams to understand insect biodiversity change. *Science* 388 (6742), eadq2110. <https://doi.org/10.1126/science.adq2110>.
- Dolezal, J., Fibich, P., Altman, J., Takahashi, K., Hara, T., 2024. Diversity effects and compensatory dynamics drive productivity and stability in temperate old-growth forests. *J. Ecol.* 112 (10), 2249–2263. <https://doi.org/10.1111/1365-2745.14391>.
- Ewers, R.M., Boyle, M.J.W., Gleave, R.A., Plowman, N.S., Benedick, S., Bernard, H., Bishop, T.R., Bakhtiar, E.Y., Chey, V.K., Chung, A.Y.C., Davies, R.G., Edwards, D.P., Eggleton, P., Fayle, T.M., Hardwick, S.R., Homathei, R., Kitching, R.L., Khoo, M.S., Luke, S.H., Turner, E.C., 2015. Logging cuts the functional importance of

- invertebrates in tropical rainforest. *Nat. Commun.* 6 (1), 6836. <https://doi.org/10.1038/ncomms7836>.
- Ewers, R.M., Orme, C.D.L., Pearse, W.D., Zulkifli, N., Yvon-Durocher, G., Yusah, K.M., Yoh, N., Yeo, D.C.J., Wong, A., Williamson, J., Wilkinson, C.L., Wiederkehr, F., Webber, B.L., Wearn, O.R., Wai, L., Vollans, M., Twining, J.P., Turner, E.C., Tobias, J.A., Banks-Leite, C., 2024. Thresholds for adding degraded tropical forest to the conservation estate. *Nature* 631 (8022), 808–813. <https://doi.org/10.1038/s41586-024-07657-w>.
- Ewers, R.M., Thorpe, S., Didham, R.K., 2007. Synergistic interactions between edge and area effects in a heavily fragmented landscape. *Ecology* 88 (1), 96–106. [https://doi.org/10.1890/0012-9658\(2007\)88%255B96:SIBEA%255D2.0.CO;2](https://doi.org/10.1890/0012-9658(2007)88%255B96:SIBEA%255D2.0.CO;2).
- Fahrig, L., 2017. Ecological responses to habitat fragmentation per Se, 2017 *Annu. Rev. Ecol. Evol. Syst.* 48 (48), 1–23. <https://doi.org/10.1146/annurev-ecolsys-110316-022612>.
- Fahrig, L., Arroyo-Rodríguez, V., Bennett, J.R., Boucher-Lalonde, V., Cazetta, E., Currie, D.J., Eigenbrod, F., Ford, A.T., Harrison, S.P., Jaeger, J.A.G., Koper, N., Martin, A.E., Martin, J.-L., Metzger, J.P., Morrison, P., Rhodes, J.R., Saunders, D.A., Simberloff, D., Smith, A.C., Watling, J.L., 2019. Is habitat fragmentation bad for biodiversity? *Biol. Conserv.* 230, 179–186. <https://doi.org/10.1016/j.biocon.2018.12.026>.
- Fairbairn, A.J., Meyer, S.T., Mühlbauer, M., Jung, K., Apfelbeck, B., Berthoin, K., Frank, A., Guthmann, L., Jokisch, J., Kerler, K., Müller, N., Obster, C., Unterbichler, M., Webersberger, J., Matejka, J., Depner, P., Weisser, W.W., 2024. Urban biodiversity is affected by human-designed features of public squares. *Nat. Cities* 1 (10), 706–715. <https://doi.org/10.1038/s44284-024-00126-5>.
- Fenoglio, M.S., Rossetti, M.R., Videla, M., 2020. Negative effects of urbanization on terrestrial arthropod communities: a meta-analysis. *Glob. Ecol. Biogeogr.* 29 (8), 1412–1429. <https://doi.org/10.1111/gcb.13107>.
- Fiordaliso, W., Reverte, S., Ghisbain, G., Wood, T., Ruelle, E., Lefebvre, A., Reese, A., Lookx, M., Michez, D., Tougeron, K., 2025. Reconciling community-level responses of wild bees to highly anthropized landscapes. *Landscape Urban Plan.* 259, 105347. <https://doi.org/10.1016/j.landurbplan.2025.105347>.
- Fletcher, R., 2025. Biodiversity declines across fragmented forests. *Nature*. <https://doi.org/10.1038/d41586-025-00672-5>.
- Fletcher, R.J., Didham, R.K., Banks-Leite, C., Barlow, J., Ewers, R.M., Rosindell, J., Holt, R.D., Gonzalez, A., Pardini, R., Damschen, E.I., Melo, F.P.L., Ries, L., Prevedello, J.A., Tschamtké, T., Laurance, W.F., Lovejoy, T., Haddad, N.M., 2018. Is habitat fragmentation good for biodiversity? *Biol. Conserv.* 226, 9–15. <https://doi.org/10.1016/j.biocon.2018.07.022>.
- Forman, R.T.T., Alexander, L.E., 1998. Roads and their major ecological effects. *Annu. Rev. Ecol. Evol. Syst.* 29 (29), 207–231. <https://doi.org/10.1146/annurev.ecolsys.29.1.207>.
- Godoy, O., Gómez-Aparicio, L., Matías, L., Pérez-Ramos, I.M., Allan, E., 2020. An excess of niche differences maximizes ecosystem functioning. *Article 1. Nat. Commun.* 11 (1). <https://doi.org/10.1038/s41467-020-17960-1>.
- Grimm, N.B., Faeth, S.H., Golubiewski, N.E., Redman, C.L., Wu, J., Bai, X., Briggs, J.M., 2008. Global change and the ecology of cities. *Science* 319 (5864), 756–760. <https://doi.org/10.1126/science.1150195>.
- Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster, B.L., Jenkins, C.N., King, A.J., Laurance, W.F., Levey, D.J., Margules, C.R., Townshend, J.R., 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. *Sci. Adv.* 1 (2), e1500052. <https://doi.org/10.1126/sciadv.1500052>.
- 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. *Nat. Commun.* 14 (1), 4751. <https://doi.org/10.1038/s41467-023-39746-1>.
- Harper, K.A., Macdonald, S.E., Burton, P.J., Chen, J., Brosfoske, K.D., Saunders, S.C., Euskirchen, E.S., Roberts, D., Jaiteh, M.S., Eessen, P.-A., 2005. Edge influence on forest structure and composition in fragmented landscapes. *Conserv. Biol.* 19 (3), 768–782. <https://doi.org/10.1111/j.1523-1739.2005.00045.x>.
- Harrison, M.L.K., Banks-Leite, C., 2020. Edge effects on trophic cascades in tropical rainforests. *Conserv. Biol.* 34 (4), 977–987. <https://doi.org/10.1111/cobi.13438>.
- Hartig, F., Lohse, L., & leite, M. de S (2024). *DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models* (Version 0.4.7) [Computer software]. <https://cran.r-project.org/web/packages/DHARMA/>.
- Hausmann, A., Segerer, A.H., Greifenstein, T., Knubben, J., Morinière, J., Bozicevic, V., Doczkal, D., Günter, A., Ulrich, W., Habel, J.C., 2020. Toward a standardized quantitative and qualitative insect monitoring scheme. *Ecol. Evol.* 10 (9), 4009–4020. <https://doi.org/10.1002/ece3.6166>.
- Heidrich, L., Bae, S., Levick, S., Seibold, S., Weisser, W., Krzyszek, P., Magdon, P., Nauss, T., Schall, P., Serebryanyk, A., Wöllauer, S., Ammer, C., Bässler, C., Doerfler, I., Fischer, M., Gossner, M.M., Heurich, M., Hothorn, T., Jung, K., Müller, J., 2020. Heterogeneity–diversity relationships differ between and within trophic levels in temperate forests. *Nat. Ecol. & Evol.* 4 (9), 1204–1212. <https://doi.org/10.1038/s41559-020-1245-z>.
- Keck, F., Peller, T., Alther, R., Barouillet, C., Blackman, R., Capo, E., Chonova, T., Couton, M., Fehlinger, L., Kirschner, D., Knüsel, M., Munerel, L., Oester, R., Tapolczai, K., Zhang, H., Altermatt, F., 2025. The global human impact on biodiversity. *Nature* 1–6. <https://doi.org/10.1038/s41586-025-08752-2>.
- Kennedy, C.M., Lonsdorf, E., Neel, M.C., Williams, N.M., Ricketts, T.H., Winfree, R., Bommarco, R., Brittain, C., Burley, A.L., Cariveau, D., Carvalheiro, L.G., Chacoff, N. P., Cunningham, S.A., Danforth, B.N., Dudenhöffer, J.-H., Elle, E., Gaines, H.R., Garibaldi, L.A., Gratton, C., Kremen, C., 2013. A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecol. Lett.* 16 (5), 584–599. <https://doi.org/10.1111/ele.12082>.
- Koh, I., Lonsdorf, E.V., Williams, N.M., Brittain, C., Isaacs, R., Gibbs, J., Ricketts, T.H., 2016. Modeling the status, trends, and impacts of wild bee abundance in the United States. *Proc. Natl. Acad. Sci.* 113 (1), 140–145. <https://doi.org/10.1073/pnas.1517685113>.
- Laforest-Lapointe, I., Paquette, A., Messier, C., Kembel, S.W., 2017. Leaf bacterial diversity mediates plant diversity and ecosystem function relationships. *Nature* 546 (7656), 145–147. <https://doi.org/10.1038/nature22399>.
- Li, Y., Schmid, B., Schuldt, A., Li, S., Wang, M.-Q., Fornoff, F., Staab, M., Guo, P.-F., Anttonen, P., Chesters, D., Bruelheide, H., Zhu, C.-D., Ma, K., Liu, X., 2023. Multitrophic arthropod diversity mediates tree diversity effects on primary productivity. *Nat. Ecol. & Evol.* 7 (6), 832–840. <https://doi.org/10.1038/s41559-023-02049-1>.
- Li, Y., Schuldt, A., Ebeling, A., Eisenhauer, N., Huang, Y., Albert, G., Albracht, C., Amyntas, A., Bonkowski, M., Bruelheide, H., Bröcher, M., Chesters, D., Chen, J., Chen, Y., Chen, J.-T., Ciobanu, M., Deng, X., Fornoff, F., Gleixner, G., Liu, X., 2024. Plant diversity enhances ecosystem multifunctionality via multitrophic diversity. *Nat. Ecol. & Evol.* 8 (11), 2037–2047. <https://doi.org/10.1038/s41559-024-02517-2>.
- Liang, M., Yang, Q., Chase, J.M., Isbell, F., Loreau, M., Schmid, B., Seabloom, E.W., Tilman, D., Wang, S., 2025. Unifying spatial scaling laws of biodiversity and ecosystem stability. *Science* 387 (6740), ead12373. <https://doi.org/10.1126/science.ad12373>.
- Lindenmayer, D.B., Laurance, W.F., 2017. The ecology, distribution, conservation and management of large old trees. *Biol. Rev.* 92 (3), 1434–1458. <https://doi.org/10.1111/brv.12290>.
- Marder, E., Smiley, T.M., Yanites, B.J., Kravitz, K., 2025. Direct effects of mountain uplift and topography on biodiversity. *Science* 387 (6740), 1287–1291. <https://doi.org/10.1126/science.adp7290>.
- Marsh, C.J., Turner, E.C., Blonder, B.W., Bongalov, B., Both, S., Cruz, R.S., Elias, D.M.O., Hemprich-Bennett, D., Jotan, P., Kemp, V., Kritzer, U.H., Milne, S., Milodowski, D. T., Mitchell, S.L., Pilloco, M.M., Nunes, M.H., Riutta, T., Robinson, S.J.B., Slade, E.M., Hector, A., 2025. Tropical forest clearance impacts biodiversity and function, whereas logging changes structure. *Science* 387 (6730), 171–175. <https://doi.org/10.1126/science.adf9856>.
- Murcia, C., 1995. Edge effects in fragmented forests: implications for conservation. *Trends Ecol. & Evol.* 10 (2), 58–62. [https://doi.org/10.1016/S0169-5347\(00\)88977-6](https://doi.org/10.1016/S0169-5347(00)88977-6).
- National Bureau of Statistics of China. (2024). *China City Statistical Yearbook 2024*. Novotny, V., Basset, Y., 2005. Host specificity of insect herbivores in tropical forests. *Proc. R. Soc. B Biol. Sci.* <https://doi.org/10.1098/rspb.2004.3023>.
- Novotny, V., Miller, S.E., Baje, L., Balagawi, S., Basset, Y., Cizek, L., Craft, K.J., Dem, F., Drew, R.A.I., Hulcr, J., Leps, J., Lewis, O.T., Pokon, R., Stewart, A.J.A., Allan Samuelson, G., Weiblen, G.D., 2010. Guild-specific patterns of species richness and host specialization in plant–herbivore food webs from a tropical forest. *J. Anim. Ecol.* 79 (6), 1193–1203. <https://doi.org/10.1111/j.1365-2656.2010.01728.x>.
- Ollerton, J., Winfree, R., Tarrant, S., 2011. How many flowering plants are pollinated by animals? *Oikos* 120 (3), 321–326. <https://doi.org/10.1111/j.1600-0706.2010.18644.x>.
- Orr, M.C., Hughes, A.C., Chesters, D., Pickering, J., Zhu, C.-D., Ascher, J.S., 2021. Global patterns and drivers of bee distribution. *e4 Curr. Biol.* 31 (3), 451–458. <https://doi.org/10.1016/j.cub.2020.10.053>.
- Penone, C., Allan, E., Soliveres, S., Felipe-Lucia, M.R., Gossner, M.M., Seibold, S., Simons, N.K., Schall, P., van der Plas, F., Manning, P., Manzanedo, R.D., Boch, S., Prati, D., Ammer, C., Bauhus, J., Buscot, F., Ehbrecht, M., Goldmann, K., Jung, K., Fischer, M., 2019. Specialisation and diversity of multiple trophic groups are promoted by different forest features. *Ecol. Lett.* 22 (1), 170–180. <https://doi.org/10.1111/ele.13182>.
- Pereira, F.W., Carneiro, L., Gonçalves, R.B., 2021. More losses than gains in ground-nesting bees over 60 years of urbanization. *Urban Ecosyst.* 24 (2), 233–242. <https://doi.org/10.1007/s11252-020-01030-1>.
- Pfeifer, M., Lefebvre, V., Peres, C.A., Banks-Leite, C., Wearn, O.R., Marsh, C.J., Butchart, S.H.M., Arroyo-Rodríguez, V., Barlow, J., Cerezo, A., Cisneros, L., D’Cruze, N., Faria, D., Hadley, A., Harris, S.M., Klingbeil, B.T., Kormann, U., Lens, L., Medina-Rangel, G.F., Ewers, R.M., 2017. Creation of forest edges has a global impact on forest vertebrates. *Nature* 551 (7679), 187–191. <https://doi.org/10.1038/nature24457>.
- Priyadarshana, T.S., Woodcock, B.A., Jain, A., Martínez-Núñez, C., Goodale, E., Pagani-Núñez, E., Gebert, F., Lee, J.S.H., Slade, E.M., 2025. The direct and indirect effects of road verges and urban greening on butterflies in a tropical city-state. *Landscape Urban Plan.* 258, 105335. <https://doi.org/10.1016/j.landurbplan.2025.105335>.
- Ries, L., Sisk, T.D., 2004. A predictive model of edge effects. *Ecology* 85 (11), 2917–2926. <https://doi.org/10.1890/03-8021>.
- Sánchez-Bayo, F., Wyckhuys, K.A.G., 2019. Worldwide decline of the entomofauna: a review of its drivers. *Biol. Conserv.* 232, 8–27. <https://doi.org/10.1016/j.biocon.2019.01.020>.
- 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. *Conserv. Urban Plan.* 256, 105273. <https://doi.org/10.1016/j.landurbplan.2024.105273>.
- Schuldt, A., Ebeling, A., Kunz, M., Staab, M., Guimarães-Steinicke, C., Bachmann, D., Buchmann, N., Durka, W., Fichtner, A., Fornoff, F., Härdtle, W., Hertzog, L.R., Klein, A.-M., Roscher, C., Schaller, J., von Oheimb, G., Weigelt, A., Weisser, W., Wirth, C., Eisenhauer, N., 2019. Multiple plant diversity components drive consumer

- communities across ecosystems. *Nat. Commun.* 10 (1), 1460. <https://doi.org/10.1038/s41467-019-09448-8>.
- Seibold, S., Gossner, M.M., Simons, N.K., Blüthgen, N., Müller, J., Ambarlı, D., Ammer, C., Bauhus, J., Fischer, M., Habel, J.C., Linsenmair, K.E., Nauss, T., Penone, C., Prati, D., Schall, P., Schulze, E.-D., Vogt, J., Wöllauer, S., Weisser, W.W., 2019. Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature* 574 (7780), 671–674. <https://doi.org/10.1038/s41586-019-1684-3>.
- Shannon, C.E., 1948. A mathematical theory of communication. *Bell Syst. Tech. J.* 27 (3), 379–423. <https://doi.org/10.1002/j.1538-7305.1948.tb01338.x>.
- Shangrao Bureau of Statistics. (2022). *Shangrao Statistical Yearbook 2022*. (https://navi.cnki.net/knavi/detail?p=ltvxuOoU4kNN0lQyVretflNgDnZ_YC5rVshZJ9ntDL_HFIBB4MR1jegd0SnaKyRVV65gxWAYQkFkzwHT2uXKDXIDG7LN867b36oPOCF5s0=&uniplatform=NZKPT).
- Shipley, J.R., Gossner, M.M., Rigling, A., Krumm, F., 2023. Conserving forest insect biodiversity requires the protection of key habitat features. *Trends Ecol. & Evol.* 38 (9), 788–791. <https://doi.org/10.1016/j.tree.2023.05.015>.
- Skaldina, O., Nylund, A., Ramula, S., 2024. Neglected puzzle pieces of urban green infrastructure: richness, cover, and composition of insect-pollinated plants in traffic-related green spaces. *Landsc. Ecol.* 39 (4), 80. <https://doi.org/10.1007/s10980-024-01881-5>.
- Soliveres, S., van der Plas, F., Manning, P., Prati, D., Gossner, M.M., Renner, S.C., Alt, F., Arndt, H., Baumgartner, V., Binkenstein, J., Birkhofer, K., Blaser, S., Blüthgen, N., Boch, S., Böhm, S., Börschig, C., Buscot, F., Diekötter, T., Heinze, J., Allan, E., 2016. Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality. *Nature* 536 (7617), 456–459. <https://doi.org/10.1038/nature19092>.
- Staab, M., Schuldt, A., 2020. The influence of tree diversity on natural enemies—a review of the “enemies” hypothesis in forests. *Curr. For. Rep.* 6 (4), 243–259. <https://doi.org/10.1007/s40725-020-00123-6>.
- Stein, A., Krefl, H., 2015. Terminology and quantification of environmental heterogeneity in species-richness research. *Biol. Rev. Camb. Philos. Soc.* 90 (3), 815–836. <https://doi.org/10.1111/brv.12135>.
- Theodorou, P., Radzevičiūtė, R., Lentendu, G., Kahnt, B., Husemann, M., Bleidorn, C., Settele, J., Schweiger, O., Grosse, I., Wubet, T., Murray, T.E., Paxton, R.J., 2020. Urban areas as hotspots for bees and pollination but not a panacea for all insects. *Nat. Commun.* 11 (1), 576. <https://doi.org/10.1038/s41467-020-14496-6>.
- Trombulak, S.C., Frissell, C.A., 2000. Review of ecological effects of roads on terrestrial and aquatic communities. *Conserv. Biol.* 14 (1), 18–30. <https://doi.org/10.1046/j.1523-1739.2000.99084.x>.
- Tschamntke, T., Karp, D.S., Chaplin-Kramer, R., Batáry, P., DeClerck, F., Gratton, C., Hunt, L., Ives, A., Jonsson, M., Larsen, A., Martin, E.A., Martínez-Salinas, A., Meehan, T.D., O'Rourke, M., Poveda, K., Rosenheim, J.A., Rusch, A., Schellhorn, N., Wanger, T.C., Zhang, W., 2016. When natural habitat fails to enhance biological pest control – Five hypotheses. *Biol. Conserv.* 204, 449–458. <https://doi.org/10.1016/j.biocon.2016.10.001>.
- Uhler, J., Redlich, S., Zhang, J., Hothorn, T., Tobisch, C., Ewald, J., Thorn, S., Seibold, S., Mitesser, O., Morinière, J., Bozicevic, V., Benjamin, C.S., Englmeier, J., Fricke, U., Ganuza, C., Haensel, M., Riebel, R., Rojas-Botero, S., Rummier, T., Müller, J., 2021. Relationship of insect biomass and richness with land use along a climate gradient. *Nat. Commun.* 12 (1), 5946. <https://doi.org/10.1038/s41467-021-26181-3>.
- van Klink, R., Bowler, D.E., Gongalsky, K.B., Shen, M., Swengel, S.R., Chase, J.M., 2024. Disproportionate declines of formerly abundant species underlie insect loss. *Nature* 628 (8007), 359–364. <https://doi.org/10.1038/s41586-023-06861-4>.
- Vázquez-González, C., Castagneyrol, B., Muiruri, E.W., Barbaro, L., Abdala-Roberts, L., Barsoum, N., Fründ, J., Glynn, C., Jactel, H., McShea, W.J., Mereu, S., Mooney, K.A., Morillas, L., Nell, C., Nock, C.A., Paquette, A., Parker, J.D., Parker, W.C., Roales, J., Koricheva, J., 2024. Tree diversity enhances predation by birds but not by arthropods across climate gradients. *Ecol. Lett.* 27 (5), e14427. <https://doi.org/10.1111/ele.14427>.
- Wong, M.K.L., Didham, R.K., 2024. Global meta-analysis reveals overall higher nocturnal than diurnal activity in insect communities. *Nat. Commun.* 15 (1), 3236. <https://doi.org/10.1038/s41467-024-47645-2>.
- Woodcock, B.A., Savage, J., Bullock, J.M., Nowakowski, M., Orr, R., Tallwin, J.R.B., Pywell, R.F., 2014. Enhancing floral resources for pollinators in productive agricultural grasslands. *Biol. Conserv.* 171, 44–51. <https://doi.org/10.1016/j.biocon.2014.01.023>.
- Yachi, S., Loreau, M., 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proc. Natl. Acad. Sci.* 96 (4), 1463–1468. <https://doi.org/10.1073/pnas.96.4.1463>.
- Yang, G., Crowther, T.W., Lauber, T., Zohner, C.M., Smith, G.R., 2025. A globally consistent negative effect of edge on aboveground forest biomass. *Nat. Ecol. & Evol.* 1–10. <https://doi.org/10.1038/s41559-025-02840-2>.