Urban densification and vegetation composition reshape ecological networks across trophic layers

Kilian Perrelet[1,*], Sebastian Ruile[1,2], Merin Reji Chacko[1,3], Joan Casanelles-Abella[1,4], Bertrand Fournier[5], Marco Moretti[1*]

[1]*Biodiversity and Conservation Biology, Swiss Federal Institute for Forest, Snow, and Landscape Research WSL, Birmensdorf, Switzerland*

[2]*Department of Environmental Systems Science, ETH Zurich, Zurich, Switzerland*

[3]*Ecological Networks, Technische Universität Darmstadt, Darmstadt, Germany*

[4]*Urban Productive Ecosystems, TUM School of Life Sciences, Technical University of Munich, Freising, Germany*

[5]*Institute of Environmental Sciences and Geography, University of Potsdam, Potsdam, Germany*

*corresponding authors

Kilian Perrelet, Zürcherstrasse 111, Birmensdorf, Zürich, Switzerland, kilian.perrelet@gmail.com

Keywords:

Urban ecology; Metaweb; Food web; Plant diversity; Pollination; Herbivory; Predation

Abstract

Urban densification reshapes biodiversity, yet its effects on ecological networks across trophic levels remain unclear. Using a metaweb approach, we reconstructed bipartite, multitrophic, and combined food webs across 60 urban green spaces along gradients of urban densification and vegetation complexity. Densification reduced taxonomic and interaction richness, promoted interaction generalization, and homogenized networks. Its effects depended on network type, altering connectance, nestedness, and modularity differently in bipartite and multitrophic networks while increasing dependencies among trophic layers, ultimately reducing the robustness of combined food webs. Higher plant richness partly mitigated these effects by promoting interaction diversity, trophic specialization, and robustness, although responses varied across network types. Non-native plants also induced network-specific shifts, favoring highly connected consumers in bipartite networks while leaving overall structure largely unchanged. Our results show that urban density and vegetation composition jointly restructure ecological networks in a network-type-dependent manner, and that single-guild perspectives may misrepresent ecosystem-level responses in cities.

Introduction

Cities now house nearly 60% of the global population and represent some of the fastest-growing ecosystems on Earth (Rivkin et al. 2019, United Nations 2022). Urban growth is an extreme form of habitat conversion with profound impacts on biodiversity and ecosystem functioning (Grimm et al. 2008, Simkin et al. 2022). To limit sprawl, urban densification—concentrating populations and impervious surfaces within existing areas—has been promoted as a strategy to protect valuable peri-urban areas (Sushinsky et al. 2013, Concepción et al. 2016, Savary et al. 2026). Yet, while densification may reduce the loss and degradation of peri-urban areas, it often comes at the expense of urban green spaces, undermining biodiversity, ecosystem services, and human well-being (Haaland and van den Bosch 2015, Lin et al. 2015, Bille et al. 2023). Should densification continue to be favored, it remains unclear whether improved habitat quality through various greening strategies (e.g., increased vegetation complexity) can offset the ecological costs of compact urban growth (Beninde et al. 2015, Wenzel et al. 2020).

Urbanization (both sprawl and densification) is commonly assessed via its effects on species richness and composition (Knapp et al. 2021). However, these metrics overlook how species are embedded within complex multitrophic interaction networks, including plant–pollinator, plant–herbivore, and predator–prey systems that govern ecosystem processes, energy flows, population dynamics, and ecosystem stability (Johnson et al. 2014, Keyes et al. 2021). By filtering out specialists and favoring generalists, urbanization can restructure ecological networks, producing smaller but more densely connected structures (Banaszak-Cibicka and Żmihorski 2012, Start et al. 2019, da Cunha-Silva et al. 2025). These changes can alter emergent properties such as nestedness, reflecting specialization, and modularity, reflecting compartmentalization, with consequences for robustness to cascading extinctions (Banaszak-Cibicka and Żmihorski 2012, Start et al. 2019, da

Cunha-Silva et al. 2025). Yet, urban landscapes offer opportunities for intervention, as greening strategies that modify habitat design and management, as well as resource amount and quality, can mitigate biodiversity loss and strengthen ecological interactions (i.e., intermediate landscape-complexity hypothesis; Tscharntke et al. 2012). By enhancing plant diversity, structural complexity, and native species representation, urban greening strategies can directly support primary consumers (Zaninotto et al. 2023, Schmack and Egerer 2023), while providing indirect (although sometimes weaker) benefits to higher trophic levels through increased prey (Burks and Philpott 2017, Ning et al. 2025). Likewise, reducing disturbance and increasing stewardship, often expressed through increased time allocated to management (Bennett et al. 2018), can further benefit multiple trophic levels and reinforce ecological network resilience (Harrison and Winfree 2015, Proske et al. 2022).

Although these findings are encouraging, most studies focus on a single interaction type (e.g., plant–pollinator networks), without consideration for cascading effects across trophic levels (Moreno-García et al. 2025). Yet, evidence of predatory (e.g., Philpott et al. 2020), parasite (e.g., Start et al. 2019), and, more recently, multitrophic networks (e.g., Perrelet et al. 2025, Straka et al. 2025) report divergent responses to urban densification and greening interventions. Such discrepancies likely arise because urbanization and vegetation complexity filter species differently across trophic levels, reshaping species composition, interactions, and ultimately network structure (Rocha and Fellowes 2018, Theodorou 2022). For example, bees and their natural enemies respond differently to urban densification, producing contrasting changes in prey and predator communities (Martínez-Núñez et al. 2024), while connectance (i.e., the proportion of realized interactions) may increase in bipartite networks through the persistence of generalists but decline in multitrophic food webs following the loss of highly connected predators (Start et al. 2019, Perrelet et al. 2025). Consequently, focusing on a single interaction type may overlook how urban densification and

greening strategies reshape different trophic levels and energy flows between them, potentially ignoring cascading synergistic or antagonistic effects across networks and risking incomplete or conflicting management recommendations (Welti and Joern 2015, Pilosof et al. 2017, O'Connor et al. 2026).

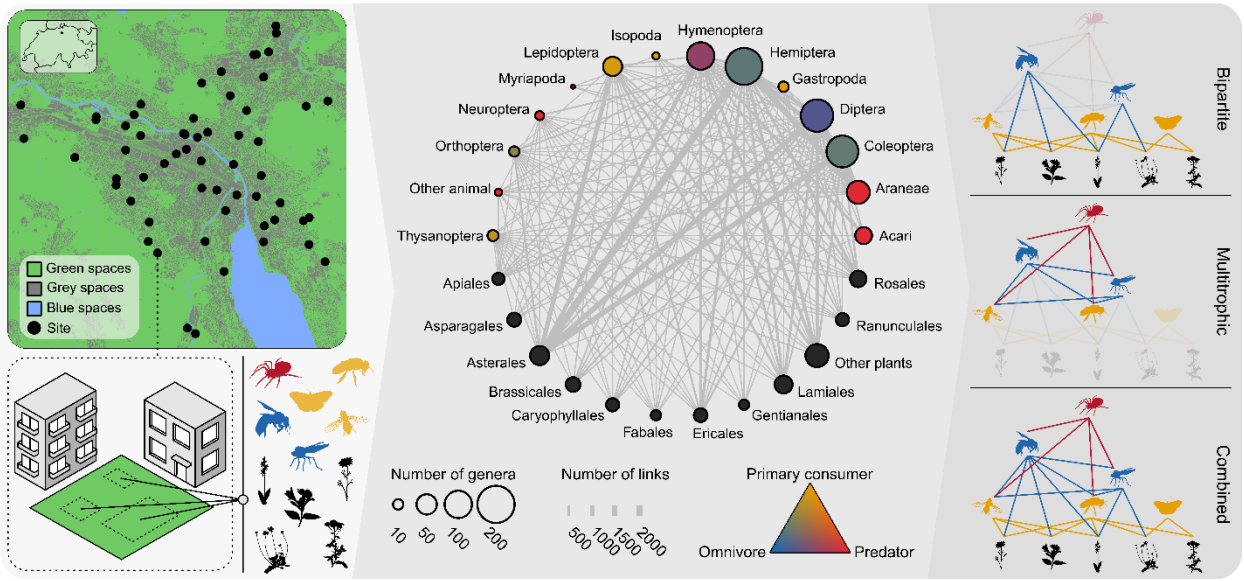
Urban ecological networks are rarely studied beyond plant–primary consumer interactions, largely because consumer–consumer links (e.g., predator–prey) are difficult to observe, especially in urban areas where private property can limited site access (Gelmi-Candusso et al. 2023). However, recent advances in metaweb frameworks, which delineate regional interaction pools and infer local networks through species co-occurrences (Dunne 2006), along with large-scale species interaction databases (e.g., Reji Chacko et al. 2025b) now enable the reconstruction of potential ecological networks across multiple interaction types (Ho et al. 2022, Reji Chacko et al. 2025a, Adhurya and Park 2025). Here, we apply a metaweb approach to 60 urban sites across gradients of urban densification and vegetation complexity, focusing on bipartite (plant–consumer) and multitrophic (consumer–consumer) networks, as well as their combination. We hypothesize that (1) urban densification will reduce network size and favor generalists, yielding smaller, more connected networks; (2) responses of bipartite and multitrophic networks will differ due to contrasting sensitivities of primary consumers relative to predators, and (3) urban greening strategies will help mitigate these effects, with stronger benefits expected in bipartite networks due to the closer association of primary consumers with vegetation. By resolving networks across trophic layers, we aim to identify dependencies among layers and assess how local greening can mitigate urbanization-driven changes in network structure.

Methods

Site selection

This study was conducted in Zurich, Switzerland's largest city (92 km^2, ~450,000 inhabitants), using data from Ruile et al. (2026). Zurich is well suited to study urban densification, as rapid population growth exceeds most Western European agglomerations (United Nations 2018), while policies explicitly promote densification to limit sprawl (Stadt Zürich 2019). Despite high impervious cover, ~35 km^2 of heterogeneous green space remain, including parks, ruderal sites, and private or real estate-managed gardens.

To capture broad variation in invertebrate communities while minimizing habitat-type bias, we selected 60 sites spanning five urban green space types: parks, allotments, private gardens, residential estate gardens, and ruderal sites (12 per type, with one private garden later excluded due to lost access). Following a space-for-time substitution approach, sites were selected to span two largely orthogonal gradients: urban densification and vegetation structural diversity, ensuring wide environmental coverage across the study area. Urban densification was measured as the proportion of impervious surface within a 500 m radius, and vegetation complexity was quantified based on lawn cover and the number of habitat types present (e.g., meadow, shrubland, trees, flower beds, vegetable beds, wetland). Further details on site selection are provided in Casanelles-Abella et al. (2026).



120 *Figure 1: Site locations and local food web inference. Left: Sampling locations (black dots) with*
121 *schematic transects (dashed lines) and observed communities at each site. Middle: Regional*
122 *metaweb used for local network inference (visualized at the order level, except Myriapoda; Reji*
123 *Chacko et al. 2025b). Circle size reflects the number of genera, color indicates trophic composition*
124 *(primary consumers, omnivores, strict predators), and line thickness represents interaction counts*
125 *between groups. Right: Inferred local networks at a site, including bipartite (plant–consumer),*
126 *multitrophic (consumer–consumer), and "combined" networks, derived from species co-*
127 *occurrence (left) and the regional metaweb (middle).*

128

129 *Species data collection*

130 In 2024, invertebrates were sampled along transects at each site on three occasions between April
131 and August under favorable conditions (temperature >15 °C, wind <13 kmh^{-1}; Grange et al. 2021).
132 The number of transects scaled with habitat heterogeneity, but total sampled area was fixed at 100
133 m^2 per site to standardize effort. Transects encompassed all vegetation up to 2 m in height,
134 including overhanging branches. In allotments, transects covered the entire area; in private gardens,
135 100 m^2 was divided equally into central and peripheral transects; in ruderal sites, transects were
136 placed randomly; and in parks and residential estate areas, transects were allocated proportionally

according to mapped habitat areas, excluding habitats covering <5% of the site (Casanelles-Abella et al. 2026).

Flowering plants were identified along transects, and insects landing on the reproductive parts of the flowers were collected with hand nets, recording each visit as a plant–pollinator interaction. Survey speed was adjusted to flower complexity to maintain comparable observation effort per flower. Specimens were stored in –20 °C, individually pinned and sent to experts for taxonomic identification. To sample herbivores, detritivores, and predators, transects were subdivided into 5 m^2 subplots, and invertebrates were collected from all strata (leaves, stems, ground) of the most dominant plant within each subplot, based on coverage. Collection was performed by vacuuming the vegetation, and all specimens were preserved in 97% ethanol. For these groups, taxonomic identification used DNA metabarcoding, with DNA extraction, amplification, library preparation, and sequencing performed by AllGenetics & Biology SL (A Coruña, Spain). Reads were quality-filtered, merged, dereplicated, and clustered into OTUs, which were filtered to remove low-abundance reads (<0.5% of total sample reads), those containing ambiguous nucleotides or chimera, and those detected in positive or negative controls. OTUs were rarefied to the 15th percentile of reads per sample to mitigate sequencing bias. Taxonomic assignment was performed using BLAST against the NCBI nucleotide database, with identity thresholds of 90% for family and 95% for genus levels, retaining matches with >90% query coverage and the lowest E-value. Further details are provided in Ruile et al. (2026). Species-level assignments were not retained to ensure compatibility with the metaweb framework (see *Local food web inferences*).

Environmental predictors

We evaluated the influence of urban densification (hereafter "urbanization" for simplicity) and five urban greening strategies (changes in plant richness, % non-native species, % woody species,

disturbance intensity, and time investment), on ecological networks. Urbanization was quantified as the proportion of impervious surface within a 1,000 m buffer around each site, derived from a 10 m-resolution habitat map of Switzerland (Price et al. 2024). Human population density within the same buffer was also extracted but excluded due to strong collinearity with impervious surface (Pearson r = 0.81). The 1,000 m buffer was chosen due to its stronger influence on arthropod richness than smaller spatial scales (Chatelain et al. 2023), although sensitivity analyses using 150 and 500 m buffers produced qualitatively similar results (Figs. S2–4) .

Urban greening strategies were measured at the site level to reflect design and management decisions available to gardeners and practitioners. Design variables included plant richness, the proportion of non-native species, and the proportion of woody species. Plant richness was measured as the number of plants per transect. Non-native species were defined as species that do not occur naturally in Switzerland based on national checklists (Federal Office for the Environment 2022), and woody species were defined as shrubs and trees, excluding herbs and lianas. Because transects were dominated by herbaceous vegetation, structural complexity was highly collinear with woody cover in preliminary analyses and was therefore excluded in favor of the latter for interpretability. Management behavior was assessed using a questionnaire adapted from previously validated research (Tresch et al. 2019) and described in Ruile et al. (2026b). Questionnaires were completed by individuals responsible for decisions regarding planting and management of the respective green space and were used to quantified three dimensions of management: disturbance intensity, based on the frequency of high-intensity interventions such as mowing; time investment, used as a proxy for ecological stewardship (Bennett et al. 2018); and biodiversity-friendly practices (e.g., reduced pesticide use). Because time investment and biodiversity-friendly practices were strongly correlated, only time investment was retained. Other correlations among environmental variables (hereafter “covariates”) were generally low to

moderate ($r \approx 0.3–0.4$), except for a stronger correlation between time investment and disturbance intensity ($r = 0.68$; Fig S1). Together, these variables captured environmental variation across urban green space types (allotments, private and residential estate gardens, parks, and ruderal sites). We therefore used continuous predictors instead of categorical site types, as they better reflect underlying environmental gradients.

Local food web inferences

Local food webs were inferred using a metaweb approach, which aggregates documented interactions among taxa within a predefined region (Dunne 2006). We used a Swiss national metaweb encompassing plant–pollinator, herbivore–plant, and predator–prey interactions, compiled from empirical observations, and primary and grey literature (Reji Chacko et al. 2025b), and supplemented it with additional published interactions to address underrepresented urban pollination links (Reji Chacko et al. 2026). The metaweb was resolved primarily at the genus level, retaining family-level information only when genus-level data were unavailable. This resolution accommodates less-documented taxa (e.g., soil fauna) and accounts for diet shifts (typically occurring among closely related species; Pearse and Altermatt 2013), while remaining sufficient to capture variation in network structure along environmental gradients (Thompson and Townsend 2000, Potapov et al. 2019).

Local networks were constructed by subsetting the metaweb based on co-occurring taxa at each site, following the assumption that documented interactions may occur locally (Morales-Castilla et al. 2015). Although this assumes fixed feeding behavior, metaweb approaches are increasingly used to overcome practical constraints in sampling interactions (e.g., Ho et al. 2022, Reji Chacko et al. 2025a), particularly in urban systems where access to private land is limited (e.g., Perrelet et al. 2025). By standardizing potential biases across sites and network types, this framework enables

comparative analyses along environmental gradients, provided that interpretations focus on relative changes along gradients rather than absolute network metrics (Pellissier et al. 2018). While metawebs have been criticized at broad spatial or temporal scales (Brimacombe et al. 2024), temporally explicit co-occurrence within sites provides a biologically plausible basis for potential interactions.

We validated the metaweb by comparing predicted plant–pollinator interactions with field observations (see *Species data collection*). Of the 2,763 observed interactions, 2,428 (87.9%) were correctly inferred by the metaweb, whereas 335 (12.1%) were not predicted; an additional 6,584 inferred interactions were not observed in the field (Fig. S5). Unpredicted observed interactions were incorporated into subsequent analyses. Given that interactions accumulate more slowly than species with sampling effort, these values are plausible. Moreover, network metrics derived from observed and inferred networks (e.g., connectance, modularity, robustness; see *Network-level* analysis) were significantly correlated ($r = 0.3–0.8$; Fig. S6) and showed largely similar relationships with environmental factors, although some effects were only significant in observed or inferred networks (Fig. S7). Together, these results support the metaweb approach, which helps mitigate undersampling while enabling inference of difficult-to-observe interactions (e.g., predator–prey). Nonetheless, we stress that all analyses are based on potential rather than realized interactions, and only a subset may occur at each site.

We distinguished three network types: bipartite networks (plants and detritus interacting with primary consumers), multitrophic networks (interactions among consumers), and combined networks incorporating both (Fig. 1). This classification allowed us to (i) evaluate whether commonly studied networks, such as plant–pollinator networks, exhibit similar dynamics to more complex trophic systems, (ii) assess dependencies across interaction types, and (iii) distinguish networks directly influenced by urban greening strategies from those affected indirectly.

Interactions were assigned by resource type: links involving plants or detritus were classified as bipartite, whereas links among animal taxa were classified as multitrophic. Based on the metaweb, consumers were categorized into three trophic groups as primary consumers (feeding exclusively on plants or detritus), predators (feeding exclusively on consumers), and omnivores (feeding on both, including across life stages). Accordingly, bipartite networks included herbivory, pollination, and plant–omnivore interactions, whereas multitrophic networks comprised predator–prey and consumer–omnivore interactions. We did not further subdivide primary consumers (e.g., herbivores vs. pollinators), as interaction-type information in the metaweb were often insufficient to reliably distinguish between these processes.

Link-level analysis

To examine variation in trophic group richness and interaction structure, we quantified, for each site, the number of taxa in the three trophic groups (primary consumers, omnivores, and predators) as well as plants, together with the number of links among them (e.g., plant–omnivore interactions). To test whether observed interaction patterns deviated from expectations based on taxonomic richness alone, we implemented a role-constrained null model. This model preserved group-specific richness, total link number, and trophic role identity (i.e., basal resources consumed by primary consumers and omnivores, consumers consumed only by omnivores and predators) while randomly redistributing links across biologically permissible feeding pairs. We generated 100 null networks, recalculated link frequencies, and derived standardized effect sizes (z-scores) to quantify deviations from null expectations for each trophic pathway. For clarity, interactions involving omnivores (primary consumer–omnivore, omnivore–omnivore, and predator–omnivore) were grouped as consumer–omnivore links, and a similar grouping was applied for predator-related interactions. Finally, to assess the effects of urbanization and greening strategies on feeding

patterns, taxonomic richness, link richness, and z-scores were regressed against environmental covariates using (generalized) linear models (negative binomial distribution for richness, Gaussian for z-scores).

Network-level analysis

To evaluate shifts in generalism and network structure, we quantified common degree-distribution properties—median, skewness, and coefficient of variation—which capture complementary aspects of interaction patterns. The median reflects typical species generalism, skewness the balance between sparsely and highly connected species, and the coefficient of variation interaction heterogeneity and uneven connectivity across species. As these properties can co-occur, metrics were moderately correlated, except for a stronger association between skewness and coefficient of variation in multitrophic networks (Fig. S8). Null models preserving node and link richness (with resource nodes constrained to remain basal) were used to express degree-distribution metrics as z-scores, quantifying deviations beyond expectations from network size and connectance. We also measured standard network metrics, including node richness, connectance, nestedness, modularity, and robustness (R50, i.e., the mean proportion of primary extinctions needed to remove 50% of nodes, based on 100 simulations of random primary extinctions and secondary cascades; Jonsson et al. 2015). The same null models as for degree metrics were implemented, confirming that all network metrics deviated from null expectations (Fig. S9). Details on network metric calculations are provided in *Supplementary Material I*.

We then applied a dual modeling strategy to assess environmental effects. First, degree-distribution metrics (median, skewness, coefficient of variation) were modeled as functions of individual covariates using linear models, with standardized effect sizes and 95% confidence intervals reported via coefficient plots. Second, to account for interdependencies among structural network

properties, we applied piecewise structural equation modeling (SEM), allowing separation of direct environmental effects from indirect effects mediated through other metrics. SEMs followed established ecological and mathematical dependencies: node richness was modeled as a function of the covariate; connectance as a function of node richness and the covariate; modularity and nestedness as functions of connectance, node richness, and the covariate; and robustness as a function of all preceding properties, following Neff et al. (2021). This framework reflects the rationale that changes in species richness can alter connectance, facilitating modular or nested organization and ultimately influencing robustness. We ensured that model assumptions were met and tested overall model fit and individual path independence claims (see Tables S1 and S2). We then retrieved standardized path coefficients and assessed significance via 1,000-bootstrap resamples to obtain 95% confidence intervals. SEMs were conducted separately for bipartite, multitrophic, and combined networks, and independently for urbanization and each of the six urban greening strategies.

Results

Using the metaweb, we constructed 177 networks, equally divided among three types: bipartite networks (mean ± SD nodes = 137 ± 32; mean interactions = 1032 ± 480), multitrophic networks (98 ± 27; 1461 ± 633), and combined networks (161 ± 37; 429 ± 200; note that values do not sum across types because species may act as consumers in bipartite networks and as prey in multitrophic networks).

We found that urbanization reduced the taxonomic richness of all trophic groups—primary consumers, omnivores, and predators—as well as the number of links among them (Fig. 2A–B). Despite this decline, taxonomic composition remained relatively stable, dominated by

Hymenoptera, Hemiptera, Diptera, Collembola, and Araneae (Fig. S10). However, trophic structure shifted: the proportion of omnivores declined (Fig. S11), and their interaction patterns changed, leading to an increase in consumer–omnivore interactions and a decline in plant–omnivore interactions beyond expectations from species loss alone (Fig. 2C). Urban greening strategies partly counteracted these shifts: higher plant richness—and, to a lesser extent, time investment—restored taxonomic and interaction richness and shifted interactions back toward plant-based links, increasing plant–omnivore interactions and reducing consumer–consumer interactions relative to null expectations (Fig. 2). Non-native plant dominance further promoted plant–omnivore interactions while reducing plant–primary consumer interactions. Other drivers had weaker effects overall.

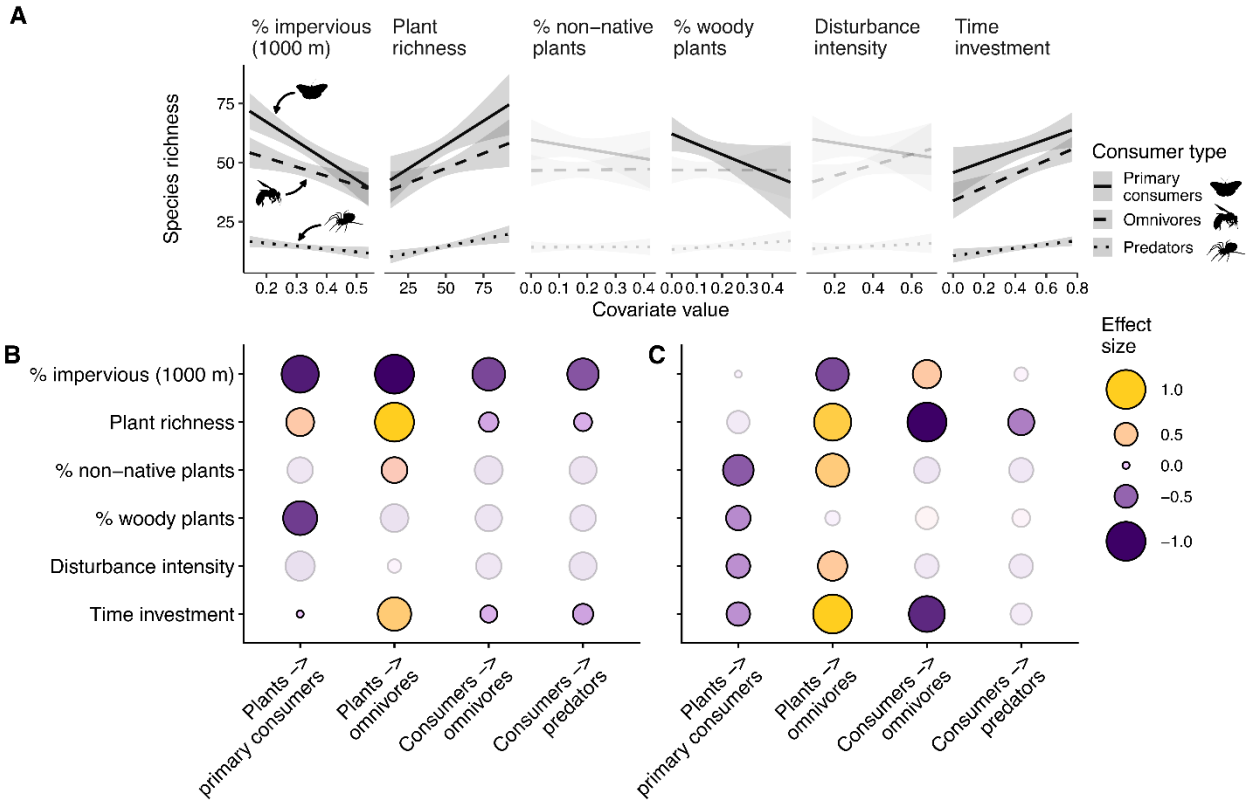


Figure 2: Effects of urbanization and urban greening strategies (plant richness, proportion of alien and woody plants, disturbance intensity, and time investment) on trophic structure and interaction organization in local food webs. (A) Relationships between covariates and richness of primary consumers (solid), omnivores (dashed), and predators (dotted); non-significant relationships are

shown with reduced opacity. (B–C) Effects of covariates on trophic link richness (B) and deviations in link frequencies from null expectations (z-scores; C). Significant relationships in (C) indicate changes in interaction frequencies beyond those explained by species and link richness and trophic group proportions. Bubble size indicates effect magnitude, color indicates direction, and transparency indicates statistical support. For simplicity, interactions involving primary consumers, omnivores, or predators as prey are grouped as consumer → omnivore and consumer → predator interactions.

Urbanization also reshaped degree distributions across network types (Fig. 3). Along the urban gradient, networks included more well-connected nodes (higher median degree) and fewer poorly connected nodes (lower skewness), resulting in more homogeneous degree distributions (lower coefficient of variation; Fig 3). These patterns were broadly consistent across bipartite and multitrophic networks—although shifts in median degree were less consistent—and were most pronounced in combined networks.

Urban greening strategies partly mitigated these shifts, although effects were network-dependent (Fig. 3). Higher plant richness reduced median degree, increased the prevalence of poorly connected nodes (higher skewness), and restored heterogeneity (higher coefficient of variation), particularly in bipartite and combined networks (Fig. 3). Other strategies showed network-specific responses. Non-native plants reduced degree median and favored poorly connected nodes in multitrophic networks (higher skewness), but increased median values in bipartite networks. Time investment had little effect on multitrophic networks but increased heterogeneity in bipartite and combined networks (higher skewness and variance). Once again, woody plant dominance and disturbance again had comparatively minor effects (Fig. 3).

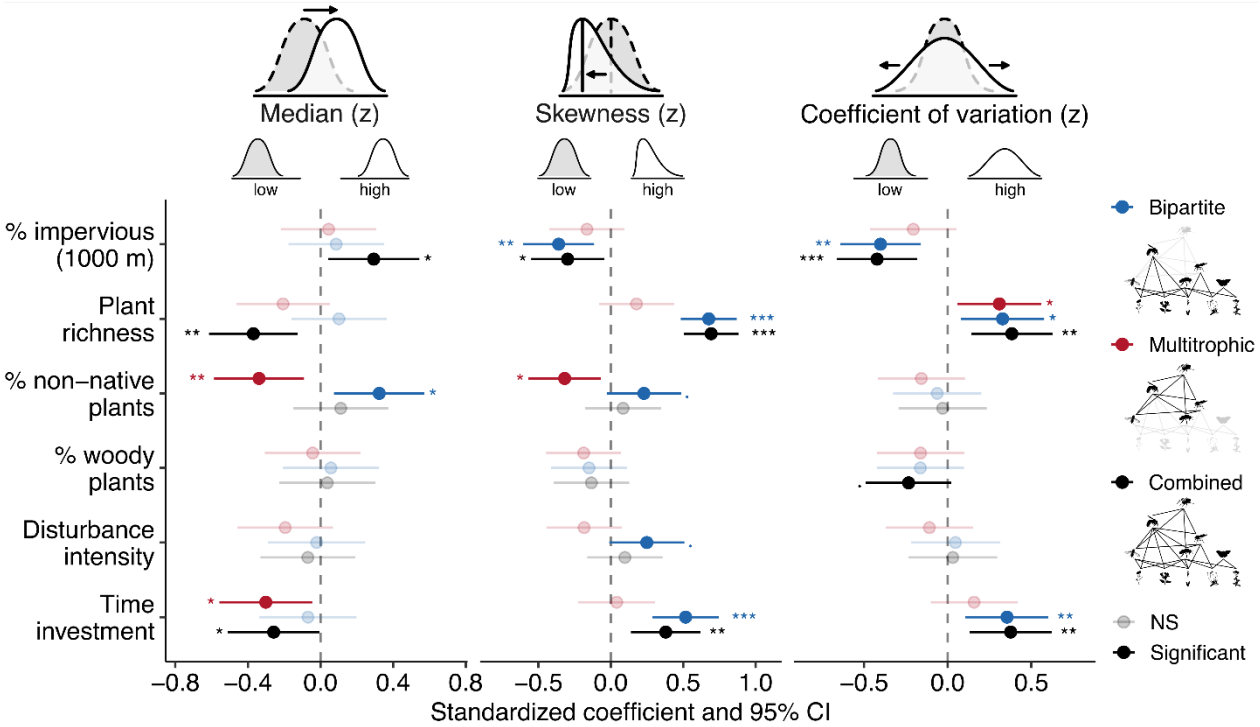
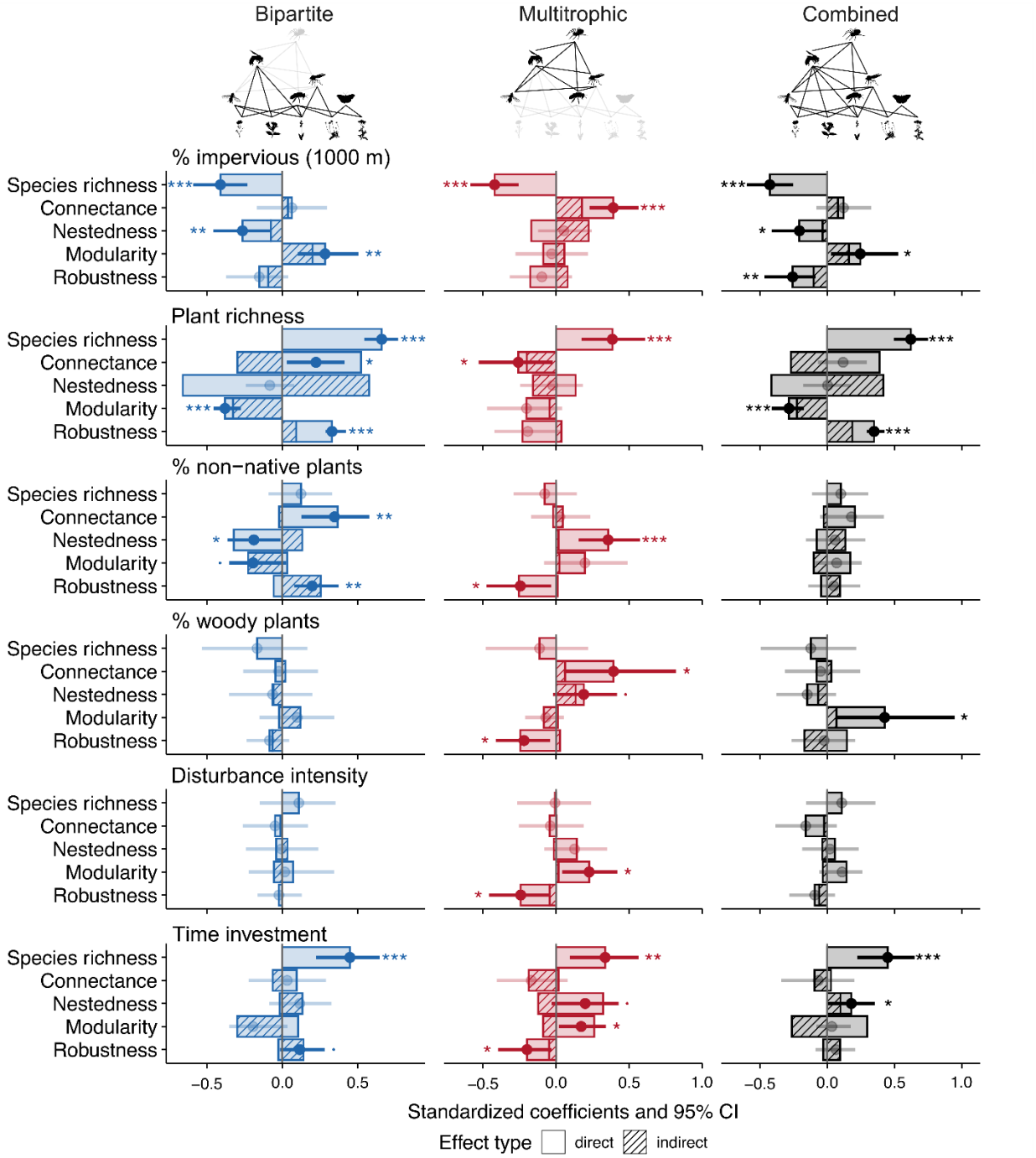


*Figure 3: Influence of urbanization and urban greening strategies (plant richness, proportion of non-native species and woody plants, disturbance intensity, and time investment) on node degree distributions across network types (color-coded). Dots represent standardized coefficients, and lines indicate 95% confidence intervals. All metrics were z-scored to account for effects of node and link richness, as indicated with "(z)". Non-significant relationships are shown in lighter shades. Symbols denote significance levels (· $p < 0.1$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$). Since skewness values were always positive, lower skewness reflects more even degree distributions rather than a shift toward highly connected nodes (which would produce negative skewness).*

SEM analyses showed that urbanization reshaped network structure through direct and indirect pathways. While it directly reduced consumer richness, its effects on network structures were more moderate, partly indirect, and network-specific (Fig. 4): in multitrophic networks, urbanization increased connectance, whereas in bipartite networks it increased modularity and reduced nestedness (Fig. S12). In combined food webs, these effects did not combine additively: instead,

352 urbanization exerted its strongest influence, simultaneously increasing modularity, decreasing
353 nestedness, and markedly reducing robustness (Fig. 4).

354 Urban greening strategies often mitigated these urban-associated shifts, but responses frequently
355 diverged across network types (Fig. 4). In combined networks, patterns generally reflected those
356 of subnetworks, although some effects were dampened (e.g., nestedness with non-native plants) or
357 amplified (e.g., modularity with woody plants; Fig. 4). While increases in species richness were
358 consistent across network types, structural responses were not: connectance, nestedness, and
359 modularity often changed in only one network type or even in opposite directions (e.g.,
360 connectance with plant richness), resulting in relatively stable overall structure in combined
361 networks (Fig. 4, S8). Similar contrasts emerged for robustness: it increased in bipartite networks
362 with plant richness and a higher proportion of non-native plants, but decreased in multitrophic
363 networks with increasing plant richness, woody plant proportion, disturbance intensity, and time
364 investment. In combined food webs, these opposing effects offset one another, leading to non-
365 significant changes, except for a clear increase with plant richness.



366 *Figure 4: Direct and indirect effects of urbanization and urban greening strategies on food web*
367 *structure across network types (color-coded) based on structural equation models (SEMs).*
368 *Patterns distinguish effect types (solid = direct; hashed = indirect). Dots represent total*
369 *standardized coefficients, and lines indicate 95% confidence intervals derived from 5,000*
370 *bootstrap resamples. Non-significant relationships are shown in lighter shades. Symbols denote*
371 *significance levels (· $p < 0.1$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$). The underlying SEMs from*
372 *which these effects are derived are presented in Figure S12.*

Discussion

Our study showed that urbanization can be a dominant force structuring ecological networks, reshaping composition and structure across trophic levels. Its effects were pervasive but network-specific, highlighting the importance of considering dependencies among interaction types. However, urban greening strategies, especially increased plant species richness, mitigated many of these effects and in some cases reversed them, underscoring their potential to buffer networks against urban densification.

Urbanization reduced species and link richness, resulting in smaller networks and altered interaction structure. Consumer–consumer interactions became overrepresented, whereas plant–omnivore links declined relative to null expectations, suggesting that although predator declines may weaken top-down control (Eötvös et al. 2018), remaining omnivores may maintain important regulatory roles through increased predation on consumers (Hironaka and Koike 2013). Degree distributions shifted toward higher medians with reduced skewness and variability, indicating a loss of specialists and increased dominance of generalized interactions (Fournier et al. 2020, Hahs et al. 2023). Moreover, the effects of urbanization manifested differently across network types: bipartite networks became less nested and more modular, potentially reflecting reduced overlap among plant–consumer interactions (Graf et al. 2024), whereas multitrophic networks showed increased connectance, likely associated with stronger consumer–omnivore interactions and intraguild predation (Perrelet et al. 2026). In combined food webs, these shifts coincided with reduced robustness, suggesting additive effects across subnetworks. Thus, urbanization impacts on network stability likely emerge from the combination of trophic-level-specific filtering, shifts in specialization, and altered multitrophic dependencies, highlighting the need to incorporate multiple

interaction types when assessing ecological network responses (Pilosof et al. 2017; Reji Chacko et al., 2026).

In the context of the intermediate landscape complexity hypothesis (Tscharntke et al. 2012), cities retain heterogeneous habitat mosaics that provide opportunities for local interventions to mitigate the negative effects of urban densification (Lepczyk et al. 2017). Among the five urban greening strategies assessed, higher plant richness—and, to a lesser extent, greater time investment in green space management—supported higher consumer richness and larger, more heterogeneous networks, likely by increasing feeding resource diversity (Wenzel et al. 2020, Kral-O'Brien et al. 2021, Schmack and Egerer 2023). These factors also shifted degree distributions in the opposite direction to urbanization, decreasing median degree while increasing skewness and variance, consistent with greater coexistence of specialists and generalists, especially in bipartite networks (Ebeling et al. 2018). In these networks, greater plant richness and time investment translated into lower modularity and increased robustness. This pattern may arises from two complementary mechanisms: greater resource and consumer diversity, providing more feeding options in generalist-dominated networks, and the restoration of plant–omnivore links, which reoriented energy flows toward basal resources, thereby increasing connectance and ultimately robustness. By expanding the diversity of trophic pathways, increasing plant richness may thus enhance the stability of ecosystem functions supported by primary consumers (McDougall et al. 2022). In contrast, multitrophic networks responded more weakly, suggesting that predator–prey interactions may be less sensitive to plant diversity (Scherber et al. 2010, Giling et al. 2019). Increased time investment, reflecting greater ecological stewardship and associated with careful, often biodiversity-friendly rather than intensive maintenance practices (Bennett et al. 2018, Ruile et al. 2026a), produced qualitatively similar but generally weaker effects, with more limited implications for network robustness.

The effects of non-native plant dominance were network-specific. In bipartite networks, non-native plants increased connectance and the prevalence of well-connected taxa without reducing poorly connected nodes (i.e., unchanged skewness), resulting in highly connected hubs alongside persistent species with fewer interactions (Poisot and Gravel 2014). Together with an overrepresentation of plant–omnivore interactions, this pattern likely reflects the addition of new interactions involving a subset of well-connected generalists, particularly omnivores, rather than widespread accessibility of non-native plants to consumers (Salisbury et al. 2017, Seitz et al. 2020). This concentration of interactions among few generalists may increase dependence on these taxa for key ecosystem functions, such as pollination (Liang et al. 2023). In multitrophic networks, effects were weaker—consistent with the indirect role of plant origin on predator–prey interactions unless habitat structure is altered (Grutters et al. 2015)—but included reduced median degree, increased poorly connected nodes, greater nestedness, and lower robustness. These changes may reflect weakened consumer–omnivore interactions and reduced energy transfer to higher trophic levels (Bezemer et al. 2014). At the combined network level, these contrasting responses largely offset one another.

Woody plant prevalence and disturbance intensity had comparatively modest effects. Woody prevalence reduced plant–primary consumer interactions in bipartite networks, likely through loss of rare links, while increasing predator prevalence and connectance in multitrophic networks, consistent with greater structural habitat complexity (Philpott and Bichier 2017). Because predators are more vulnerable to secondary extinctions, this increase also reduced robustness (Perrelet et al. 2026). At the scale of combined food webs, these shifts—reduced plant–primary consumer interactions and increased predator prevalence—likely partially decoupled upper trophic levels from basal resources, resulting in greater modularity and highlighting dependencies among trophic levels. Such decoupling may reduce the efficiency with which primary production is transferred to

443 higher trophic levels (Perrelet et al. 2025). Disturbance intensity, by contrast, had limited overall
444 effects, possibly due to contrasting responses within trophic groups (e.g., differing sensitivities of
445 herbivores versus pollinators to mowing; Hudewenz et al. 2012, Proske et al. 2022). Nonetheless,
446 it promoted plant–omnivore interactions, increasing modularity and reducing robustness in
447 multitrophic networks potentially by weakening consumer–consumer links (Hironaka and Koike
448 2013).

449 To infer network dynamics across interaction types, we used a metaweb approach that enables
450 standardized reconstruction of trophic interactions across multiple network types. However, our
451 analyses relied on unweighted networks, which do not capture variation in interaction strength and
452 can obscure important aspects of energy flows, species dependencies, and network robustness
453 (Berlow et al. 2004, Bastolla et al. 2009). Although weighting interactions by abundance can
454 approximate interaction frequency or strength in some contexts (Sauve et al. 2016), abundance data
455 was not available for all plant species, and even when available, may not reliably capture interaction
456 strength across network types: a given plant species can exert contrasting effects across trophic
457 guilds due to differences in morphology (e.g., few flowers but many leaves) or chemical signaling
458 (floral scent vs. plant defense), thereby disproportionately influencing herbivory relative to
459 pollination (Fontaine and Thébault 2015, Lucas-Barbosa 2016, Wang et al. 2024). This limitation
460 aligns with our classification of interactions into bipartite and multitrophic networks, which
461 necessarily masks fine-scale ecological specificity, such as varying sensitivities among herbivores
462 and pollinators (Sauve et al. 2016, Wang et al. 2024). Nevertheless, this framework enables
463 comparisons across commonly studied (e.g., plant–pollinator) and more complex multitrophic
464 networks, while distinguishing interactions directly influenced by urban greening from those
465 indirectly mediated through higher trophic levels (Pilosof et al. 2017). Lastly, although ecological
466 networks vary seasonally (Souza et al. 2018), our analysis represents a temporal snapshot. We

argue that partitioning by sampling date, while possible, would have conflicted with the metaweb objective of defining the potential space of trophic interactions rather than realized interactions (Adhurya and Park 2025). Despite these constraints, our approach provides a comprehensive perspective on how urbanization and urban greening strategies jointly shape trophic structure, emphasizing the importance of multitrophic dependencies in urban ecosystems.

Conclusion

Urban densification reshaped ecological networks beyond species loss, favoring generalized interactions, producing smaller and more homogeneous networks, and shifting interaction structure toward consumer–consumer rather than plant–consumer links. Moreover, its effects varied across network types, increasing modularity in bipartite networks and connectance and nestedness in multitrophic networks, ultimately reducing robustness in combined food webs. These differences indicate that changes at different interaction levels are interconnected, with shifts in one part of the network propagating to others and jointly shaping overall stability. Thus, identical environmental pressures can generate contrasting structural responses depending on interaction type, with cascading consequences at the scale of whole networks, highlighting the need for a multitrophic perspective to capture ecosystem-level responses. Nonetheless, urban greening strategies buffered many of these impacts. Increasing plant richness, and to a lesser extent time investment, consistently supported larger, more heterogeneous, and more robust networks, allowing specialists and generalists to coexist. Other factors produced more network-specific effects: the prevalence of non-native plants left multitrophic and combined networks largely unchanged but reorganized bipartite interactions, concentrating links among highly connected consumers rather than benefiting a broader range of consumers.

Overall, urban ecological networks emerge from the interplay between broad-scale urbanization and local urban greening strategies, with outcomes contingent on interaction type. This underscores that strategies based on single network types may misrepresent ecosystem-level dynamics, and that maintaining diverse, functionally rich, and preferably native plant communities are key for sustaining robust networks in increasingly compact cities.

References

Adhurya, S. and Park, Y.-S. 2025. Metaweb approaches for understanding complex ecological interactions: A review. - Ecological Informatics 91: 103367.

Banaszak-Cibicka, W. and Żmihorski, M. 2012. Wild bees along an urban gradient: winners and losers. - J Insect Conserv 16: 331–343.

Bastolla, U., Fortuna, M. A., Pascual-García, A., Ferrera, A., Luque, B. and Bascompte, J. 2009. The architecture of mutualistic networks minimizes competition and increases biodiversity. - Nature 458: 1018–1020.

Beninde, J., Veith, M. and Hochkirch, A. 2015. Biodiversity in cities needs space: a meta-analysis of factors determining intra-urban biodiversity variation. - Ecology Letters 18: 581–592.

Bennett, N. J., Whitty, T. S., Finkbeiner, E., Pittman, J., Bassett, H., Gelcich, S. and Allison, E. H. 2018. Environmental Stewardship: A Conceptual Review and Analytical Framework. - Environmental Management 61: 597–614.

Berlow, E. L., Neutel, A.-M., Cohen, J. E., De Ruiter, P. C., Ebenman, B., Emmerson, M., Fox, J. W., Jansen, V. A. A., Iwan Jones, J., Kokkoris, G. D., Logofet, D. O., McKane, A. J., Montoya, J. M. and Petchey, O. 2004. Interaction strengths in food webs: issues and opportunities. - Journal of Animal Ecology 73: 585–598.

Bezemer, T. M., Harvey, J. A. and Cronin, J. T. 2014. Response of Native Insect Communities to Invasive Plants. - Annual Review of Entomology 59: 119–141.

Bille, R. A., Jensen, K. E. and Buitenwerf, R. 2023. Global patterns in urban green space are strongly linked to human development and population density. - Urban Forestry & Urban Greening 86: 127980.

Brimacombe, C., Bodner, K. and Fortin, M.-J. 2024. Applying a method before its proof of concept: A cautionary tale using inferred food webs. - Global Change Biology 30: e17360.

Burks, J. M. and Philpott, S. M. 2017. Local and Landscape Drivers of Parasitoid Abundance, Richness, and Composition in Urban Gardens. - Environ Entomol 46: 201–209.

Casanelles-Abella, J., Ruile, S. R., Bergamini, A., Dädlow, G. M. L., Grothe, V., Fournier, B., Perrelet, K. and Moretti, M. 2026. Social-ecological signatures in plant species composition across Swiss cities and urban green space types. - Plants, People, Planet in press.

Chatelain, M., Rüdisser, J. and Traugott, M. 2023. Urban-driven decrease in arthropod richness and diversity associated with group-specific changes in arthropod abundance. - Front. Ecol. Evol. in press.

Concepción, E. D., Obrist, M. K., Moretti, M., Altermatt, F., Baur, B. and Nobis, M. P. 2016. Impacts of urban sprawl on species richness of plants, butterflies, gastropods and birds: not only built-up area matters. - Urban Ecosyst 19: 225–242.

da Cunha-Silva, R. R., Barreto, E. and Almeida-Neto, M. 2025. Urbanization influences the structure of plant–insect pollination networks through changes in pollinator species richness. - Arthropod-Plant Interactions 19: 50.

Dunne, J. A. 2006. The network structure of food webs (M Pascual and JA Dunne, Eds.). - Ecological networks: linking structure and dynamics: 27–86.

Ebeling, A., Rzanny, M., Lange, M., Eisenhauer, N., Hertzog, L. R., Meyer, S. T. and Weisser, W. W. 2018. Plant diversity induces shifts in the functional structure and diversity across trophic levels. - Oikos 127: 208–219.

Eötvös, C. B., Magura, T. and Lövei, G. L. 2018. A meta-analysis indicates reduced predation pressure with increasing urbanization. - Landscape and Urban Planning 180: 54–59.

Federal Office for the Environment 2022. Alien Species in Switzerland. An inventory of alien species and their impact. in press.

Fontaine, C. and Thébault, E. 2015. Comparing the conservatism of ecological interactions in plant–pollinator and plant–herbivore networks. - Popul Ecol 57: 29–36.

Fournier, B., Frey, D. and Moretti, M. 2020. The origin of urban communities: From the regional species pool to community assemblages in city. - Journal of Biogeography 47: 615–629.

Giling, D. P., Ebeling, A., Eisenhauer, N., Meyer, S. T., Roscher, C., Rzanny, M., Voigt, W., Weisser, W. W. and Hines, J. 2019. Plant diversity alters the representation of motifs in food webs. - Nat Commun 10: 1226.

Graf, L. V., Meyer, F. S., Jeronimo, F. F. and Gonçalves, R. B. 2024. Urbanization as a driver of changes in mutualistic networks between bees and plants. - Urban Ecosyst 28: 30.

Grange, M. C., Munoz, F., Moretti, M., Varona-Y-Varona, S., Renaud, J., Colace, M.-P., Gueguen, M. and Gallien, L. 2021. Designing sampling protocols for plant-pollinator interactions - timing, meteorology, flowering variations and failed captures matter. - Botany Letters 168: 324–332.

Grimm, N. B., Faeth, S. H., Golubiewski, N. E., Redman, C. L., Wu, J., Bai, X. and Briggs, J. M. 2008. Global Change and the Ecology of Cities. - Science 319: 756–760.

Grutters, B. M., Pollux, B. J., Verberk, W. C. and Bakker, E. S. 2015. Native and non-native plants provide similar refuge to invertebrate prey, but less than artificial plants. - PLoS One 10: e0124455.

560 Haaland, C. and van den Bosch, C. K. 2015. Challenges and strategies for urban green-space planning in
561 cities undergoing densification: A review. - Urban For. Urban Green. 14: 760–771.

562 Hahs, A. K., Fournier, B., Aronson, M. F. J., Nilon, C. H., Moretti, M., et al. 2023. Urbanisation generates
563 multiple trait syndromes for terrestrial animal taxa worldwide. - Nat Commun 14: 4751.

564 Harrison, T. and Winfree, R. 2015. Urban drivers of plant-pollinator interactions. - Functional Ecology 29:
565 879–888.

566 Hironaka, Y. and Koike, F. 2013. Guild structure in the food web of grassland arthropod communities
567 along an urban—rural landscape gradient. - Ecoscience 20: 148–160.

568 Ho, H.-C., Brodersen, J., Gossner, M. M., Graham, C. H., Kaeser, S., Reji Chacko, M., Seehausen, O.,
569 Zimmermann, N. E., Pellissier, L. and Altermatt, F. 2022. Blue and green food webs respond
570 differently to elevation and land use. - Nat Commun 13: 6415.

571 Hudewenz, A., Klein, A.-M., Scherber, C., Stanke, L., Tscharntke, T., Vogel, A., Weigelt, A., Weisser, W.
572 W. and Ebeling, A. 2012. Herbivore and pollinator responses to grassland management intensity
573 along experimental changes in plant species richness. - Biological Conservation 150: 42–52.

574 Johnson, S., Domínguez-García, V., Donetti, L. and Muñoz, M. A. 2014. Trophic coherence determines
575 food-web stability. - Proceedings of the National Academy of Sciences 111: 17923–17928.

576 Jonsson, T., Berg, S., Pimenov, A., Palmer, C. and Emmerson, M. 2015. The reliability of R50 as a
577 measure of vulnerability of food webs to sequential species deletions. - Oikos 124: 446–457.

578 Keyes, A. A., McLaughlin, J. P., Barner, A. K. and Dee, L. E. 2021. An ecological network approach to
579 predict ecosystem service vulnerability to species losses. - Nat Commun 12: 1586.

580 Knapp, S., Aronson, M. F., Carpenter, E., Herrera-Montes, A., Jung, K., Kotze, D. J., La Sorte, F. A.,
581 Lepczyk, C. A., MacGregor-Fors, I., MacIvor, J. S., Moretti, M., Nilon, C. H., Piana, M. R.,
582 Rega-Brodsky, C. C., Salisbury, A., Threlfall, C. G., Trisos, C., Williams, N. S. G. and Hahs, A.
583 K. 2021. A Research Agenda for Urban Biodiversity in the Global Extinction Crisis. - BioScience
584 71: 268–279.

585 Kral-O'Brien, K. C., O'Brien, P. L., Hovick, T. J. and Harmon, J. P. 2021. Meta-analysis: Higher Plant
586 Richness Supports Higher Pollinator Richness Across Many Land Use Types. - Ann Entomol Soc
587 Am 114: 267–275.

588 Lepczyk, C. A., Aronson, M. F., Evans, K. L., Goddard, M. A., Lerman, S. B. and MacIvor, J. S. 2017.
589 Biodiversity in the City: Fundamental Questions for Understanding the Ecology of Urban Green
590 Spaces for Biodiversity Conservation. - BioScience 67: 799–807.

591 Liang, H., He, Y.-D., Theodorou, P. and Yang, C.-F. 2023. The effects of urbanization on pollinators and
592 pollination: A meta-analysis. - Ecology Letters 26: 1629–1642.

593 Lin, B., Meyers, J. and Barnett, G. 2015. Understanding the potential loss and inequities of green space
594 distribution with urban densification. - Urban Forestry & Urban Greening 14: 952–958.

595 Lucas-Barbosa, D. 2016. Integrating Studies on Plant–Pollinator and Plant–Herbivore Interactions. -
596 Trends in Plant Science 21: 125–133.

Martínez-Núñez, C., Casanelles Abella, J., Frey, D., Zanetta, A. and Moretti, M. 2024. Local and landscape factors shape alpha and beta trophic interaction diversity in urban gardens. - Proc Biol Sci 291: 20232501.

McDougall, R., Kristiansen, P., Latty, T., Jones, J. and Rader, R. 2022. Pollination service delivery is complex: Urban garden crop yields are best explained by local canopy cover and garden scale plant species richness. - Journal of Applied Ecology 59: 1248–1257.

Morales-Castilla, I., Matias, M. G., Gravel, D. and Araújo, M. B. 2015. Inferring biotic interactions from proxies. - Trends in Ecology & Evolution 30: 347–356.

Moreno-García, P., Savage, A., Salgado, A. L., Tartaglia, E. S., Cocciardi, J. M., Aronson, M. F. J., Jarzyna, M. A., Alberti, M. and Li, D. 2025. The effects of urbanization on species interactions. - Nat Cities 2: 693–702.

Neff, F., Brändle, M., Ambarlı, D., Ammer, C., Bauhus, J., Boch, S., Hölzel, N., Klaus, V. H., Kleinebecker, T., Prati, D., Schall, P., Schäfer, D., Schulze, E.-D., Seibold, S., Simons, N. K., Weisser, W. W., Pellissier, L. and Gossner, M. M. 2021. Changes in plant-herbivore network structure and robustness along land-use intensity gradients in grasslands and forests. - Science Advances 7: eabf3985.

Ning, Y., Li, L., Xu, W., Zhang, Y., Wu, H. and Li, H. 2025. Insects in urban green spaces directly and indirectly affect ecosystem functions by interacting with plants to build ecological networks. - Urban Forestry & Urban Greening 113: 129032.

O'Connor, L. M. J., Thuiller, W., Brose, U., Chenevois, É., Freund, C., Gauzens, B., Gaüzere, P., Graham, C., Harfoot, M., Hirt, M. R., Lavergne, S., Maiorano, L., Moilanen, A., Verburg, P. H., Visconti, P. and Pollock, L. J. 2026. The Untapped Potential of Food Webs in Systematic Conservation Planning. - Conservation Letters 19: e70002.

Pearse, I. S. and Altermatt, F. 2013. Predicting novel trophic interactions in a non-native world. - Ecology Letters 16: 1088–1094.

Pellissier, L., Albouy, C., Bascompte, J., Farwig, N., Graham, C., Loreau, M., Maglianesi, M. A., Melián, C. J., Pitteloud, C., Roslin, T., Rohr, R., Saavedra, S., Thuiller, W., Woodward, G., Zimmermann, N. E. and Gravel, D. 2018. Comparing species interaction networks along environmental gradients. - Biological Reviews 93: 785–800.

Perrelet, K., Cook, L. M., Reji Chacko, M., Altermatt, F. and Moretti, M. 2025. Urbanisation Drives the Decoupling, Simplification, and Homogenization of Aquatic and Terrestrial Food Webs. - Ecology Letters 28: e70212.

Perrelet, K., Cook, L. M., Reji Chacko, M., Altermatt, F. and Moretti, M. 2026. Food webs on green roofs are unique but less robust than their ground-level counterparts. - Journal of Applied Ecology 63: e70306.

Philpott, S. M. and Bichier, P. 2017. Local and landscape drivers of predation services in urban gardens. - Ecological Applications 27: 966–976.

Philpott, S. M., Lucatero, A., Bichier, P., Egerer, M. H., Jha, S., Lin, B. and Liere, H. 2020. Natural enemy–herbivore networks along local management and landscape gradients in urban agroecosystems. - Ecological Applications in press.

Pilosof, S., Porter, M. A., Pascual, M. and Kéfi, S. 2017. The multilayer nature of ecological networks. - Nat Ecol Evol 1: 0101.

Poisot, T. and Gravel, D. 2014. When is an ecological network complex? Connectance drives degree distribution and emerging network properties. - PeerJ 2: e251.

Potapov, A. M., Scheu, S. and Tiunov, A. V. 2019. Trophic consistency of supraspecific taxa in below-ground invertebrate communities: Comparison across lineages and taxonomic ranks. - Functional Ecology 33: 1172–1183.

Price, B., Kolecka, N., Huber, N., Rüetschi, M., Nussbaumer, A. and Ginzler, C. 2024. The Habitat Map of Switzerland v1_1 2024.

Proske, A., Lokatis, S. and Rolff, J. 2022. Impact of mowing frequency on arthropod abundance and diversity in urban habitats: A meta-analysis. - Urban For. Urban Green. 76: 127714.

Reji Chacko, M., Albouy, C., Altermatt, F., Boussange, V., Brändle, M., Farwig, N., Gossner, M. M., Ho, H.-C., Joss, A., Neff, F. and Pellissier, L. 2025a. Species loss in key habitats accelerates regional food web disruption. - Commun Biol 8: 988.

Reji Chacko, M., Albouy, C., Altermatt, F., Casanelles-Abella, J., Brändle, M., Boussange, V., Campell, F., Ellis, W. N., Fopp, F., Gossner, M. M., Ho, H.-C., Joss, A., Kipf, P., Neff, F., Petrović, A., Prié, V., Tomanović, Ž., Zimmerli, N. and Pellissier, L. 2025b. A species-level multi-trophic metaweb for Switzerland. - Sci Data 12: 1164.

Reji Chacko, M., Casanelles-Abella, J., Casciano, G., Fournier, B., Frey, D. J., Perrelet, K. and Moretti, M. 2026. Urban densification reduces food-web robustness despite partial gains through local habitat improvements. - EcoEvoRxiv in press.

Rivkin, L. R., Santangelo, J. S., Alberti, M., Aronson, M. F., de Keyzer, C. W., Diamond, S. E., Fortin, M.-J., Frazee, L. J., Gorton, A. J., Hendry, A. P., Liu, Y., Losos, J. B., MacIvor, J. S., Martin, R. A., McDonnell, M. J., Miles, L. S., Munshi-South, J., Ness, R. W., Newman, A. E. M., Stothart, M. R., Theodorou, P., Thompson, K. A., Verrelli, B. C., Whitehead, A., Winchell, K. M. and Johnson, M. T. J. 2019. A roadmap for urban evolutionary ecology. - Evolutionary Applications 12: 384–398.

Rocha, E. A. and Fellowes, M. D. E. 2018. Does urbanization explain differences in interactions between an insect herbivore and its natural enemies and mutualists? - Urban Ecosyst 21: 405–417.

Ruile, S., Moretti, M., Ghazoul, J., Fournier, B., Grothe, V., Dädlow, L. and Abella, J. C. 2026a. The human handprint in shaping plant diversity in urban environments. in press.

Ruile, S., Knecht, A., Knuser, A., Hug, L., Grimm, M., Perrelet, K., Grothe, V., Dädlow, L., Fournier, B., Abella, J. C. and Moretti, M. 2026b. A comprehensive dataset on plant-associated invertebrates and gardening activities, from 100 sites across five urban green space types in Zurich, Lugano, and Geneva, Switzerland. in press.

Salisbury, A., Al-Beidh, S., Armitage, J., Bird, S., Bostock, H., Platoni, A., Tatchell, M., Thompson, K. and Perry, J. 2017. Enhancing gardens as habitats for plant-associated invertebrates: should we plant native or exotic species? - Biodivers Conserv 26: 2657–2673.

Sauve, A. M. C., Thébault, E., Pocock, M. J. O. and Fontaine, C. 2016. How plants connect pollination and herbivory networks and their contribution to community stability. - Ecology 97: 908–917.

677 Savary, P., Tannier, C. and Foltête, J.-C. 2026. The negative impact of urban sprawl on biodiversity: A
678 simulation approach to genetic diversity in European cities. - Landscape and Urban Planning 269:
679 105586.

680 Scherber, C., Eisenhauer, N., Weisser, W. W., Schmid, B., Voigt, W., Fischer, M., Schulze, E.-D.,
681 Roscher, C., Weigelt, A., Allan, E., Beßler, H., Bonkowski, M., Buchmann, N., Buscot, F.,
682 Clement, L. W., Ebeling, A., Engels, C., Halle, S., Kertscher, I., Klein, A.-M., Koller, R., König,
683 S., Kowalski, E., Kummer, V., Kuu, A., Lange, M., Lauterbach, D., Middelhoff, C., Migunova, V.
684 D., Milcu, A., Müller, R., Partsch, S., Petermann, J. S., Renker, C., Rottstock, T., Sabais, A.,
685 Scheu, S., Schumacher, J., Temperton, V. M. and Tscharntke, T. 2010. Bottom-up effects of plant
686 diversity on multitrophic interactions in a biodiversity experiment. - Nature 468: 553–556.

687 Schmack, J. M. and Egerer, M. 2023. Floral richness and seasonality influences bee and non-bee flower
688 interactions in urban community gardens. - Urban Ecosyst 26: 1099–1112.

689 Seitz, N., vanEngelsdorp, D. and Leonhardt, S. D. 2020. Are native and non-native pollinator friendly
690 plants equally valuable for native wild bee communities? - Ecology and Evolution 10: 12838–
691 12850.

692 Simkin, R. D., Seto, K. C., McDonald, R. I. and Jetz, W. 2022. Biodiversity impacts and conservation
693 implications of urban land expansion projected to 2050. - Proceedings of the National Academy of
694 Sciences 119: e2117297119.

695 Souza, C. S., Maruyama, P. K., Aoki, C., Sigrist, M. R., Raizer, J., Gross, C. L. and de Araujo, A. C.
696 2018. Temporal variation in plant–pollinator networks from seasonal tropical environments:
697 Higher specialization when resources are scarce. - Journal of Ecology 106: 2409–2420.

698 Stadt Zürich, H. 2019. Kommunaler Richtplan Siedlung, Landschaft, öffentliche Bauten und Anlagen. in
699 press.

700 Start, D., Barbour, M. A. and Bonner, C. 2019. Urbanization reshapes a food web. - Journal of Animal
701 Ecology 89: 808–816.

702 Straka, T. M., Radchuk, V., Kowarik, I., von der Lippe, M. and Buchholz, S. 2025. Urbanization Impacts
703 Top Predators and Alters Biotic Interactions in Predator–Prey–Mutualistic Communities of Urban
704 Dry Grasslands. - Ecology and Evolution 15: e70791.

705 Sushinsky, J. R., Rhodes, J. R., Possingham, H. P., Gill, T. K. and Fuller, R. A. 2013. How should we
706 grow cities to minimize their biodiversity impacts? - Global Change Biology 19: 401–410.

707 Theodorou, P. 2022. The effects of urbanisation on ecological interactions. - Current Opinion in Insect
708 Science 52: 100922.

709 Thompson, R. M. and Townsend, C. R. 2000. Is resolution the solution?: the effect of taxonomic
710 resolution on the calculated properties of three stream food webs. - Freshwater Biology 44: 413–
711 422.

712 Tresch, S., Frey, D., Le Bayon, R.-C., Zanetta, A., Rasche, F., Fliessbach, A. and Moretti, M. 2019. Litter
713 decomposition driven by soil fauna, plant diversity and soil management in urban gardens. -
714 Science of The Total Environment 658: 1614–1629.

715 Tscharntke, T., Tylianakis, J. M., Rand, T. A., Didham, R. K., Fahrig, L., Batáry, P., Bengtsson, J.,
716 Clough, Y., Crist, T. O., Dormann, C. F., Ewers, R. M., Fründ, J., Holt, R. D., Holzschuh, A.,

Klein, A. M., Kleijn, D., Kremen, C., Landis, D. A., Laurance, W., Lindenmayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., van der Putten, W. H. and Westphal, C. 2012. Landscape moderation of biodiversity patterns and processes - eight hypotheses. - Biological Reviews 87: 661–685.

United Nations, D. of E. and S. A., Population Division 2018. The World's Cities in 2018—Data Booklet.

United Nations 2022. World Cities Report 2022: Envisaging the future of cities. - United Nations Human Settlements Programme: Nairobi, Kenya: 41–44.

Wang, X., Fu, X., Shi, M., Xue, C., Yang, J., Zhao, Z., Li, S. and Tu, T. 2024. Multiple interaction networks reveal that Lepidoptera larvae and adults prefer various host plants for diet and pollination. - Integrative Zoology 19: 763–776.

Welti, E. A. R. and Joern, A. 2015. Structure of trophic and mutualistic networks across broad environmental gradients. - Ecology and Evolution 5: 326–334.

Wenzel, A., Grass, I., Belavadi, V. V. and Tscharntke, T. 2020. How urbanization is driving pollinator diversity and pollination – A systematic review. - Biological Conservation 241: 108321.

Zaninotto, V., Thebault, E. and Dajoz, I. 2023. Native and exotic plants play different roles in urban pollination networks across seasons. - Oecologia 201: 525–536.

Author contributions

K.P., M.R., and M.M. conceived and designed the study. S.R and M.R. conducted field work, and K.P. and M.M. collected data from the literature and existing databases. K.P. analyzed the data. K.P. wrote the initial draft. All authors commented on and approved the final manuscript.

Data availability

Analysis files and R script are available on GitHub (https://github.com/KPerrelet/urban_network_types) and Zenodo (https://doi.org/10.5281/zenodo.22657711).

Acknowledgments

We thank all the participating stakeholders for their invaluable contribution to the PAPPUS Project. All icons used in the figures were either created by the authors or sourced from the public domain.

Funding

This work is supported by the Swiss National Science Foundation (SNF) Synergia Program within the project Plants and People in Urban Systems [PAPPUS] (Grant Number 501100001711-213584).

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.

Supplementary Material for "Urban densification and vegetation composition reshape ecological networks across trophic layers"

Kilian Perrelet[1,*], Sebastian Ruile[1,2], Merin Reji Chacko[1,3], Joan Casanelles-Abella[1,4], Bertrand Fournier[5], Marco Moretti[1*]

[1]*Biodiversity and Conservation Biology, Swiss Federal Institute for Forest, Snow, and Landscape Research WSL, Birmensdorf, Switzerland*

[2]*Department of Environmental Systems Science, ETH Zurich, Zurich, Switzerland*

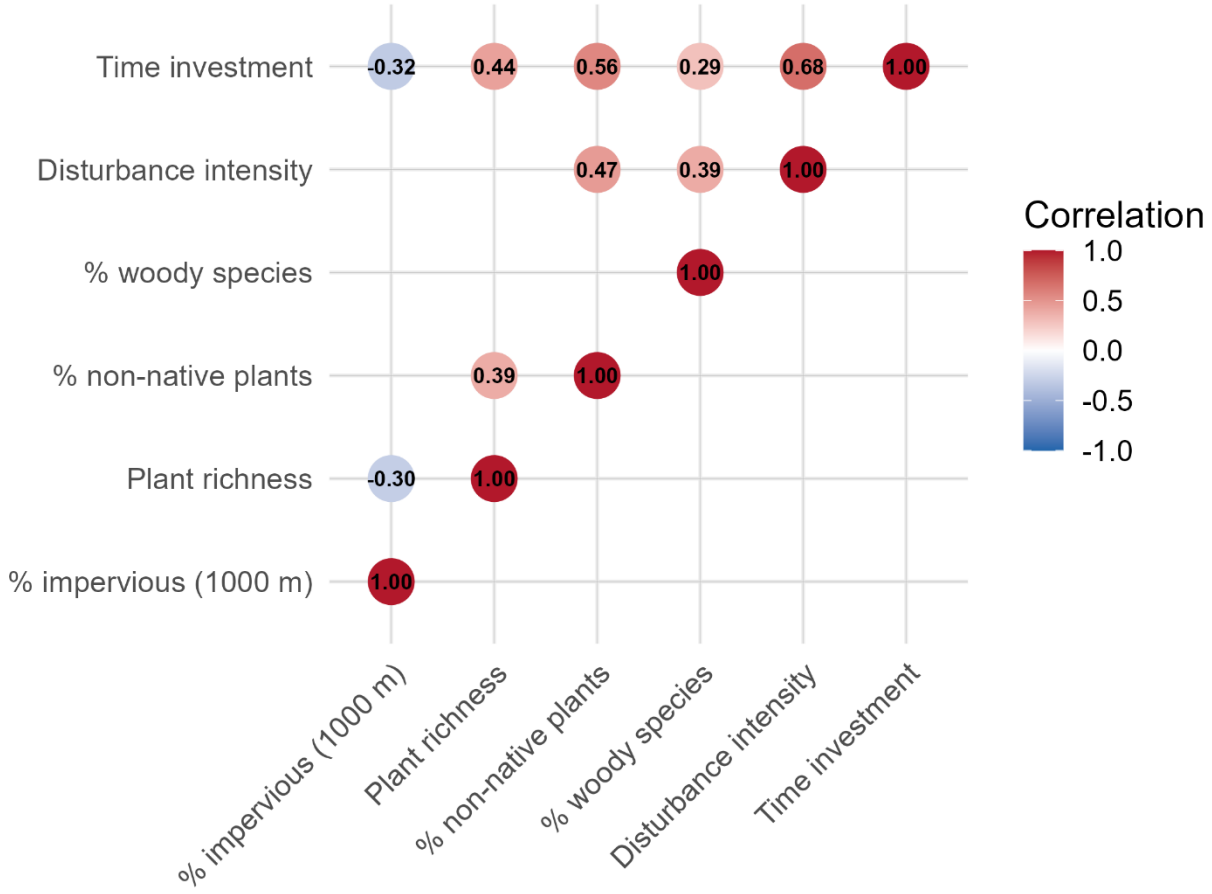
[3]*Ecological Networks, Technische Universität Darmstadt, Darmstadt, Germany*

[4]*Urban Productive Ecosystems, TUM School of Life Sciences, Technical University of Munich, Freising, Germany*

[5]*Institute of Environmental Sciences and Geography, University of Potsdam, Potsdam, Germany*

*corresponding authors

Kilian Perrelet, Zürcherstrasse 111, Birmensdorf, Zürich, Switzerland, kilian.perrelet@gmail.com



771 *Figure S1: Correlation matrix illustrating pairwise associations among covariates (Pearson*
772 *correlation; color-coded by strength and direction). Non-significant correlations are not shown.*

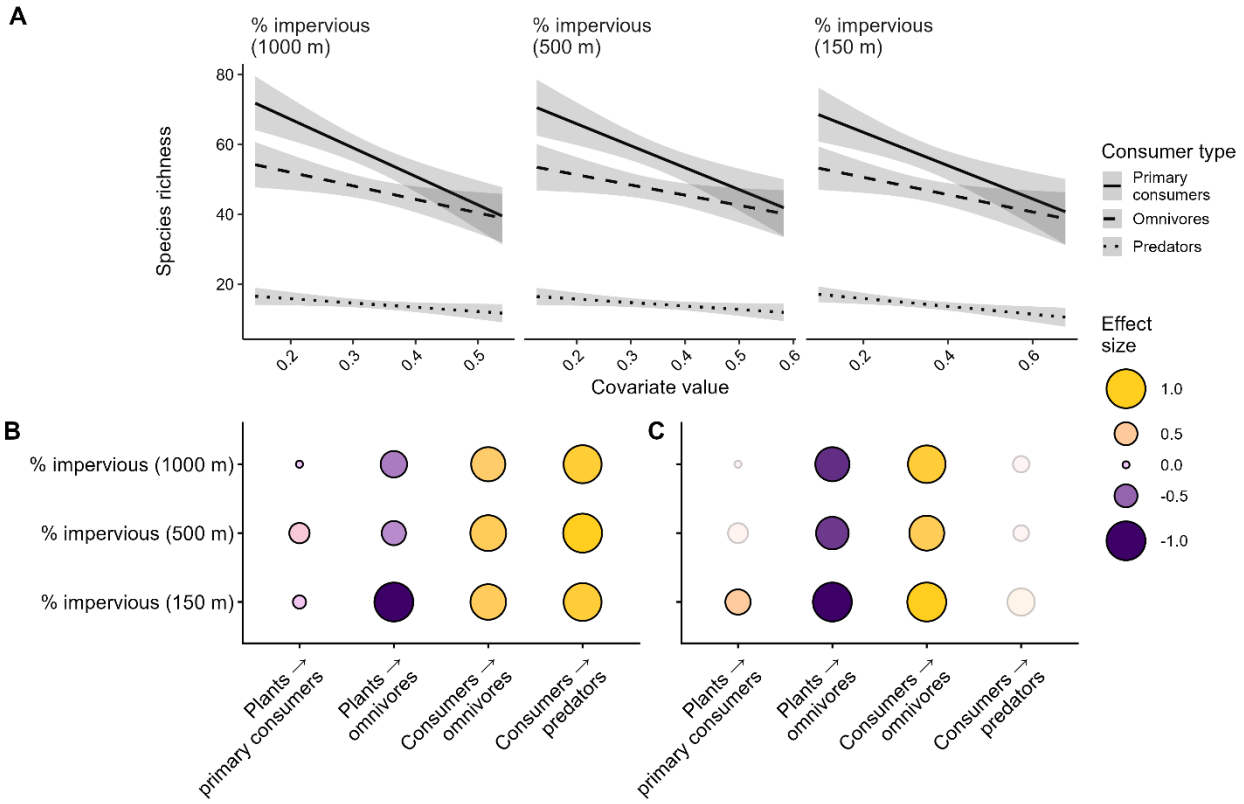


Figure S2: Effects of urbanization across multiple spatial scales (1000 m, 500, 150 m buffer) on trophic structure and interaction organization in local food webs. (A) Relationships between covariates and richness of primary consumers (solid), omnivores (dashed), and predators (dotted); non-significant relationships are shown with reduced opacity. (B–C) Effects of covariates on trophic link richness (B) and deviations in link frequencies from null expectations (z-scores; C). Significant relationships in (C) indicate changes in interaction frequencies beyond those explained by species and link richness and trophic group proportions. Bubble size indicates effect magnitude, color indicates direction, and transparency indicates statistical support. For simplicity, interactions involving primary consumers, omnivores, or predators as prey are grouped as consumer → omnivore and consumer → predator interactions.

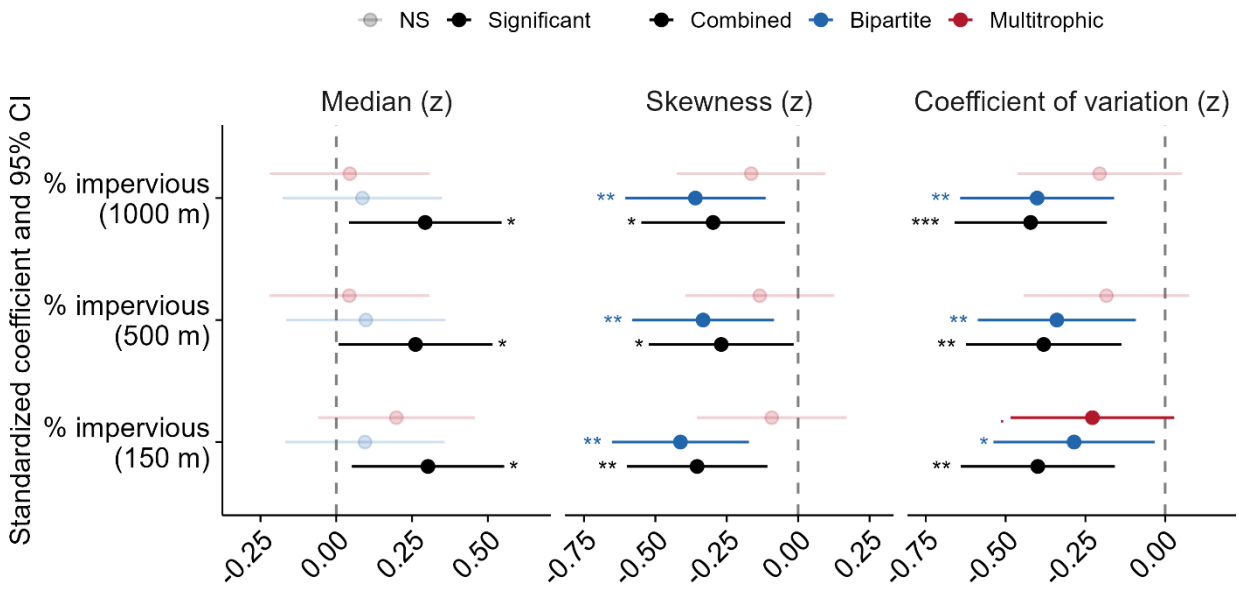


*Figure S3: Influence of urbanization across multiple spatial scales (1000 m, 500, 150 m buffer) on node degree distributions across network types (color-coded). Dots represent standardized coefficients, and lines indicate 95% confidence intervals. All metrics were z-scored to account for effects of node and link richness, as indicated with "(z)". Non-significant relationships are shown in lighter shades. Symbols denote significance levels (· $p < 0.1$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$). Since skewness values were always positive, lower skewness reflects more even degree distributions rather than a shift toward highly connected nodes (which would produce negative skewness).*

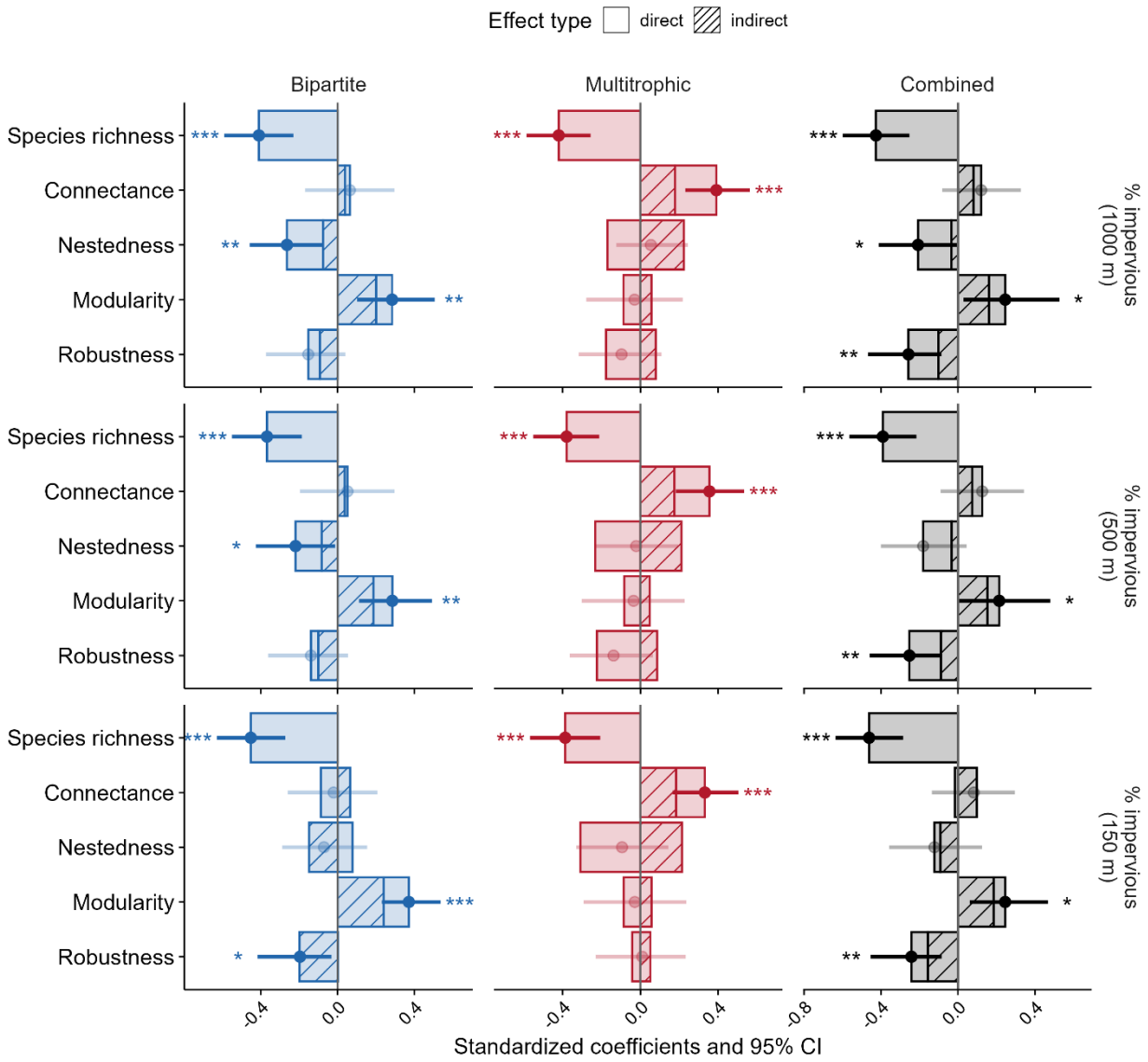


*Figure S4: Direct and indirect effects of urbanization at multiple spatial scales (1000 m, 500, 150 m buffer) across network types (color-coded) based on structural equation models (SEMs). Patterns distinguish effect types (solid = direct; hashed = indirect). Dots represent total standardized coefficients, and lines indicate 95% confidence intervals derived from 5,000 bootstrap resamples. Non-significant relationships are shown in lighter shades. Symbols denote significance levels (· $p < 0.1$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$). The underlying SEMs from which these effects are derived are presented in Figure S12.*

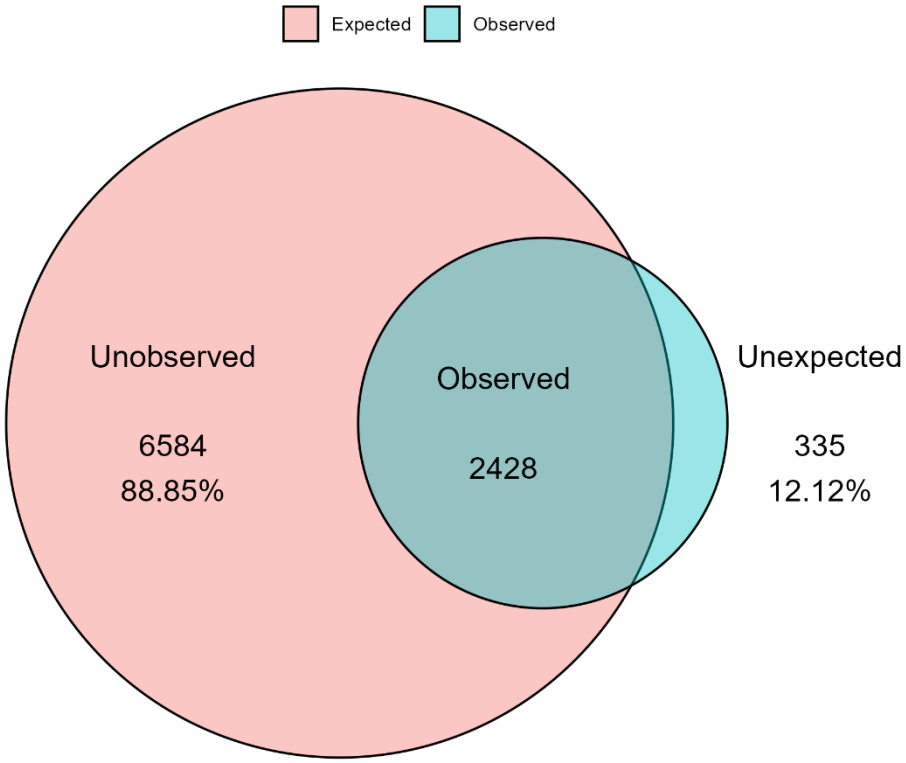


Figure S5: Venn diagram showing predicted versus observed interactions based on the metaweb. Interactions present in the metaweb but not observed locally are labeled "unobserved", those both predicted and observed are labeled "observed", and interactions observed but not included in the metaweb are labeled "unexpected".

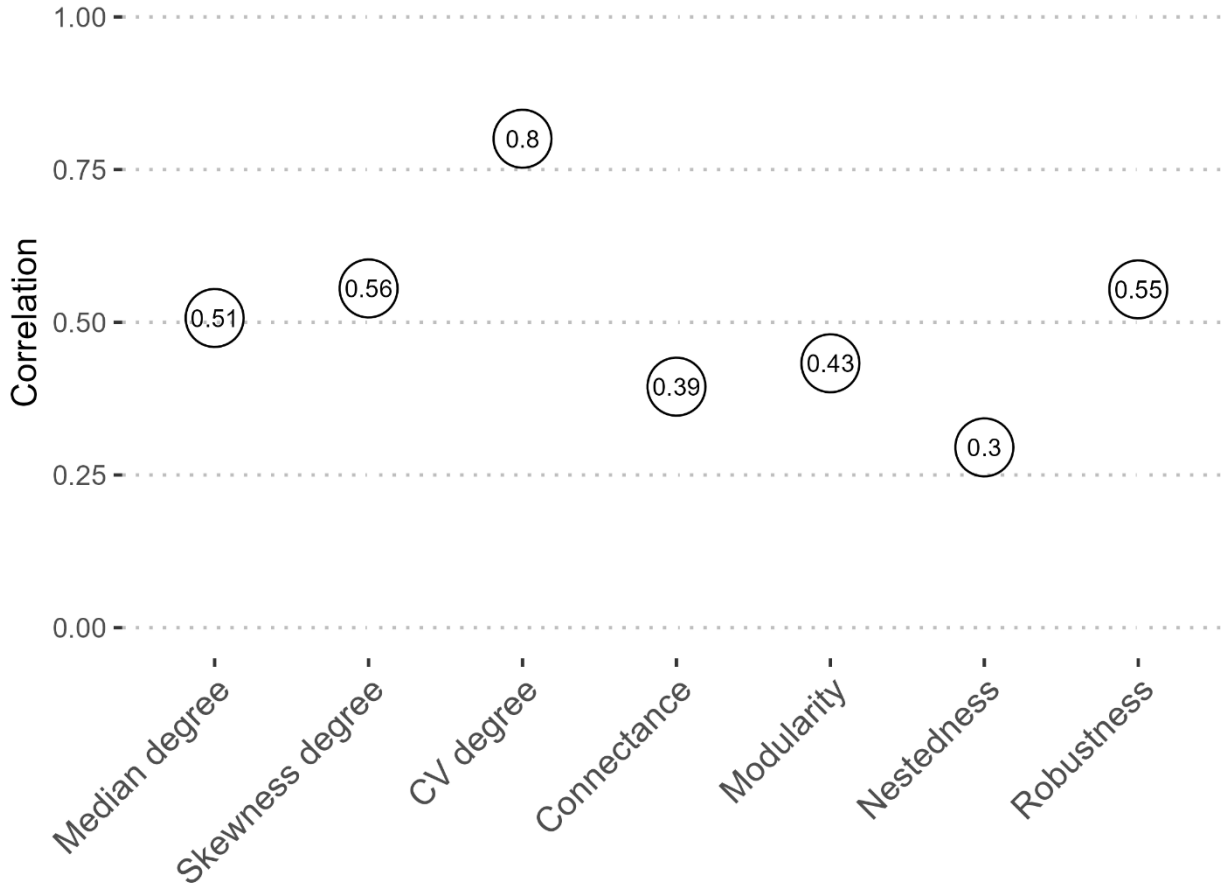


Figure S6: Correlation between network metrics derived from observed versus metaweb-based plant–primary consumers interactions. Points represent Pearson's correlation coefficients (r) for each metric, with corresponding values indicated. All correlations are highly significant ($p < 0.0001$).

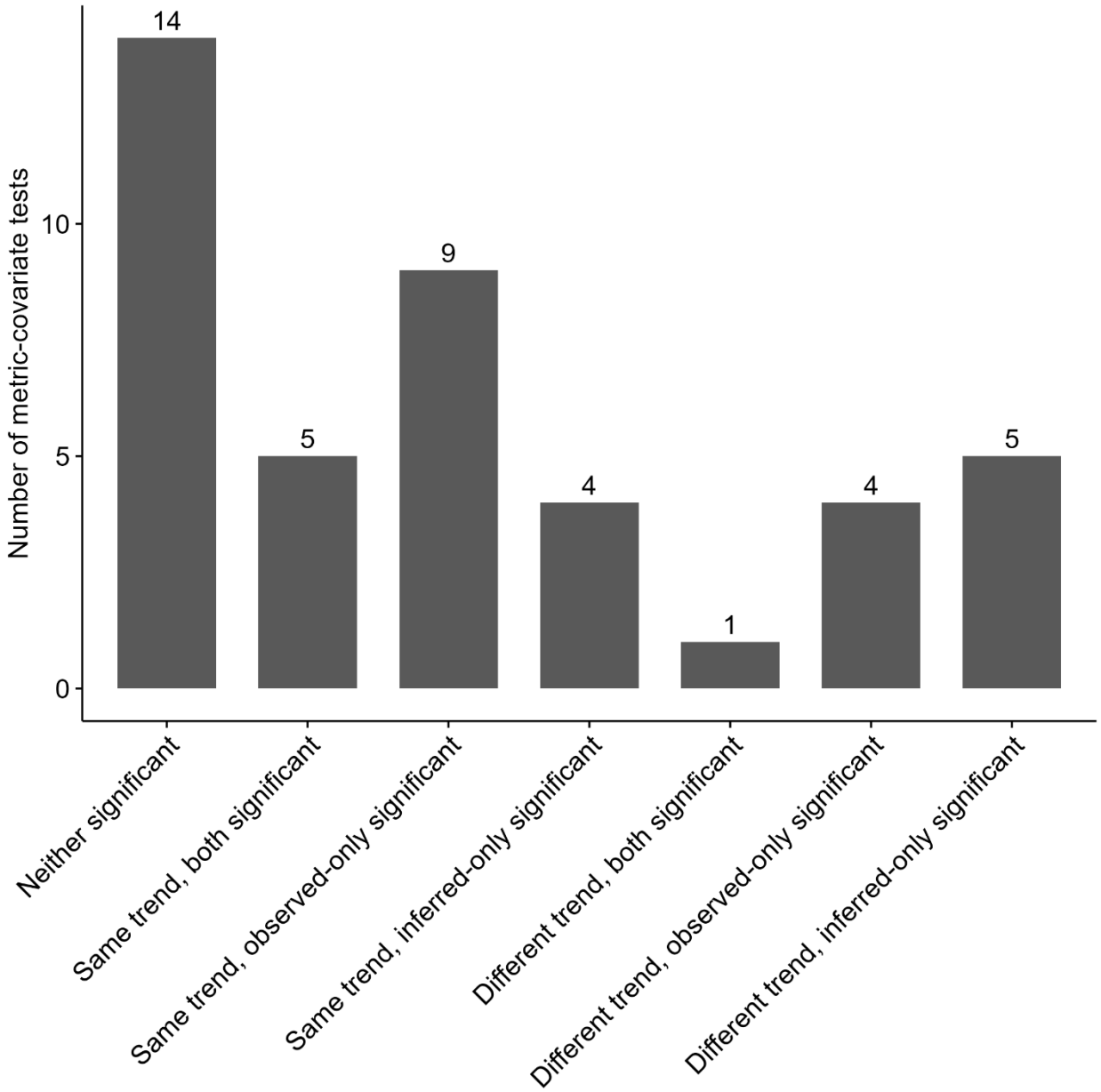


Figure S7: Agreement in the direction and significance of relationships between plant–primary consumer network metrics and environmental covariates derived from observed versus metaweb-based ("inferred") interactions. Bars indicate the number of metric-covariate relationships classified by whether observed-only and inferred estimates had the same or opposite direction, and whether significance was detected in both, one, or neither dataset. Significance was assessed at $p < 0.05$.

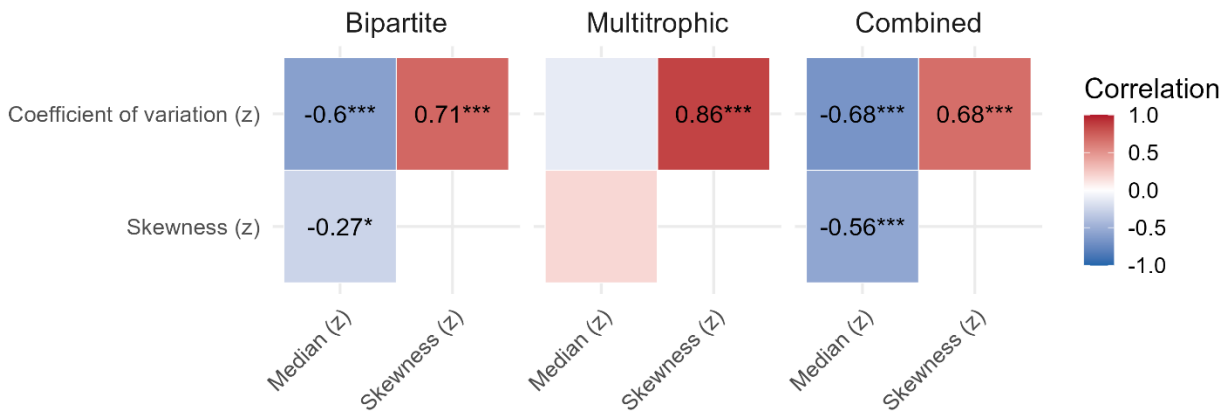


Figure S8: Pearson correlation matrices showing associations among degree distribution metrics (median degree, degree skewness, and coefficient of variation; all z-scored) for bipartite, multitrophic, and complete networks. Tile values and color indicates correlation strength and direction (blue = negative, red = positive), while asterisks denote significant correlations (P < 0.05; ** P < 0.01; *** P < 0.001).*

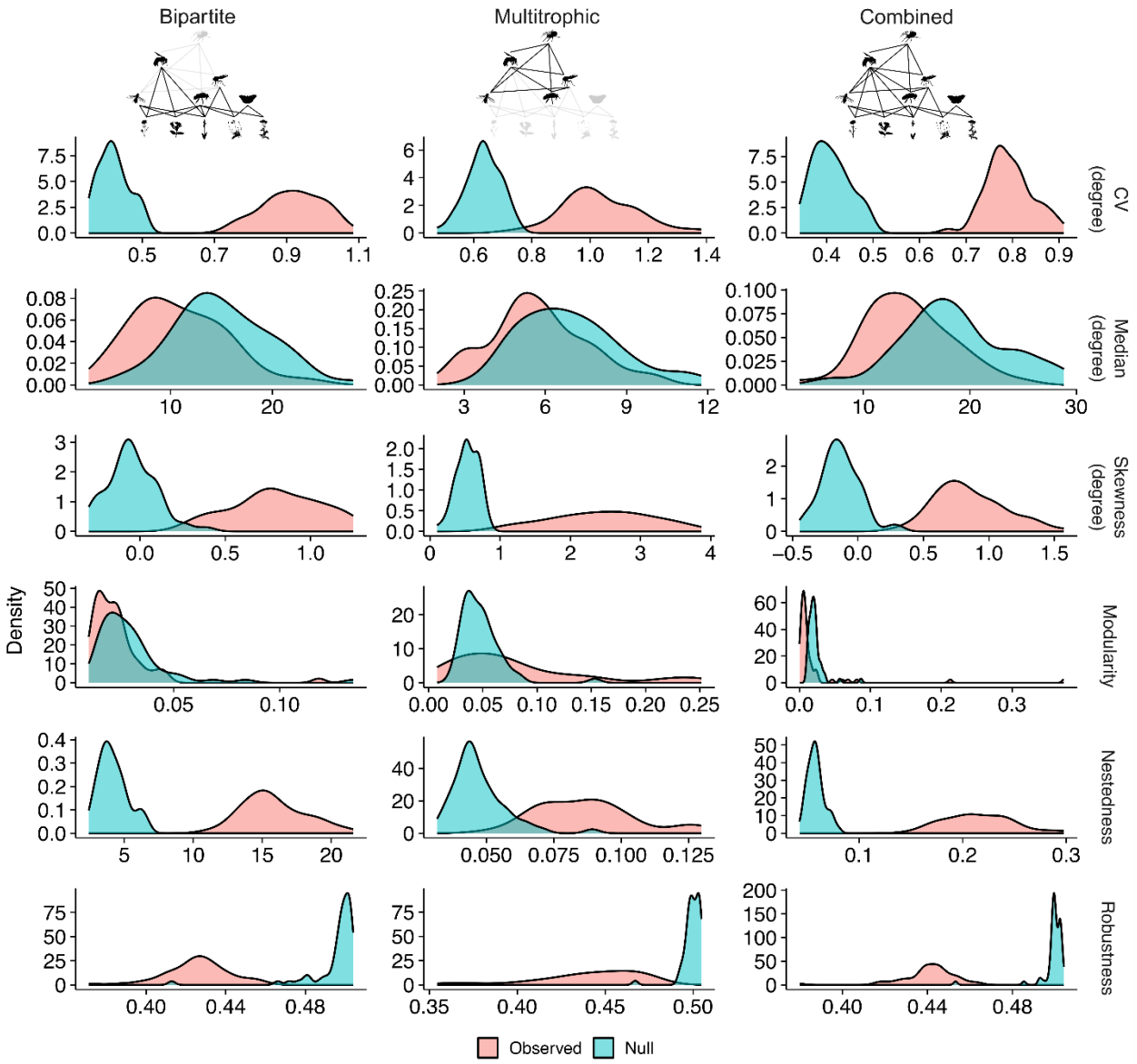
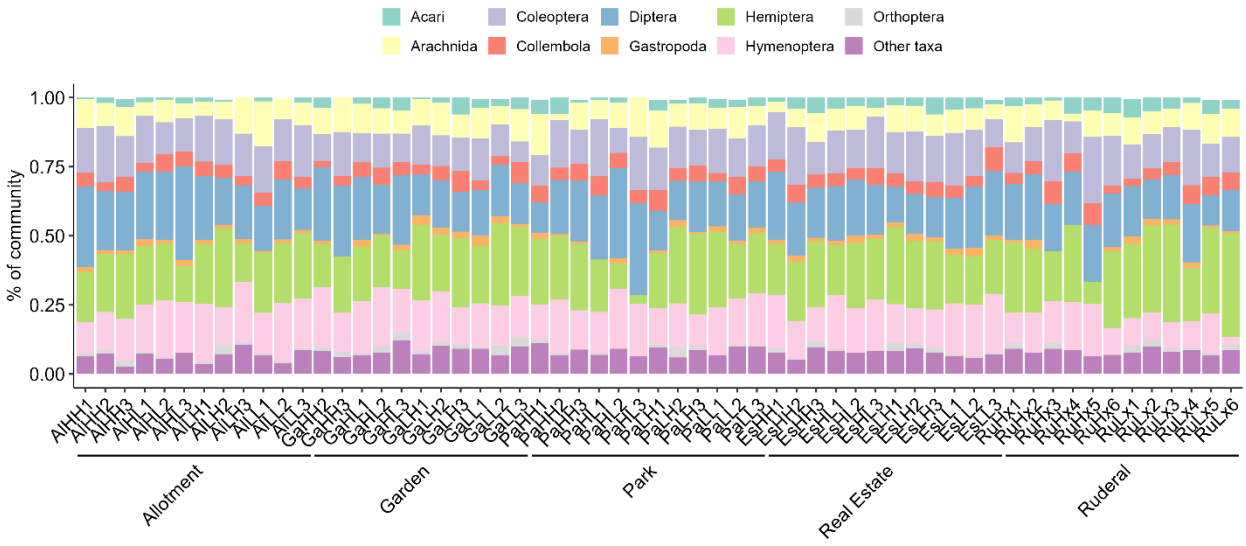


Figure S9: Comparison of network properties between metaweb-derived networks ("observed," blue) and null models ("null," red). All distributions differ significantly (Kolmogorov–Smirnov tests; $p < 0.001$, except modularity in bipartite networks, for which $p < 0.05$).



820 *Figure S10: Community composition across all sites, grouped by urban green space type. Each*

821 *bar represents an individual site.*

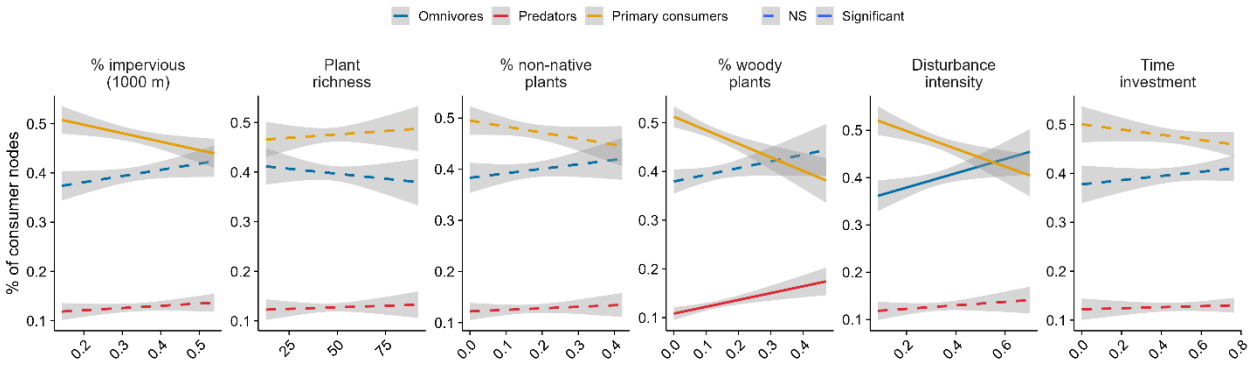
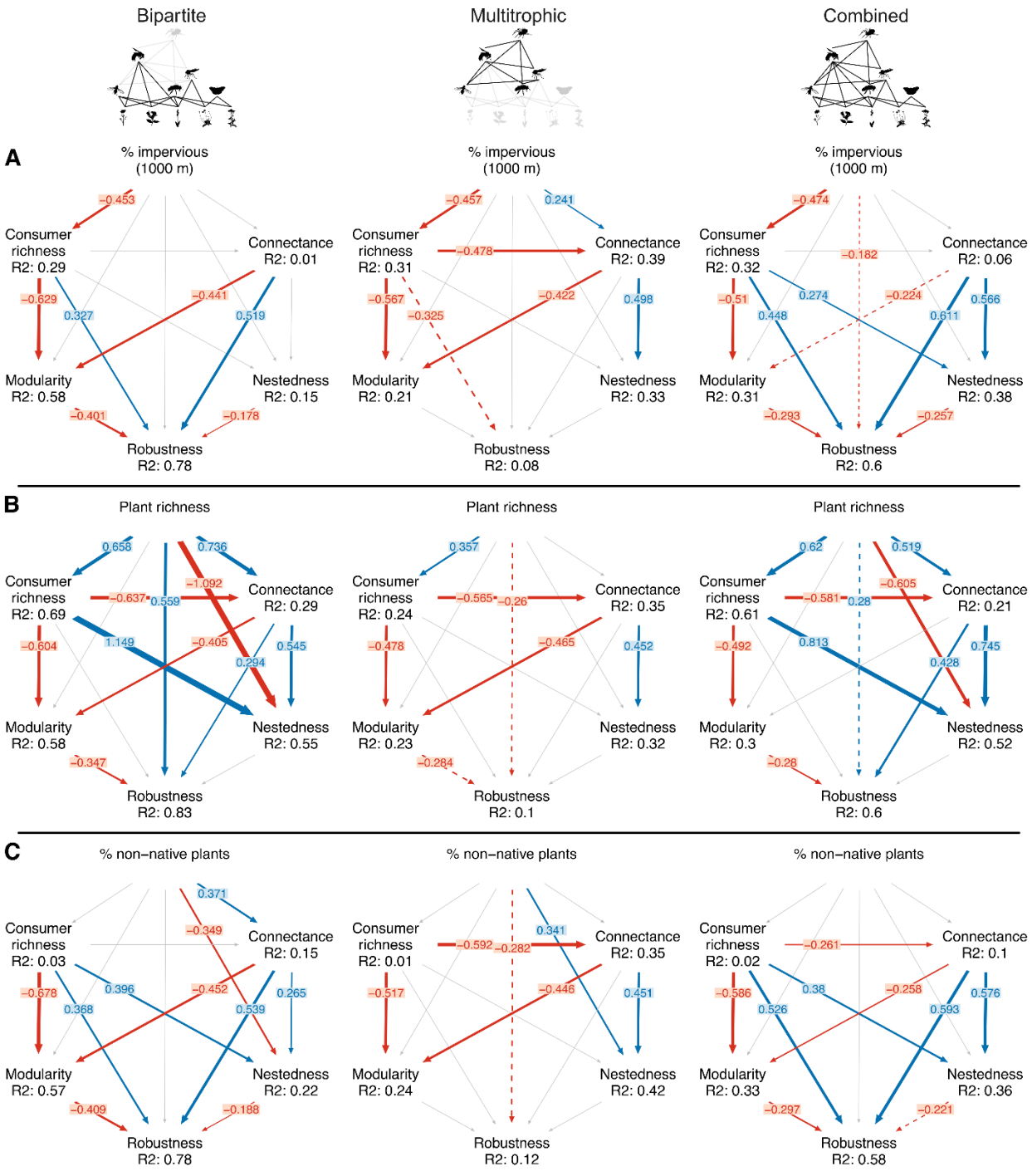


Figure S11: Regression lines showing the proportion of plants, bipartite consumers, and multitrophic consumers (color-coded) in relation to environmental covariates. Solid lines indicate significant correlations with each covariate, whereas dashed lines indicate non-significant relationships.


Bipartite
Multitrophic
Combined
A
% impervious (1000 m)
Consumer richness R2: 0.29
Connectance R2: 0.01
Modularity R2: 0.58
Nestedness R2: 0.15
Robustness R2: 0.78
−0.453
−0.629
0.327
−0.441
0.519
−0.401
−0.178
% impervious (1000 m)
Consumer richness R2: 0.31
Connectance R2: 0.39
Modularity R2: 0.21
Nestedness R2: 0.33
Robustness R2: 0.08
−0.457
0.241
−0.478
−0.567
−0.325
−0.422
0.498
% impervious (1000 m)
Consumer richness R2: 0.32
Connectance R2: 0.06
Modularity R2: 0.31
Nestedness R2: 0.38
Robustness R2: 0.6
−0.474
−0.182
−0.51
0.274
0.448
−0.224
0.566
0.611
−0.293
−0.257
B
Plant richness
Consumer richness R2: 0.69
Connectance R2: 0.29
Modularity R2: 0.58
Nestedness R2: 0.55
Robustness R2: 0.83
0.658
0.736
−1.092
−0.637
0.559
−0.604
1.149
−0.405
0.294
0.545
−0.347
Plant richness
Consumer richness R2: 0.24
Connectance R2: 0.35
Modularity R2: 0.23
Nestedness R2: 0.32
Robustness R2: 0.1
0.357
−0.565
−0.26
−0.478
−0.465
0.452
−0.284
Plant richness
Consumer richness R2: 0.61
Connectance R2: 0.21
Modularity R2: 0.3
Nestedness R2: 0.52
Robustness R2: 0.6
0.62
0.519
−0.605
−0.581
0.28
−0.492
0.813
0.428
0.745
−0.28
C
% non−native plants
Consumer richness R2: 0.03
Connectance R2: 0.15
Modularity R2: 0.57
Nestedness R2: 0.22
Robustness R2: 0.78
0.371
−0.349
−0.678
0.396
0.368
−0.452
0.539
0.265
−0.409
−0.188
% non−native plants
Consumer richness R2: 0.01
Connectance R2: 0.35
Modularity R2: 0.24
Nestedness R2: 0.42
Robustness R2: 0.12
0.341
−0.592
−0.282
−0.517
−0.446
0.451
% non−native plants
Consumer richness R2: 0.02
Connectance R2: 0.1
Modularity R2: 0.33
Nestedness R2: 0.36
Robustness R2: 0.58
−0.261
−0.586
0.38
0.526
−0.258
0.593
0.576
−0.297
−0.221

826

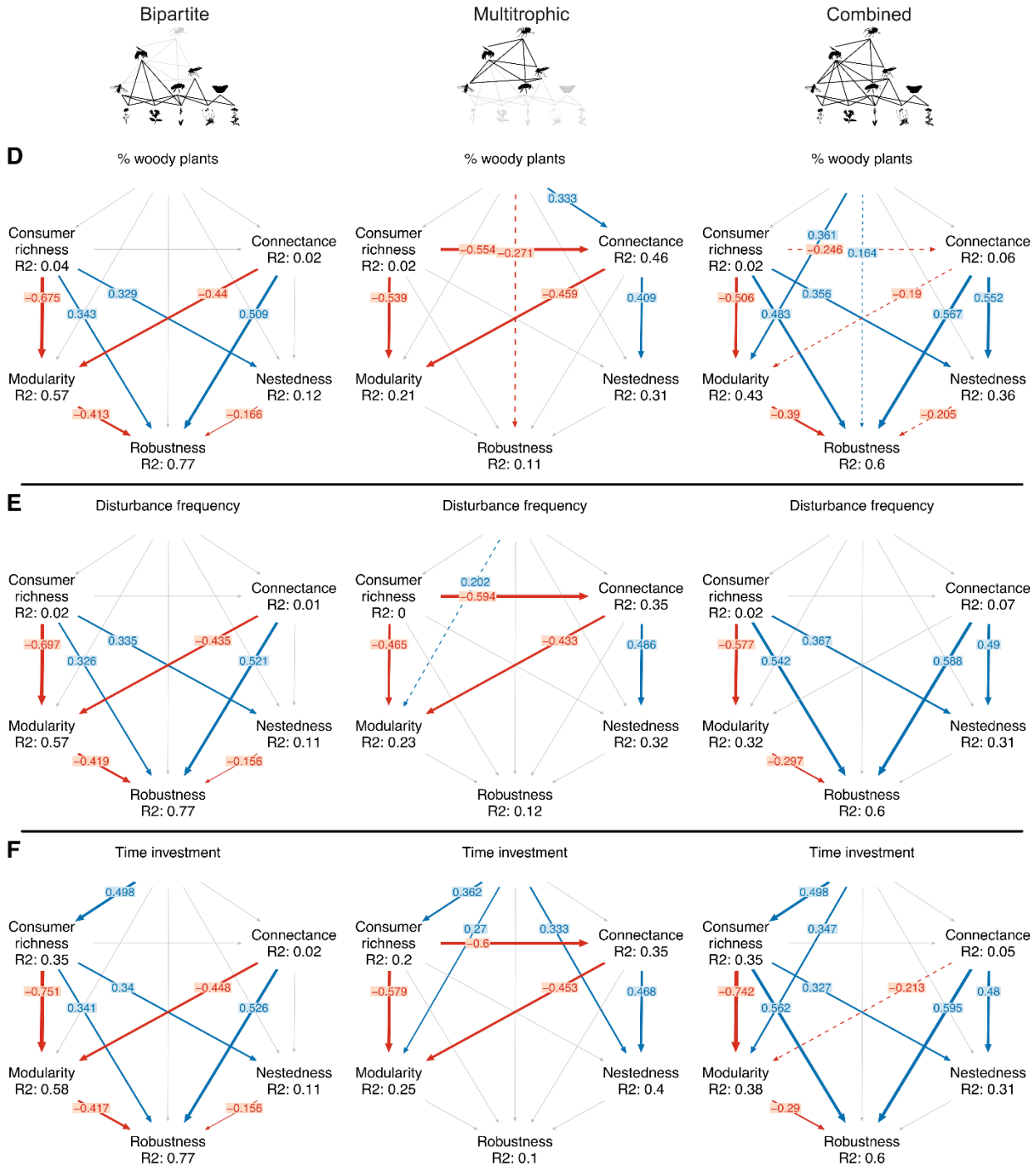


Figure S12: Structural equation models (A–F) depicting relationships among structural food web properties for each individual covariate. Blue arrows indicate significant positive relationships, red arrows indicate significant negative relationships ($\alpha \leq 0.05$), and dashed arrows denote marginally significant relationships ($\alpha \leq 0.1$). Arrow thickness reflects coefficient magnitude, while grey arrows represent non-significant paths (coefficients not shown).

Table S1: Independence claims tested within structural equation models (SEMs) evaluating relationships between environmental covariates and network structure for bipartite, multitrophic, and complete networks. Each claim represents a hypothesized absence of a direct relationship between variables implied by the model structure. For each model, critical values, p-values, and degrees of freedom are reported to assess whether independence assumptions are supported based on standard significance thresholds.

		Independence claim	Critical value	p-value	df
% impervious (1000 m)	Bipartite	nestedness ~ modularity	-0.254	0.800	54
	Multitrophic	nestedness ~ modularity	1.394	0.169	54
	Complete	nestedness ~ modularity	-0.638	0.526	54
Plant richness	Bipartite	nestedness ~ modularity	-1.232	0.223	54
	Multitrophic	nestedness ~ modularity	1.787	0.080	54
	Complete	nestedness ~ modularity	-1.232	0.223	54
% non-native plants	Bipartite	nestedness ~ modularity	-0.328	0.745	54
	Multitrophic	nestedness ~ modularity	1.010	0.317	54
	Complete	nestedness ~ modularity	-0.651	0.518	54
% woody plants	Bipartite	nestedness ~ modularity	-0.438	0.663	54
	Multitrophic	nestedness ~ modularity	1.507	0.138	54
	Complete	nestedness ~ modularity	-0.516	0.608	54
Disturbance intensity	Bipartite	nestedness ~ modularity	-0.406	0.687	54
	Multitrophic	nestedness ~ modularity	0.726	0.471	54
	Complete	nestedness ~ modularity	-0.749	0.457	54
Time investment	Bipartite	nestedness ~ modularity	-0.421	0.675	54
	Multitrophic	nestedness ~ modularity	0.203	0.840	54
	Complete	nestedness ~ modularity	-0.971	0.336	54

Table S2: Goodness-of-fit statistics for the structural equation models (SEM) evaluating relationships between environmental covariates and network structure for bipartite, multitrophic, and complete networks. Fit was evaluated using Fisher's C and Chi-squared tests, with corresponding values, p-values, and degrees of freedom reported for each model.

		Metric	Value	p-value	df
% impervious (1000 m)	Bipartite	Chi-Squared	0.071	0.790	1
		Fisher's C	0.446	0.800	2
	Multitrophic	Chi-Squared	2.085	0.149	1
		Fisher's C	3.554	0.169	2
	Complete	Chi-Squared	0.443	0.506	1
		Fisher's C	1.283	0.526	2
Plant richness	Bipartite	Chi-Squared	1.635	0.201	1
		Fisher's C	2.998	0.223	2
	Multitrophic	Chi-Squared	3.391	0.066	1
		Fisher's C	5.064	0.080	2
	Complete	Chi-Squared	1.636	0.201	1
		Fisher's C	2.999	0.223	2
% non-native plants	Bipartite	Chi-Squared	0.117	0.732	1
		Fisher's C	0.590	0.745	2
	Multitrophic	Chi-Squared	1.105	0.293	1
		Fisher's C	2.298	0.317	2
	Complete	Chi-Squared	0.461	0.497	1
		Fisher's C	1.316	0.518	2
% woody plants	Bipartite	Chi-Squared	0.209	0.647	1
		Fisher's C	0.821	0.663	2
	Multitrophic	Chi-Squared	2.430	0.119	1
		Fisher's C	3.965	0.138	2
	Complete	Chi-Squared	0.291	0.590	1
		Fisher's C	0.996	0.608	2
Disturbance intensity	Bipartite	Chi-Squared	0.180	0.671	1
		Fisher's C	0.752	0.687	2
	Multitrophic	Chi-Squared	0.575	0.448	1
		Fisher's C	1.506	0.471	2
	Complete	Chi-Squared	0.611	0.434	1
		Fisher's C	1.564	0.457	2
Time investment	Bipartite	Chi-Squared	0.194	0.659	1
		Fisher's C	0.785	0.675	2
	Multitrophic	Chi-Squared	0.045	0.832	1
		Fisher's C	0.348	0.840	2
	Complete	Chi-Squared	1.023	0.312	1
		Fisher's C	2.179	0.336	2

Supplementary Material I

For each local food web, we calculated connectance as the proportion of realized trophic links relative to all possible links. Modularity was estimated using Newman's algorithm, which performs well in both bipartite and unipartite networks (Thébault, 2013), and nestedness using NODF (Almeida-Neto et al., 2008) or UNODF for unipartite networks, which is better suited to square adjacency matrices where all nodes can potentially interact (Cantor et al., 2017). Robustness (R50) was quantified through stochastic extinction simulations in which species were sequentially removed and secondary extinctions occurred when species lost all of their resources (Jonsson et al., 2015). Robustness was defined as the normalized proportion of primary extinctions required to eliminate 50% of the original species richness, averaged across replicates. Species without consumers (e.g., basal plants or prey without predators) were excluded from secondary extinction dynamics because they do not contribute to extinction cascades. Because the ecological interpretation of raw modularity and nestedness values differs between bipartite and unipartite networks, we stress that our goal was not to compare absolute metric values across network types. Instead, we assessed whether their variation among sites (and responses to environmental gradients) was congruent across network types.

References

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

Cantor, M., Pires, M. M., Marquitti, F. M. D., Raimundo, R. L. G., Sebastián-González, E.,

Coltri, P. P., Perez, S. I., Barneche, D. R., Brandt, D. Y. C., Nunes, K., Daura-Jorge, F. G., Floeter, S. R., and Jr, P. R. G. (2017). Nestedness across biological scales. PLOS ONE, 12(2), e0171691. https://doi.org/10.1371/journal.pone.0171691

Jonsson, T., Berg, S., Pimenov, A., Palmer, C., and Emmerson, M. (2015). The reliability of R50 as a measure of vulnerability of food webs to sequential species deletions. Oikos, 124(4), 446–457. https://doi.org/10.1111/oik.01588

Thébault, E. (2013). Identifying compartments in presence–absence matrices and bipartite networks: Insights into modularity measures. Journal of Biogeography, 40(4), 759–768. https://doi.org/10.1111/jbi.12015