



Urban environments increase generalization of hummingbird–plant networks across climate gradients

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Urbanization has reshaped the distribution of biodiversity on Earth, but we are only beginning to understand its effects on ecological communities. While urbanization may have homogenization effects strong enough to blur the large-scale patterns in interaction networks, urban community patterns may still be associated with climate gradients reflecting large-scale biogeographical processes. Using 103 hummingbird–plant mutualistic networks across continental Americas, including 176 hummingbird and 1,180 plant species, we asked how urbanization affects species interactions over large climate gradients. Urban networks were more generalized, exhibiting greater interaction overlap. Higher generalization was also associated with lower precipitation in both urban and natural areas, indicating that climate affects networks irrespective of habitat type. Urban habitats also showed lower hummingbird functional trait diversity and over/underrepresentation of specific clades. From the plant side, urban communities had a higher prevalence of nonnative nectar plants, which were more frequently visited by the hummingbird species occurring in both urban and natural areas. Therefore, urbanization affected hummingbird–plant interactions through both the composition of species and traits, as well as floral resource availability. Taken together, we show that urbanization consistently modifies ecological communities and their interactions, but climate still plays a role in affecting the structure of these novel communities over the scale of continents.

functional diversity | Latin America | Neotropics | pollination | urbanization

We humans have drastically transformed the environment surrounding us, particularly through urbanization in which land conversion changes natural habitats into novel environments designed for human settlement (1). Urbanization alters the distribution of species, but we know little about how it affects species interactions and consequently ecological and evolutionary processes (2–4). Ecological interactions in species communities can be depicted as complex networks of interactions (Fig. 1), describing the modes and frequencies of interactions (5). For instance, many ecological networks are characterized by the presence of modules, i.e., subsets of species highly connected through interactions, reflecting a certain level of niche specialization (6). In turn, the conformation of networks into modules may confer some robustness against species extinctions by limiting the spread of secondary extinctions to within modules (7, 8), although such evidence is not unequivocal (9). By changing the network structure, anthropogenic impacts can result in the loss of network robustness and ecosystem function (10–12).

Biotic pollination is a major ecosystem function and involves diverse groups of animals, even in urban areas (13). However, urbanization has been shown to reduce their richness and abundance (14, 15) and cause changes in their functional diversity (16). Such effects in urban environments are also mirrored by reduced plant reproductive success (17), which can be linked to changes in the structural properties of pollination networks (12, 18).

Significance

Urbanization causes dramatic changes in biodiversity. However, we still understand little about its effects on species interactions over broad spatial gradients. We leveraged a large dataset on hummingbird interactions with nectar flowers from Mexico to Brazil and evaluated the influence of both urbanization and climate. Hummingbird–plant communities were consistently more generalized in urban than in natural habitats, and communities located in areas with higher precipitation showed more specialized interactions for both habitat types. Therefore, while urbanization consistently affected species interactions, such effects are still related to large-scale climate gradients. Our study highlights the complex ways in which human-induced land transformations and climate affect species interactions, which may have cascading ecological and evolutionary effects on plants, pollinators, and ecosystem functioning.

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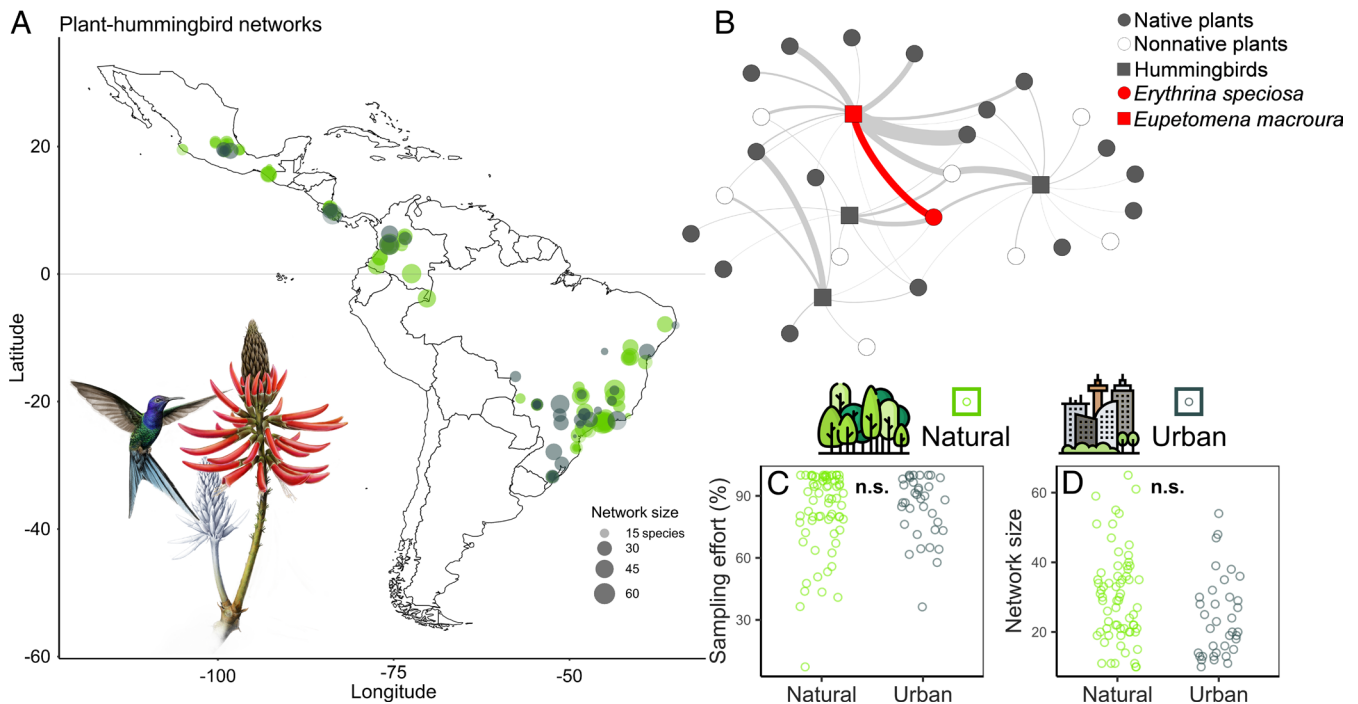


Fig. 1. Location and the characterization of the 103 hummingbird-plant networks sampled in natural ($n = 67$) and urban ($n = 36$) habitats in this study. (A–D), Map showing the distribution of the networks, with gray and green indicating urban and natural sites, respectively (A). Point size in the map refers to the network size, i.e., species richness of the hummingbird-plant network sampled in each location. The illustration on the *Left* depicts the Swallow-tailed Hummingbird *E. macroura* (Emerald clade), a large-bodied and mostly territorial hummingbird that visits both nonnative and native plants, such as the Brazilian native *Erythrina speciosa* (Fabaceae) shown here (artist: Natanael N. Santos). An illustrative urban hummingbird-plant network from Belo Horizonte, Brazil (B; urban network ID#12). Sampling effort expressing the ratio between observed and expected diversity of interactions—sampling completeness (C), and network size expressing the richness of species (D) between urban and natural habitat networks. n.s. indicates nonsignificant results. Empty points in the plots show raw data.

Despite its importance, we still lack studies investigating the effects of urbanization on the structure and stability of interaction networks and on ecological correlates such as functional diversity, especially over large geographic extents.

Here, we use an extensive dataset comprising 103 hummingbird-plant networks from both natural and urban habitats distributed widely across Latin America (Fig. 1). Urbanization and its potential impact on biodiversity are remarkably high across this region since Latin America harbors an estimated one-third of the global species richness of vascular plants and terrestrial vertebrates (19). Moreover, approximately 80% of the human population in this region lives in urban areas (20). Interactions among hummingbirds and plants constitute an ideal model system for our investigation, given the availability of highly resolved interaction network data from natural habitats across a large spatial extent (8, 21), complemented here with new data from urban habitats. We tested the hypothesis that urbanization leads to generalized species interaction networks across the American continent. For this, we first compared three network-level indices that describe distinct aspects of network organization (nestedness, modularity, and specialization) between natural and urban habitats, while testing their association with climate gradients. Then, we compared other characteristics of these networks to evaluate the potential differences of communities under urbanization, including the proportion of nonnative plant resources and network robustness to species loss. To get further insights into how urbanization affects communities and their interactions, we investigated differences in hummingbird species' functional trait composition as well as their interactions with plants at the species level. Finally, as hummingbird clades are known to show distinct traits and interaction patterns (21), we investigated clade-specific responses to urbanization.

Results

All three network metrics, regardless of whether they were corrected with Δ -transformation or not, were consistently distinct between urban and natural habitats, but the effects of precipitation on network metrics were variable. Nestedness ($\Delta wNODF$) was $\approx 65\%$ higher in urban when compared to natural habitats, on average and assuming mean annual precipitation (MAP) (Chi-square test from a model corrected for spatial autocorrelation: $\chi^2_{\text{spat}} = 13.73$, $P < 0.001$, Fig. 2A). Nestedness decreased with precipitation but only in urban sites, whereas there was no relationship between nestedness and precipitation in natural sites (interaction term was significant; $\chi^2_{\text{spat}} = 4.67$, $P = 0.03$, Fig. 2B). Specialization (H_2') was $\approx 26\%$ lower in urban when compared to natural habitats ($\chi^2_{\text{spat}} = 10.13$, $P = 0.001$; Fig. 2C), with a positive relationship with precipitation ($\chi^2_{\text{spat}} = 13.47$, $P < 0.01$) and no effect of the interaction term ($\chi^2_{\text{spat}} = 1.07$, $P = 0.30$; Fig. 2D). Modularity (ΔQ_w) was $\approx 37\%$ lower in urban than in natural habitats ($\chi^2_{\text{spat}} = 17.32$, $P < 0.001$; Fig. 2E), with a positive effect of precipitation on modularity ($\chi^2_{\text{spat}} = 8.08$, $P = 0.004$) and without a significant effect of the interaction term ($\chi^2_{\text{spat}} = 0.06$, $P = 0.80$; Fig. 2F). The proportion of nonnative plant species was on average ≈ 12 times higher in urban than in natural habitats ($\chi^2 = 551.42$, $P < 0.001$; *SI Appendix, Fig. S1A*). In contrast, network robustness (with 50% rewiring) did not differ between habitats ($F = 0.29$, $P = 0.59$; *SI Appendix, Fig. S1B*). Sampling completeness and network size were not different between urban and natural habitats ($\chi^2_{\text{spat}} = 0.04$, $P = 0.85$; and $\chi^2_{\text{spat}} = 3.49$, $P = 0.06$, respectively; Fig. 1C and D), suggesting that these factors have no strong effects on the patterns reported here.

Considering the functional composition and diversity of hummingbirds, we found a significant effect on body mass, which was $\approx 10\%$ higher in urban when compared to natural habitats [com-

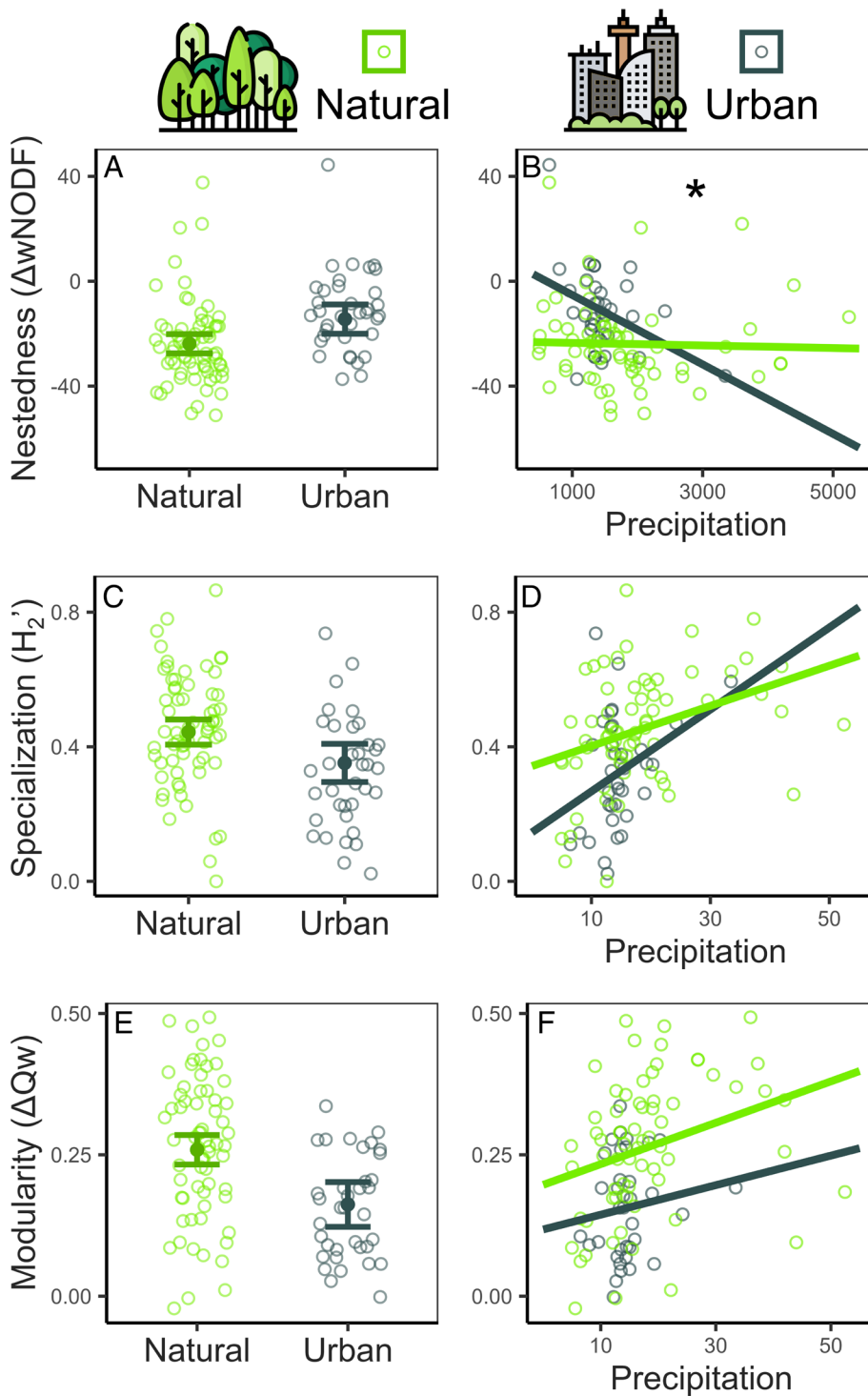


Fig. 2. Effects of urbanization and precipitation on hummingbird-plant network indices (A–F). Results from models testing the effects of habitat type, mean annual precipitation–MAP, and their interaction on network indices including nestedness ($\Delta wNODF$; A and B), specialization (H_2' ; C and D), and modularity (ΔQw ; E and F). Precipitation (in mm) was rescaled in the two latter models to improve their convergence. Points and line segments indicate predicted probabilities and 95% CIs, respectively. Asterisk (*) indicates significance of the interaction term. Empty points show raw data.

munity weighted mean (CWM) body mass: $\chi^2_{\text{spat}} = 7.60$, $P = 0.01$; Fig. 3A]. However, neither bill length nor bill curvature differed between urban and natural hummingbird communities (CWM bill length: $\chi^2_{\text{spat}} = 3.19$, $P = 0.07$; CWM bill curvature: $\chi^2_{\text{spat}} = 0.16$, $P = 0.69$; respectively; Fig. 3B and C). Moreover, functional dispersion (FD_{is}) was lower in urban networks, showing $\approx 17\%$ less trait diversity than in natural habitats ($\chi^2_{\text{spat}} = 4.76$, $P = 0.03$; Fig. 3D).

Finally, considering hummingbird species-level analyses, partner diversity was $\approx 24\%$ higher in urban when compared to natural habitats ($\chi^2 = 5.03$, $P = 0.02$; Fig. 4A), while specialization (d') was $\approx 20\%$ lower in urban habitats ($\chi^2 = 6.95$, $P = 0.01$; Fig. 4B). Considering the proportion of visits, hummingbird species interacted ≈ 18 times more with nonnative plants in urban than in

natural habitats ($\chi^2 = 122.18$, $P < 0.001$; Fig. 4C). Regarding hummingbird clades, Brilliants and Coquettes were mostly absent in the urban networks. Clade-specific analyses showed that the Emerald clade as a whole and its species tend to become less specialized and increase partner diversity when entering urban communities (Fig. 5A–D). On the contrary, hummingbirds from the Hermit clade had lower effective partner diversity in urban than in natural habitat networks (Fig. 5C and D).

Discussion

Our results show the strong effects of urbanization on hummingbird-plant networks. Notably, urbanization caused interaction

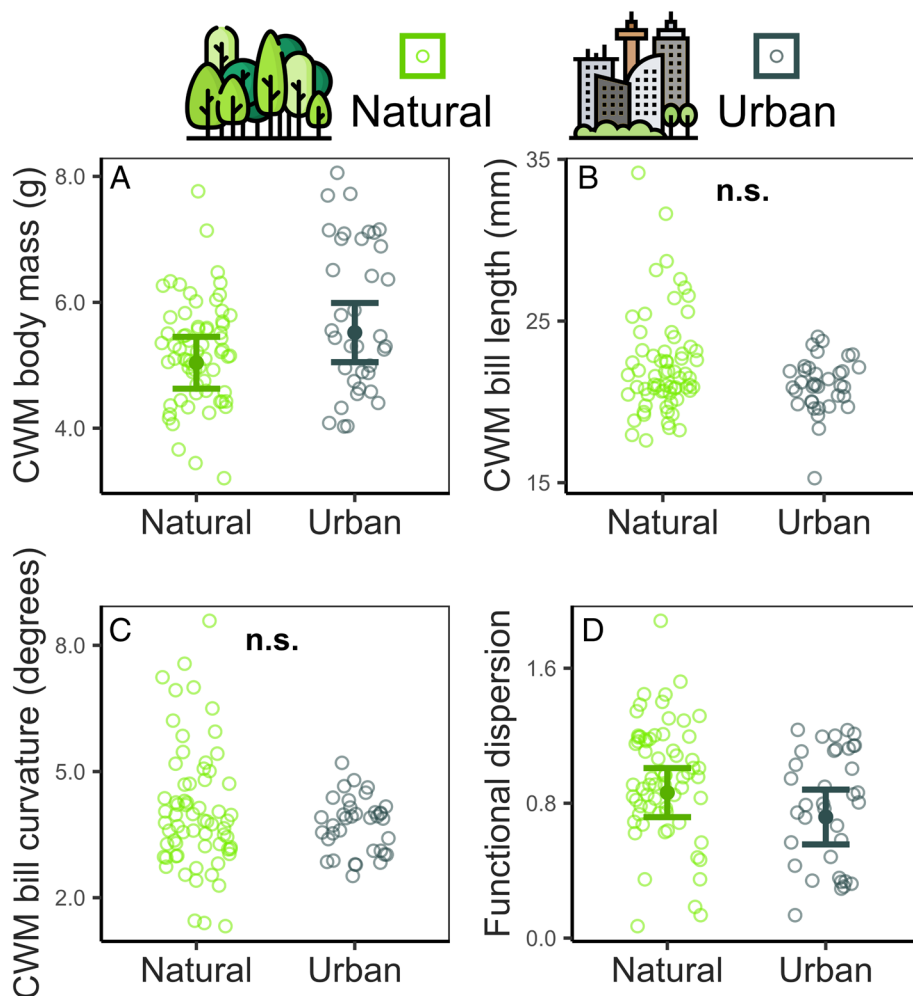


Fig. 3. Results from models testing the effects of habitat type on hummingbird functional diversity indices including CWM values of body mass (A), bill length (B), and bill curvature (C), and functional dispersion FDis (D). n.s. indicates nonsignificant results. Points and line segments indicate predicted probabilities and 95% CIs, respectively (drawn only when significant). Empty points show raw data.

networks to become more generalized, with additional effects of climate in both urban and natural communities. Species tended to have more segregated interactions, as demonstrated by high specialization and modularity in natural than in urban habitats. Additionally, interaction networks were more nested in urban networks, meaning that specialist species interacted with generalist partners while generalist species shared many interactions with each other. Hence, higher nestedness indicated less partition of floral resources by hummingbirds in urban areas. The level of resource partitioning has been shown to influence pollination ecosystem function, with higher partitioning promoting higher plant reproductive success at the community scale (12, 18). Therefore, our results indicate that urban communities potentially support reduced pollination ecosystem function when compared to natural habitats. Moreover, simulated network robustness to plant species loss indicated that both natural and urban networks may be equally robust. Once urban communities are established, it is likely that the most functionally specialized hummingbirds are already lost (10, 22). Thus, the remaining core of generalist species, as indicated by higher nestedness, probably causes communities to be robust against the loss of nectar plants (9).

Climate gradients are known to affect the structure of interaction networks and drive large-scale geographical patterns (23). If urbanization had a strong homogenizing effect on networks, it could blur the potential signal of the climate gradient (2, 24). As such, higher precipitation would lead to higher modularity and specialization and lower nestedness in natural habitats without such a tendency for urban networks. However, except for nestedness, which only decreased with higher precipitation in urban

habitats, the remaining network metrics (i.e., modularity and specialization) showed a similar positive association with precipitation for both urban and natural communities. These two habitats also responded similarly to variations in temperature, exhibiting lower nestedness in localities with higher temperatures (*SI Appendix, Fig. S2 A–F*). Therefore, large-scale climate gradients determining species distribution and assembly from the regional species pool leave a signature on the structure of both natural and urban communities (22, 24, 25). Hence, despite the role of urbanization as an ecological filter that may lead to biotic homogenization (2, 24), climate gradients still affect hummingbirds and their plants in urban communities, especially when considering precipitation.

The ecological filter represented by urbanization may lead to directional changes in functional characteristics or decreased functional diversity of communities (16, 25, 26). Accordingly, we found hummingbird communities in urban habitats to be functionally less diverse and dominated by larger species. The lower functional diversity reflects the loss of hummingbird species with distinct functional roles from urban habitats, such as those from the Hermit clade (10, 21). Therefore, flower types showing matching floral traits, e.g., longer corollas mostly visited by long-billed hummingbirds, may experience reduced pollination services when compared to the more functionally diverse natural communities (18). On the other hand, urban plant communities attractive to hummingbirds have been suggested to be dominated by highly rewarding nectar plants with larger floral displays, especially flowering trees (10). The predominance of such nectar-rich plants probably explains the overrepresentation of larger hummingbirds

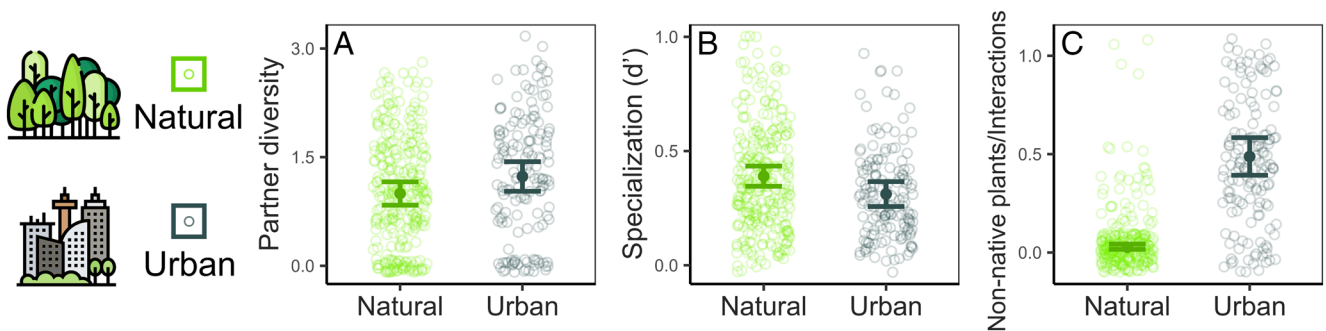


Fig. 4. Results from models testing the effects of habitat type on species level hummingbird-plant network indices, including partner diversity (A), specialization d' (B), and the proportion of nonnative plants used by hummingbird species (C). Analyses were restricted to those hummingbirds occurring in both urban and natural habitats (42 species). Points and line segments indicate predicted probabilities and 95% CIs, respectively. Empty points show raw data.

that are more likely to establish and maintain territories around nectar sources, e.g., the Swallow-tailed Hummingbird *Eupetomena macroura* in Brazil (10, 27). The tendency of some territorial species being favored in urban habitats, as found here for hummingbirds, seems to be happening with other nectarivorous bird groups, e.g., the honeyeaters in Australia (28). Such territoriality could compromise long-distance pollen dispersal, further indicating the loss of ecosystem functionality.

Interestingly, our finding on heavier hummingbirds in urban habitats contrasts with a recent report showing a global trend of

urban birds being smaller (25). Hence, how functional traits such as body mass respond to urbanization may differ according to the guild of birds being considered. Because traits such as bill length and body mass are strongly constrained phylogenetically in hummingbirds (21), our trends also reflected clade-specific hummingbird response to urbanization, with the more generalist hummingbirds in the Emerald clade being favored. In contrast, the more specialist Hermits seem to be at a disadvantage in urban areas. In this context, Brilliants and Coquettes were also mostly unrepresented in urban networks. This shows that the trait-specific

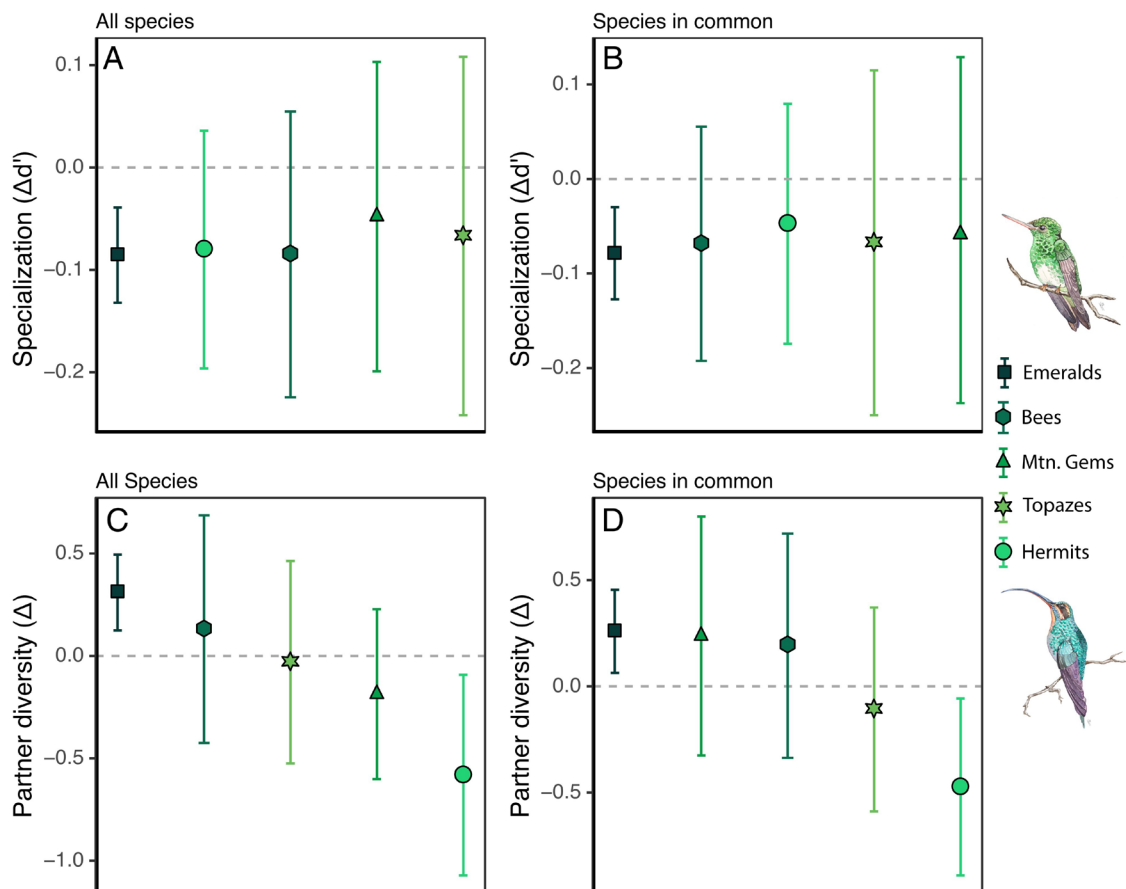


Fig. 5. Clade-specific differences in specialization d' (A and B) and partner diversity (C and D) between urban and natural environments for hummingbird species (along with the 95% CI). The average differences (Δ) derive from regression coefficients along with their CI. Coefficients based on all species within each clade derive from linear models (A and C) and coefficients based only on the species sampled in both natural and urban habitats derive from linear mixed effect models, with species identity as a random effect (B and D). Species from Brilliants and Coquette clades were poorly represented in urban networks and were therefore excluded from these analyses. The clades are sorted in the panels from Left to Right based on the CI's distance from zero, which corresponds to no significant difference between urban and natural environments when it does overlap with zero. Hummingbird illustrations highlight examples from the Emerald (*Chionomesa fimbriata*) and the Hermit clades (*Phaethornis guy*) at the Top and Bottom, respectively (artist: Katrine Hansen).

filtering of urbanization also affects the evolutionary lineages that can persist across urban communities, mirroring trait-specific losses observed in insect pollinator groups (15, 16).

Urban vegetation is rich in nonnative plant species, with these plants having relevant effects on pollinators (29, 30). We showed that hummingbirds interacted in higher proportion with nonnative plants in urban than natural habitats. This underscores the increased presence of nonnative plants in urban environments, leading hummingbirds to adjust their foraging behavior based on the available resources. Additionally, it highlights that generalist hummingbirds exhibit a greater likelihood of integrating nonnative plants into their diets (31). Therefore, our results illustrate the use of nonnative plants as nectar sources for urban pollinators in a scenario of decreased functional diversity and more generalized interactions. Nonnative nectar plants are sometimes relevant for supporting pollinators in urban environments by providing essential resources when native flowers are scarce (29, 30). Thus, replacing them with native species requires careful consideration of their ecological roles. Nevertheless, such management strategies may be needed to restore more functionally diverse communities in urban habitats.

Taken together, we show that urbanization strongly affects hummingbird–plant communities at a continental scale, but this effect is not sufficient to blur the effects of climate on mutualistic network structures, including specialization, modularity, and nestedness. In spite of these consistent patterns, we note that urban areas can be remarkably heterogeneous, varying in mode and intensity of urbanization as well as in the preurbanization biodiversity and environmental characteristics (24). Thus, a promising avenue for future studies is to explore the variation of species interaction networks along specific variables indicative of urbanization gradients (e.g., vegetation cover, population density), beyond the simple dichotomy of natural versus urban areas applied in this study, to explore the complexity of urban landscapes. Ideally, one should then contrast interaction patterns along such gradients with simultaneous sampling of more urbanized and more natural areas, to avoid introducing different time periods of sampling as we had in our dataset, where urban networks were mostly sampled more recently than natural areas (*Methods*). Such an approach could provide a more nuanced understanding of how different levels of urbanization affect interaction networks, potentially revealing tipping points of network disruption, as well as indicate which urban planning practices best foster the maintenance of species interactions. In this regard, a recent local scale study within one city found that hummingbird–plant interactions were consistently generalized along a gradient of increasing vegetation cover, but the presence of native plants increased specialization (32). Therefore, any gradient of urbanization should consider multiple effects of urban transformation.

A further promising avenue would be to address the evolutionary consequences of urbanization. Recent studies have shown that urbanization may cause evolutionary changes in traits important for interactions for both plants and pollinators (2, 33, 34). Therefore, changes in hummingbird composition and consequently on their role as pollinators could favor rapid evolutionary changes in floral morphology and mating systems (34, 35). Investigating such trends over large spatial scales could be a fruitful avenue for future research.

Despite some limitations, our results underscore that climate influences species interactions across geographical gradients even with the expected homogenizing effects of urbanization. This finding aligns with a recent experiment showing mostly similar seed predation rate variations across a large latitudinal gradient in urban and natural areas (36), thus indicating that biodiversity response

to urbanization varies across large scales. Nevertheless, urban hummingbird communities consistently had lower functional diversity than natural ones, thus potentially compromising the provisioning of ecosystem services (18). Even though many urban plants are introduced and/or maintained by humans, lowered pollination function may compromise the establishment of sustainable and biodiverse urban landscapes for those species that have self-sustainable populations and require pollination. Moreover, urban communities showed a distinct hummingbird trait composition, reflecting the over/underrepresentation of hummingbirds from specific clades; hence, both phylogenetic and functional diversity are lost. Finally, we also show that urbanization is associated with more generalized pollinator–plant interactions at the species level, indicating effects for both species composition and behavior plasticity. These findings reveal the consequences of urbanization for hummingbirds and their interactions with nectar plants, also highlighting the consistent ways in which large-scale climate gradients affect the structure of urban ecological communities.

Methods

Hummingbird–Plant Networks, Traits and Climate Data. We compiled a dataset of 103 quantitative hummingbird–plant interaction networks distributed from Mexico to Southern Brazil, comprising 176 hummingbird and 1,180 plant species (Fig. 14). While 67 of the 103 networks coming from natural areas were previously published (21), the 36 networks in urban localities consist mostly of new data collected for the present study (*SI Appendix* and *Dataset S1*) (37). Urban networks were characterized by habitats with the presence of built structures associated with denser human settlements and needed to 1) include all flowering plants (native and nonnative) known to be visited (or potentially visited) by hummingbirds in the study area, which includes ornithophilous and nonornithophilous species that produce nectar, 2) sampling should cover at least one annual cycle (all seasons sampled), 3) aim to conduct sampling for at least 10 h of observation for each plant species, and 4) the urban area sampled should cover at least one hectare (100 × 100 m). Each network represented an ecological community, summarizing interaction frequencies between pairs of hummingbird and plant species. Here, interaction frequency was defined as the total number of times a hummingbird species was observed interacting with the flowers of a given plant species, by recording visits to plant individuals, thus providing a quantitative estimate of the strength of interactions. Moreover, we included in our analyses only legitimate interactions, in which hummingbirds inserted their bills to drink nectar while touching the reproductive structures of the flowers, thereby potentially acting as pollinators and characterizing mutualistic interactions.

The 67 natural area networks were extracted from a previously published database (21), which reported 93 interaction networks from natural habitats across mainland America and islands. We only used data from the mainland networks, as those from islands are depauperated and often structured by different processes (21), and we lacked urban networks from islands. In addition, considering that urban development reflects cultural, socioeconomic, and historical drivers specific to each country/region (38), we limited the data on the natural habitats to the subset of mainland networks located in the same countries where the urban networks were also sampled (i.e., Mexico, Costa Rica, Colombia, and Brazil). This also contributed to reducing the imbalance in the statistical comparison between urban ($n = 36$) and natural habitat networks ($n = 67$). However, supplementary analyses on network metrics comparison between natural and urban interaction networks using the full mainland dataset (21), ($n = 84$) show that our results on the higher generalization of urban networks are consistent irrespective of data subsetting (*SI Appendix*, Fig. S3 A–C).

Choice of sampling sites in urban areas was made by each observer in the field, following criteria that included 1) the presence of nearby impervious pavements, 2) built structures and housing with inhabitants and/or constant human occupation, and 3) replacement, modification, and/or fragmentation of original vegetation. Hence, although there is variation within “urbanized” habitats (36), they all have been transformed by a specific type of human use. A similar dichotomous approach,

albeit limited, has been used previously, including for testing large-scale effects of urbanization (36). The assignment of communities into urban and natural habitats was supported by landscape level analysis, contrasting the proportion of built area at each study locality, with buffer areas of 1.0, 5.0, and 10.0 Km radius (SI Appendix, Fig. S4 A–C). There are some variations within each habitat category as some urban settlements could have been located next to natural vegetation areas, and some natural areas networks from Dalsgaard et al. (21) were sampled in native vegetation areas close to urban areas. We are, however, confident in the description of local environmental conditions undertaken by each data collector. Species names of the hummingbirds follow the International Ornithological Committee World List (IOC version 9.2; www.worldbirdnames.org; SI Appendix). Plant species names and families follow “World Flora Online” (<http://www.worldfloraonline.org/>). Plant species were classified as native or nonnative at the localities where they were found. For that, we used national-level online databases or up-to-date references for each of the countries in our database (see Dataset S2 for references).

For the hummingbirds, we gathered data on three morphological traits that have been proven to influence their interactions with plants: bill length, bill curvature, and body mass (21, 39) (see SI Appendix for details, Dataset S3). These traits are also known to respond to urbanization and other land-use changes (10, 22, 40). Bill length and curvature data were taken from Dalsgaard et al. (21), which measured for most species an average of five adult male and five female specimens deposited in museums. Body mass data were built upon previously gathered datasets (36, 41). For five species for which we were not able to find alternative sources, we used data available for the most closely related species (see SI Appendix for details, SI Appendix, Table S1).

Finally, we extracted from the CHELSA climate database in 10 arcmin resolution (42), (<https://chelsa-climate.org>), the MAP, in mm (hereafter, precipitation), and mean annual temperature, in °C (hereafter, temperature), for each of the 103 network localities to express the climate gradient in our study.

Network Structure. We calculated three quantitative indices that characterize different aspects of the structure of the interaction networks: i) weighted nestedness (wNODF), which describes the presence of a core of generalist species interacting among them and with specialists, generating ordered subsets of interactions (43). wNODF identifies whether sequential columns or rows (i.e., species within the matrix) are sorted by decreasing marginal totals, with more weight given to frequent interactions. ii) Quantitative modularity (Qw), which expresses the extent to which networks are organized into modules of preferentially interacting species and was estimated using the *DIRTLPAwb*+optimization algorithm (44). The algorithm rearranges the way communities can be partitioned within the observed interaction matrix, aiming to identify the conformation of species groups (i.e., modules) that maximize interactions within the modules in relation to interactions between modules, leading to optimal Qw values. iii) Complementary specialization (H_2'), which quantifies the partitioning of interactions among species relative to an expectation derived from their availability in the community [i.e., the selectiveness of interactions (45)]. H_2' is calculated by measuring the divergence between the observed interaction frequencies and random expectation of interaction when assuming that species interact with partners following their availability (where availability is estimated as species' marginal totals), then normalized to a 0 to 1 scale, showing how selectively species interact. While higher values of nestedness (from 0 to 100) indicate the prevalence of generalist core species performing most interactions, higher values of modularity and specialization (both from 0 to 1) indicate that interactions are partitioned among specific partners. We also calculated sampling completeness for each network as an index of sampling effort, by dividing the observed richness of pairwise plant and hummingbird interactions by an estimated richness of links calculated with Chao 1 estimator (46), using the frequency of each interaction as equivalent to “abundance” (47). Furthermore, since different networks may not be directly comparable given that network metrics are often affected by network size, i.e., richness of species in the network, and sampling effort (48), we applied a null model correction using the Patefield algorithm which constrains the total number of interactions performed by each species and network size (49). We then subtracted the mean metric value obtained in the null model from the value found for the empirical network [i.e., Δ -transformation (48)]. Mean metric values from the null model were obtained after 1,000 randomizations. Since the raw values of specialization H_2' are already derived from a null

model, we report the Δ -transformed nestedness and modularity in the main text, while for specialization, we report the original values (see SI Appendix, Fig. S5 A–F for complementary results). All network analyses were conducted using the R-package *bipartite* v.2.16 (50).

Network Robustness. We estimated network robustness using an algorithm that simulates sequential species extinctions in a stepwise process caused by the loss of interactions in the network and quantifies coextinction rates (8, 51). The first step removes the plant species with the fewest interactions in the network. The second step removes hummingbird species according to the probabilities equal to 1—their fraction of lost interactions in the previous step. The third step then uses the same rules to remove plants following the loss of their interactions. These steps continued until there were no more species to remove. Following this procedure, species extinctions can spread through networks depending on how the mutualistic interactions are configured (8). After each step described above, we allowed species to reconfigure 50 and 25% of their lost interactions with the remaining partners [i.e., constrained rewiring (52)]. We repeated these simulations by increasing the number of plant species removed in the first step from one to the total number of plant species in the network. This simulation series produces an attack tolerance curve, which plots the fraction of remaining hummingbird species against the fraction of eliminated plants [ATC (51)]. For each network, we calculated 1,000 ATCs and used the *loess* function in the R-package *stats* (polynomial regression fitting) to produce a single consensus ATC. Finally, we calculated the area under the consensus ATC, which defines a network's robustness to species loss, ranging from zero—expressing the lowest robustness, to one—indicating the highest robustness to extinctions (51).

Hummingbird Functional Diversity. To compare the trait composition of hummingbird communities from urban and natural habitats, we estimated the community-level weighted means of trait values [CWM (53)] for the three hummingbird traits that we compiled: bill length, bill curvature, and body mass. We additionally calculated the functional dispersion (FDis) index for each community by computing the mean distance of all species to the centroid of the community in the functional trait space, projected using a principal coordinates analysis based on pairwise Euclidean distances between hummingbird species given their traits (54). Traits were standardized to zero mean and unit variance before the calculation of Euclidean distances (55). For both CWMs and FDis, the abundance of hummingbird species in the communities was given by the sum of their interactions, which is a good proxy of their abundance (39). While CWMs indicate the mean trait composition/value of each community, higher values of hummingbird FDis indicate the co-occurrence of hummingbird species with distinct trait combinations (55). Functional diversity metrics were calculated using the function *dbFD* in the R-package *FD* v. 1.0–12.1 (55).

Species-Level Analyses. We calculated two species level indices to assess how the same hummingbird species change their interaction patterns according to whether they occurred in urban or natural habitats: i) partner diversity, which is calculated as the exponential Shannon's diversity and expresses the diversity of interaction partners for each species (56) and ii) species level complementary specialization (index d'), which quantifies how strongly interaction frequency of a given species deviates from null-model expectations in which the species interacts with partners proportionally to their availability, defined by their marginal totals (45). We also quantified the proportion of nonnative plant species used by each hummingbird species in relation to all its interacting plants in each network, expressed as the proportion of nonnative use. All these three values, partner diversity, specialization, and nonnative plants use were compared between natural and urban networks. Because we were interested in behavioral changes between habitats, as well as to reduce bias by comparing different species, we focused the analysis on those hummingbird species that were found in at least one urban and one natural network, comprising 42 species out of 176.

Statistical Analyses. Since the structure of interaction networks may be affected by sampling effort and network size (48), we tested whether networks from natural and urban habitats (i.e., habitat type—predictor) differed in sampling effort and network size (i.e., response variables) using a linear model (LM). Next, we fitted distinct LMs to the network-level response variables: nestedness, modularity, and specialization, as well as their Δ -transformed counterparts. In these models, we included habitat type (i.e., natural or urban),

precipitation, temperature, and the interaction terms as predictors (i.e., habitat*precipitation and habitat*temperature). However, we observed that the variance inflation factors (VIFs) of interaction terms were high (VIFs > 3.0) during model validation, preventing the inclusion of the two climate predictors and the interaction term together in the models. Therefore, in the main text, we report the models including only precipitation, which has been shown as the main climate factor affecting the structure of hummingbird–plant networks in previous research (39). Additional LMs with temperature as the predictor variable are reported in *SI Appendix, Fig. S2 A–F*. Thus, main LMs were fitted with urban/natural categories (i.e., habitat type), precipitation, and the interaction term (i.e., habitat*precipitation), allowing us to test the specific hypothesis of climatic gradients having a different effect in urban and natural networks. We rescaled the precipitation variable (dividing by 100) in the models testing specialization (H_2) and modularity (ΔQ_w) to improve their convergence.

Differences between habitat types (i.e., predictor variable: urban/natural) regarding functional diversity indices (CWM bill length, CWM bill curvature, CWM body mass, and FDis; as response variables) were assessed using LMs. We also used LMs to test differences between habitat types for robustness with 25 and 50% thresholds of rewiring. Since the results were similar, we only reported the results of 50% rewiring in the text. We evaluated whether the proportion of nonnative species differed between habitat types using a GLM (generalized linear model) with binomial distribution and logit link function. We took the number of nonnative species relative to the number of native ones as our response variable.

Since all analyses were based on networks that have a specific location in space, we checked for residual spatial autocorrelation using Moran's I test. If a significant result was found, we used the geographic coordinates to adjust the model for spatial dependency by specifying a structured covariance matrix. These spatial models were based on exponential autocorrelation, except for the "sampling effort" model for which we used a Matern autocorrelation to improve its fit. Whenever a spatial model was implemented, we used "spat" (in subscript) to specify. Since network data from urban habitats were sampled more recently, we also conducted a series of sensitivity analyses to demonstrate that this temporal difference does not influence the patterns reported here (*SI Appendix, Figs. S6 and S7 and Table S2*).

For species-level network analyses of hummingbirds found across both urban and natural habitats (partner diversity and specialization response variables), we employed LMMs, considering habitat type as the predictor variable and network and species identities as crossed random effects. We added a zero-inflation parameter for the model testing partner diversity. For the model considering the proportion of nonnative plants interacting with hummingbirds as the response variable, we used a GLMM (generalized linear mixed model) with binomial distribution (logit link), with network and hummingbird species identities as crossed random effects.

Spatial models, LMMs, and GLMMs were built using the R-package *glmmTMB* v.1.14.5 (57). Overdispersion, spatial dependence, and zero-inflation tests as well as models' validation were conducted by simulating the residuals 1,000 times using the R-package *DHARMa* v.0.4.5 (58). We assessed the models' significance using F tests (for LMs) or chi-square tests (for spatial models, LMMs, GLMs, and GLMMs).

Finally, we evaluated whether urban–natural differences in species-level specialization (d') and partner diversity were sensitive to the composition of hummingbird clades (Emeralds, Bees, Mt. Gems, Coquettes, Briliants, Topazes, and Hermits) by testing whether these differences persisted within each clade. We analyzed each clade individually using an LM with urban or natural habitat type as the categorical predictor variable and the values of d' and partner diversity as response variables. We extracted the coefficient from each model representing the clade's average difference in d' and partner diversity between urban and natural habitats. Subsequently, we used GLMM, with hummingbird species as random intercepts, to test whether the pattern within clades persisted for individual species found in both urban and natural habitats. In these GLMMs, only species sampled in urban and natural networks were included. The Coquettes and Briliants clades were poorly represented in urban communities, with two and zero species sampled, respectively. Thus, we excluded both clades from these analyses, which were conducted using the *lmer* function from R-package *lme4* (59). All analyses were conducted in R software v. 4.3.0 (60).

Data, Materials, and Software Availability. All data are made available as supplementary material and are deposited at Figshare repository

<https://doi.org/10.6084/m9.figshare.25393636.v3>. All other data are included in the manuscript and/or supporting information.

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1. K. C. Seto, B. Güneralp, L. R. Hutrya, Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proc. Natl. Acad. Sci. U.S.A.* **109**, 16083–16088 (2012).
2. J. S. Santangelo *et al.*, Global urban environmental change drives adaptation in white clover. *Science* **375**, 1275–1281 (2022).
3. A. L. Teixeira *et al.*, Anthropogenic impacts on plant-animal mutualisms: A global synthesis for pollination and seed dispersal. *Biol. Conserv.* **266**, 109461 (2022).
4. P. Theodorou, The effects of urbanisation on ecological interactions. *Curr. Opin. Insect Sci.* **52**, 100922 (2022).
5. P. R. Guimarães, The structure of ecological networks across levels of organization. *Annu. Rev. Ecol. Evol. Syst.* **51**, 433–460 (2020).
6. J. M. Olesen, J. Bascompte, Y. L. Dupont, P. Jordano, The modularity of pollination networks. *Proc. Natl. Acad. Sci. U.S.A.* **104**, 19891–19896 (2007).
7. D. B. Stouffer, J. Bascompte, Compartmentalization increases food-web persistence. *Proc. Natl. Acad. Sci. U.S.A.* **108**, 3648–3652 (2011).
8. J. Sonne *et al.*, Extinction, coextinction and colonization dynamics in plant-hummingbird networks under climate change. *Nat. Ecol. Evol.* **6**, 720–729 (2022).
9. E. Thébaud, C. Fontaine, Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science* **329**, 853–856 (2010).
10. P. K. Maruyama *et al.*, Plant-hummingbird interaction networks in urban areas: Generalization and the importance of trees with specialized flowers as a nectar resource for pollinator conservation. *Biol. Conserv.* **230**, 187–194 (2019).
11. M. Doré, C. Fontaine, E. Thébaud, Relative effects of anthropogenic pressures, climate, and sampling design on the structure of pollination networks at the global scale. *Glob. Change Biol.* **27**, 1266–1280 (2021).
12. A. Magrath, F. P. Molina, I. Bartomeus, Niche complementarity among pollinators increases community-level plant reproductive success. *Peer Community J.* **1**, e1 (2021).
13. V. H. D. Silva *et al.*, Diverse urban pollinators and where to find them. *Biol. Conserv.* **281**, 110036 (2023).
14. J. Millard *et al.*, Global effects of land-use intensity on local pollinator biodiversity. *Nat. Commun.* **12**, 2902 (2021).
15. H. Liang, Y.-D. He, P. Theodorou, C.-F. Yang, The effects of urbanization on pollinators and pollination: A meta-analysis. *Ecol. Lett.* **26**, 1629–1642 (2023).
16. W. Banaszak-Cibicka, Ł. Dylewski, Species and functional diversity—A better understanding of the impact of urbanization on bee communities. *Sci. Total Environ.* **774**, 145729 (2021).
17. J. M. Bennett *et al.*, Land use and pollinator dependency drives global patterns of pollen limitation in the Anthropocene. *Nat. Commun.* **11**, 3999 (2020).
18. X. Loy, B. J. Brosi, The effects of pollinator diversity on pollination function. *Ecology* **103**, e3631 (2022).
19. P. H. Raven *et al.*, The distribution of biodiversity richness in the tropics. *Sci. Adv.* **6**, eabc6228 (2020).
20. World Population Prospects 2019: Highlights (ST/ESA/SER.A/423). United Nations, Department of Economic and Social Affairs, Population Division (2019). <https://population.un.org/wpp/>. Accessed 30 August 2023.
21. B. Dalsgaard *et al.*, The influence of biogeographical and evolutionary histories on morphological trait-matching and resource specialization in mutualistic hummingbird-plant networks. *Funct. Ecol.* **35**, 1120–1133 (2021).
22. A. Puga-Caballero, M. Del coro Arizmendi, L. A. Sánchez-González, Phylogenetic and phenotypic filtering in hummingbirds from urban environments in Central Mexico. *Evol. Ecol.* **34**, 525–541 (2020).
23. B. Dalsgaard *et al.*, Specialization in plant-hummingbird networks is associated with species richness, contemporary precipitation and quaternary climate-change velocity. *PLoS One* **6**, e25891 (2011).
24. M. F. Aronson *et al.*, Biodiversity in the city: Key challenges for urban green space management. *Front. Ecol. Environ.* **15**, 189–196 (2017).
25. M. H. C. Neate-Clegg *et al.*, Traits shaping urban tolerance in birds differ around the world. *Curr. Biol.* **33**, 1677–1688.e6 (2023).
26. D. Sol *et al.*, The worldwide impact of urbanisation on avian functional diversity. *Ecol. Lett.* **23**, 962–972 (2020).
27. D. G. Justino, P. K. Maruyama, P. E. Oliveira, Floral resource availability and hummingbird territorial behaviour on a Neotropical savanna shrub. *J. Ornithol.* **153**, 189–197 (2012).
28. I. Szazima, M. Szazima, A handful of beauty and services: Flower-visiting birds at two small urbanised sites in south-eastern Brazil and Australia. *Flora* **296**, 152151 (2022).
29. M. Staab, M. H. Pereira-Peixoto, A.-M. Klein, Exotic Garden plants partly substitute for native plants as resources for pollinators when native plants become seasonally scarce. *Oecologia* **194**, 465–480 (2020).
30. P. A. Anselmo, J. C. F. Cardoso, P. R. Siqueira, P. K. M. Maruyama, Non-native plants and illegitimate interactions are highly relevant for supporting hummingbird pollinators in the urban environment. *Urban Urban Green* **86**, 128025 (2023).
31. P. K. Maruyama *et al.*, The integration of alien plants in mutualistic plant-hummingbird networks across the Americas: The importance of species traits and insularity. *Divers. Distrib.* **22**, 672–681 (2016).
32. C. Bosenbecker *et al.*, Consistent generalization of plant-hummingbird networks despite increasing vegetation cover across a tropical urban landscape. *Urban Urban Green* **101**, 128498 (2024).
33. P. Theodorou, L. M. Baltz, R. J. Paxton, A. Soro, Urbanization is associated with shifts in bumblebee body size, with cascading effects on pollination. *Evol. Appl.* **14**, 53–68 (2021).
34. S. Acoca-Pidolle *et al.*, Ongoing convergent evolution of a selfing syndrome threatens plant-pollinator interactions. *New Phytol.* **242**, 717–726 (2024). [10.1111/nph.19422](https://doi.org/10.1111/nph.19422).
35. C. R. Mackin, J. F. Peña, M. A. Blanco, N. J. Balfour, M. C. Castellanos, Rapid evolution of a floral trait following acquisition of novel pollinators. *J. Ecol.* **109**, 2234–2246 (2021).
36. A. L. Hargreaves *et al.*, Latitudinal gradients in seed predation persist in urbanized environments. *Nat. Ecol. Evol.* **8**, 1897–1906 (2024).
37. P. K. Maruyama *et al.*, Data and code for “Urban environments increase generalization of hummingbird-plant networks across climate gradients.” Figshare. <https://doi.org/10.6084/m9.figshare.25393636.v3>. Deposited 19 October 2024.
38. K. Uchida *et al.*, Urban biodiversity and the importance of scale. *Trends Ecol. Evol.* **36**, 123–131 (2021).
39. P. K. Maruyama *et al.*, Functional diversity mediates macroecological variation in plant-hummingbird interaction networks. *Glob. Ecol. Biogeogr.* **27**, 1186–1199 (2018).
40. B. A. Tinoco, V. E. Santillán, C. H. Graham, Land use change has stronger effects on functional diversity than taxonomic diversity in tropical Andean hummingbirds. *Ecol. Evol.* **8**, 3478–3490 (2018).
41. C. H. Graham, J. L. Parra, B. A. Tinoco, F. G. Stiles, J. A. McGuire, Untangling the influence of ecological and evolutionary factors on trait variation across hummingbird assemblages. *Ecology* **93**, S99–S111 (2012).
42. D. N. Karger *et al.*, Climatologies at high resolution for the earth's land surface areas. *Sci. Data* **4**, 170122 (2017).
43. M. Almeida-Neto, W. Ulrich, A straightforward computational approach for measuring nestedness using quantitative matrices. *Environ. Model. Softw.* **26**, 173–178 (2011).
44. S. J. Beckett, Improved community detection in weighted bipartite networks. *R. Soc. Open Sci.* **3**, 140536 (2016).
45. N. Blüthgen, F. Menzel, N. Blüthgen, Measuring specialization in species interaction networks. *BMC Ecol.* **6**, 9 (2006).
46. A. Chao, Nonparametric estimation of the number of classes in a population. *Scand. J. Stat.* **11**, 265–270 (1984).
47. J. Vazentin-Bugoni *et al.*, Influences of sampling effort on detected patterns and structuring processes of a Neotropical plant-hummingbird network. *J. Anim. Ecol.* **85**, 262–272 (2016).
48. B. Dalsgaard *et al.*, Opposed latitudinal patterns of network-derived and dietary specialization in avian plant-frugivore interaction systems. *Ecography* **40**, 1395–1401 (2017).
49. W. M. Patefield, Algorithm AS 159: An efficient method of generating random $R \times C$ tables with given row and column totals. *J. R. Stat. Soc. Ser. C Appl. Stat.* **30**, 91–97 (1981).
50. C. Dormann, J. Frund, N. Blüthgen, B. Gruber, Indices, graphs and null models: Analyzing bipartite ecological networks. *Open J. Ecol.* **2**, 7–24 (2009).
51. E. Burgos *et al.*, Why nestedness in mutualistic networks? *J. Theor. Biol.* **249**, 307–313 (2007).
52. M. Schleuning *et al.*, Ecological networks are more sensitive to plant than to animal extinction under climate change. *Nat. Commun.* **7**, 13965 (2016).
53. S. Lavorel *et al.*, Assessing functional diversity in the field—Methodology matters! *Funct. Ecol.* **22**, 134–147 (2008).
54. S. Villéger, N. W. Mason, D. Mouillot, New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* **89**, 2290–2301 (2008).
55. E. Liberté, P. Legendre, A distance-based framework for measuring functional diversity from multiple traits. *Ecology* **91**, 299–305 (2010).
56. C. N. Kaiser-Bunbury, N. Blüthgen, Integrating network ecology with applied conservation: A synthesis and guide to implementation. *Aob Plants* **7**, plv076 (2015).
57. M. E. Brooks *et al.*, glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R. J. J.* **9**, 378–400 (2017).
58. F. Hartig, L. Lohse, DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models (R package version 0.4.5, 2022). <https://CRAN.R-project.org/package=DHARMa>. Accessed 1 September 2022.
59. D. Bates, M. Mächler, B. Bolker, D. Walker, Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48 (2015).
60. R Core Team, *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, Vienna, Austria, 2023).