



Effects of urbanization on the trophic niche of the brown anole, a widespread invasive lizard

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ABSTRACT

Urbanization is one of the most dramatic forms of environmental change with the potential to alter trophic relationships among organisms in cities. In this study, we combine gut-content and stable isotope analyses of brown anole diets with field sampling of arthropods to assess whether and how urbanization-induced variation of basal resources influence trophic niche variation of anole populations inhabiting urban, suburban, and natural habitats. We found clear evidence for trophic niche variation across the urbanization gradient. Stable isotope analyses revealed that urban and suburban anoles had strongly elevated $\delta^{13}\text{C}$ levels and slightly lower $\delta^{15}\text{N}$ levels compared to anoles from natural forests— results consistent with increased reliance on grasses across the urbanization gradient. Isotopic niche widths were also greater in urban habitats. However, our analysis of anole diets revealed no difference in the diversity of prey consumed—despite urban habitats having the highest diversity of available prey compared to suburban and natural forest habitats. Overall, our results suggest that much of the observed variation in food web structure results from a shift in the diversity of basal resource pools across the urbanization gradient. The broader effects of a shift towards grass-dominated food webs in urban habitats remains to be understood.

1. Introduction

Urbanization is one of the most dramatic forms of environmental disturbance and can alter the trophic relationships among organisms that inhabit cities (Faeth et al., 2005). There are multiple routes through which urbanization can influence food web structure. Top-down processes have received considerable attention thus far and tend to emphasize the causes and effects of altered abundances of organisms at higher trophic levels (e.g., Marzluff et al., 2012; Fischer et al., 2012; Newsome et al., 2015; Demeny et al., 2019). Concurrently, our understanding of urbanization effects on soil biogeochemistry and plant communities has burgeoned (Pickett et al., 2008; Pouyat et al., 2007; Wheeler et al., 2017). More integrated perspectives on urban food webs that combine bottom-up and top-down insights are now emerging, providing important new understanding for how urban ecosystems function (e.g., Seress et al., 2018, 2020; Lerman et al., 2021).

An important way in which urbanization can alter urban ecosystems is through anthropogenic food subsidies. Human resources can directly enter food webs as food waste, untended pet food, and food provisioning for wildlife and feral animals. Given the reduced abundances of

invertebrates and vegetation cover in cities, anthropogenic food subsidies can be particularly important food resources in urban systems. This is an important reason why taxa that directly consume human food resources are extraordinarily abundant in urban areas (Rodewald et al., 2011; Fischer et al., 2012). Alternatively, supplemental irrigation and fertilizers can increase primary production, thus serving as an indirect nutritional pathway for subsidizing primary consumers in suburban and urban landscapes (Faeth et al., 2005). Relative to direct subsidies, these indirect pathways remain largely uncharacterized and their effects poorly understood.

Broad declines in the diversity and abundance of arthropods in urban environments can also influence the trophic ecology of species that depend on them. Arthropod declines in urban habitats can be attributed to fragmentation and thermal stress as well as the proliferation of non-native plants in urban habitats (Turner et al., 2005; Narango et al., 2017). Because non-native plants may be unsuitable food sources for native arthropods, these communities can result in trophic dead ends for primary consumers. While the loss of arthropod diversity is just starting to be investigated, alterations to basal resources and the corresponding loss of primary consumers is likely to have important consequences for

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the trophic niche of urban species. For example, habitat fragmentation has been shown to cause severe contraction of consumer trophic niches due to reduced diversity of primary producers (Layman et al., 2007; Araújo et al., 2014). Assuming that arthropod diversity declines with urbanization and that the trophic niche of anoles tracks prey availability, urbanization-induced reductions of arthropod diversity should be reflected by narrower trophic niche widths in urban populations. However, a variety of factors can influence the trophic niche of anoles (Chejanovski et al., 2017; Pringle et al., 2019; Ingram et al., 2022). Consumer selectivity, for example, can decouple the links between the diversity of available prey and trophic niche breadth—thus dampening the effects of underlying availability gradients on consumer resource use (Backwell et al., 1998; Cupples et al., 2011; Klecka and Boukal, 2012; Urban et al., 2020).

To investigate the potential for these bottom-up pathways to influence food web structure along a gradient of urbanization, we compared the trophic ecology of six populations of the brown anole lizard (*Anolis sagrei*) inhabiting forested, suburban, and urban habitats in South Florida. First, we determined whether anthropogenic food subsidies increase with urbanization. Elevated $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopes signatures reflect human foods (Jahren and Kraft, 2008) and can be used to track anthropogenic subsidies in the food web (Newsome et al., 2015; Penick

et al., 2015; Cove et al., 2018; Demeny et al., 2019; Nicholson and Cove, 2022). Given direct inputs of human-derived food waste are consumed by urbanization-tolerant arthropod prey (Penick et al., 2015), we predicted that urban populations of brown anoles will have higher concentrations of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopes in their tissues. In this case, elevated isotopic values would indicate that brown anoles consume prey that eat anthropogenically derived foods. Second, we explored whether anthropogenic reductions of prey diversity in urbanized ecosystems are reflected in the diet of the brown anole. Overall, we expected anole trophic niche width to track the diversity of available arthropod prey. And given the small home range size of individual brown anoles, and the scale at which urban biodiversity (i.e., vegetation and arthropod prey) may be altered, we predicted a contraction of trophic niche widths in urban and suburban populations relative to those from natural forests.

2. Methods

2.1. Study system

The brown anole is a small, semi-arboreal lizard found in urbanized and natural habitats across its non-native range in Florida (Kolbe et al., 2004; Lapiedra et al., 2017; Fig. 1A). This species utilizes a sit-and-wait

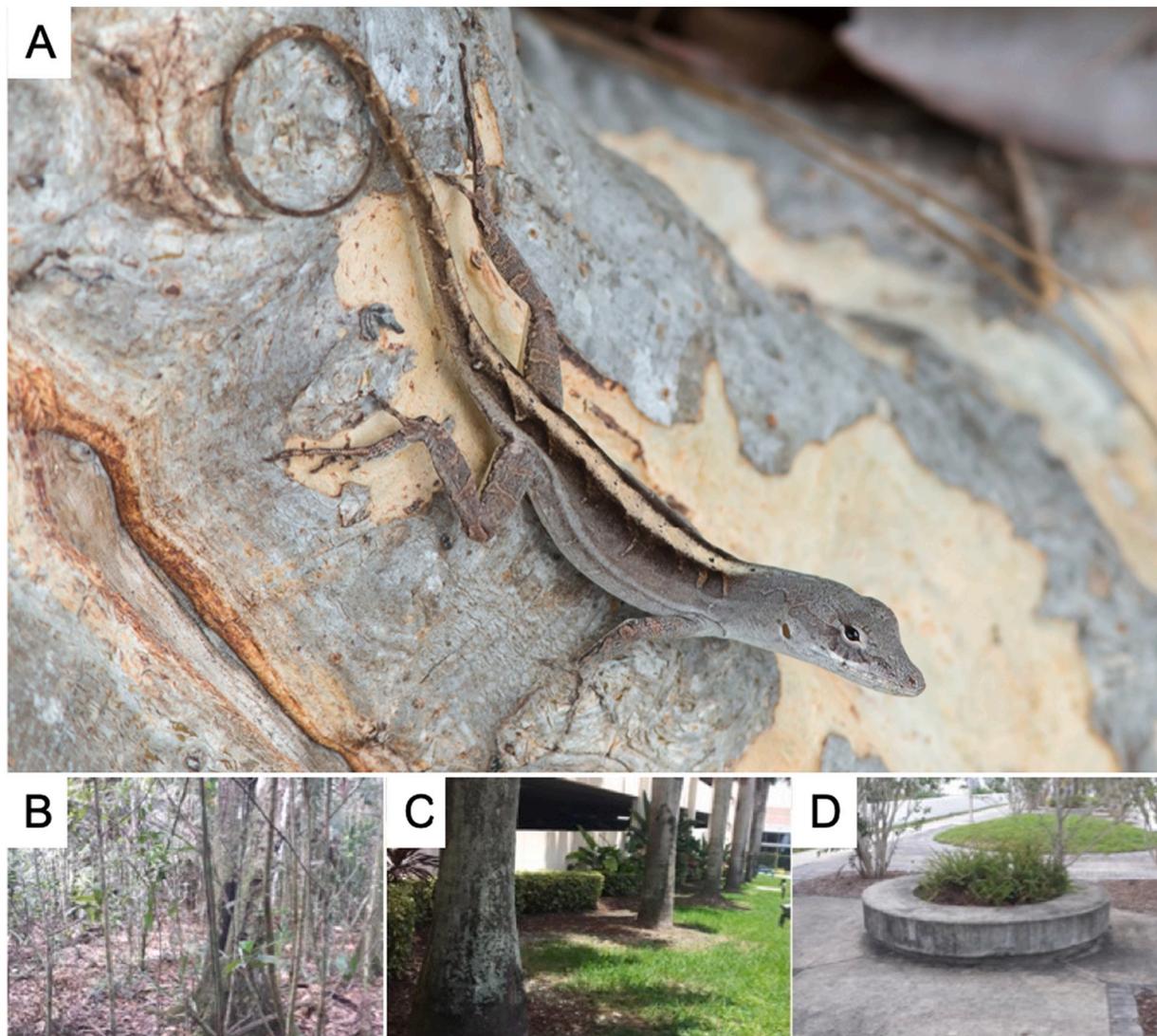


Fig. 1. Adult brown anole (*Anolis sagrei*) in typical survey posture at the base of a tree (A). Example of natural forest (B), suburban (C) and urban (D) habitats depicting major differences in coverage of impervious surfaces and grass. Anole photo credited to Jon Suh.

foraging strategy. Individuals scan for potential prey while perched on the lower portion of tree trunks (typically <2 m high) and often descend to the ground to capture prey detected by their movement (Chejanovski et al., 2017). Brown anoles are dietary generalists, but primarily consume insects, spiders, and other small arthropods (Schoener, 1968; Spiller et al., 2010; Giery et al., 2013; Kartzinel and Pringle, 2015; Stroud et al., 2017; Pringle et al., 2019; Giery and Stroud, 2019). Therefore, any anthropogenic subsidies will be routed through consumption of arthropod prey.

We compared the trophic ecology of six brown anole populations spanning a gradient of land use from heavily urbanized areas, to less urbanized suburban habitats, to natural forests in Broward County, Florida. These habitat types represent a gradient in human traffic and population density, being highest in urban habitats, which could provide the possibility of increased anthropogenic subsidies in these areas. Although we did not measure grass cover in our sites, grasses were present in our urban and suburban habitats and absent in natural forests (Fig. 1B–D). Urban habitats had high impervious surface cover and little canopy cover compared to natural forest. Forest habitats consisted of large patches of secondary forest with no impervious surface cover and relatively closed canopies (Kolbe et al., 2016; Battles and Kolbe, 2018). Suburban habitats were long stretches of continuous vegetation found along roadsides chosen to be intermediate between natural forests and urban habitats in terms of impervious surface cover and canopy cover (see Table S1 for coordinates, tree cover and non-vegetative cover for each site and Fig. S1 for a map of sites).

2.2. Nutritional subsidies

In each site, we collected tail-tips from 20 male lizards and 3–5 leaves from each of the dominant primary producers for stable isotope analysis. We averaged the $\delta^{15}\text{N}$ values of the dominant primary producers in a given site, calculated the mean, and subtracted this value from the $\delta^{15}\text{N}$ of each brown anole from that site to standardize our consumer $\delta^{15}\text{N}$ values. Additionally, variable lipid content has been shown to influence $\delta^{13}\text{C}$ values of consumers and thus we lipid-corrected our $\delta^{13}\text{C}$ data according to eq. 3 in Post et al. (2007). Finally, the change in stable isotope ratios from diet to tissue—the discrimination factor—can differ among taxa; however, this is likely to be similar in brown anoles from different habitat types and thus we do not use any discrimination factors in our analyses. We compared $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values among habitat types using Kruskal-Wallis Rank Sum Tests and Dunn's test for multiple comparisons with Bonferroni correction. Because grasses were not present at our natural forest sites, we used the $\delta^{13}\text{C}$ values of our urban and suburban primary producers to calculate the proportion of C_3 - and C_4 -based carbon contributing to the diet of brown anoles in each site through IsoError mixing models (Phillips and Gregg, 2003; Giery et al., 2013). All raw and corrected stable isotope values are listed in Table 1.

Table 1

Mean (SD) raw and corrected brown anole stable isotope values for each site. N^{15} values for consumers were corrected by pooling the N^{15} values of all primary producers within a given site, calculating the mean, and subtracting those values from that of the anoles in each site. C^{13} values were lipid-corrected according to eq. 3 in Post et al. (2007).

Study Site	Habitat Type	N^{15} Raw	N^{15} Corrected	C^{13} Raw	C^{13} Corrected
Fern Forest	Forest	5.49 (0.49)	5.49 (0.49)	-26.71 (0.78)	-24.99 (0.31)
Markham	Forest	6.32 (0.53)	6.14 (0.53)	-25.53 (1.33)	-24.07 (1.51)
Flamingo	Suburban	8.13 (0.34)	5.18 (0.34)	-20.30 (1.58)	-18.65 (2.16)
Oakland	Suburban	8.14 (0.47)	4.10 (0.47)	-21.67 (1.27)	-21.21 (1.05)
Las Olas	Urban	7.77 (0.67)	4.99 (0.69)	-21.49 (1.63)	-19.82 (4.06)
Library	Urban	5.82 (0.50)	5.67 (0.50)	-22.70 (1.54)	-21.75 (1.40)

2.3. Population niche width

To estimate diet diversity, we collected 20 male brown anoles from each site (the same males used for stable isotope analysis) which were transported to the lab at the University of Rhode Island. We euthanized and dissected each lizard, removing the entirety of the digestive tract (i. e., stomach and intestine) for gut-content analysis. Arthropod prey were identified to Order – a taxonomic resolution used in previous studies of brown anole diets (Schoener, 1968; Lister, 1976; Spiller et al., 2010; Giery et al., 2013; Kartzinel and Pringle, 2015; Stroud et al., 2017; Pringle et al., 2019; Giery and Stroud, 2019). In addition to prey abundance, we also calculated the proportion of each arthropod Order within the stomach of each lizard. Diversity of prey taxa was calculated using Simpson's Index of Diversity for prey found within the stomach of each lizard as well as prey taxa pooled for each site.

To characterize ground arthropod abundance and diversity, we deployed four pitfall traps in each site. These traps were deployed during the same season and location in which the lizards for gut-content analysis were captured. Each pitfall trap was placed at a random interval between 10 and 20 m along an established transect (transect length was no >100 m) and filled with a solution of water and a trace amount of soap to prevent arthropods from escaping. We collected pitfall traps after 24 h, preserved arthropods in isopropyl alcohol, and transported them to the lab for identification. All arthropods were identified to Order in keeping with our analysis of gut contents. We included absolute and proportional abundance, as well as taxonomic diversity as measurements of food availability, which were averaged for each site (for comparisons to prey consumption) and across habitat types (for comparisons among habitat types).

We tested for differences in the proportional availability and consumption of arthropods within each site using Welch's two-sample *t*-tests. Given that these data were not normally distributed, we compared the proportional availability, diversity, and consumption of arthropods among habitat types using Kruskal-Wallis Rank Sum followed by pairwise Dunn's tests with Bonferroni correction. Hymenoptera and Coleoptera constituted the numerical majority of items in gut contents (>50% across sites; >80% across habitats) and these groups were frequently found in our pitfall traps as well. However, we suspect that Dipterans may have been attracted to the liquid in our pitfall traps and were likely oversampled. Also, our pitfall traps might have poorly sampled spiders given that many of these taxa are arboreal. Therefore, we did not compare Dipteran and spider availability to consumption, but rather only compared availability (except spiders) and consumption of these taxa among habitat types. However, all taxa were included in calculations of diversity.

Isotopic niches were generated using the SIBER package (Jackson et al., 2011) available in R. We used the “standard.ellipse” function that employs maximum-likelihood estimators to produce ellipses that encompass approximately 40% of the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ bi-plot data within each site, thereby reducing the impact of outliers. This function provides calculations of the area of each ellipse (corrected for small sample size)

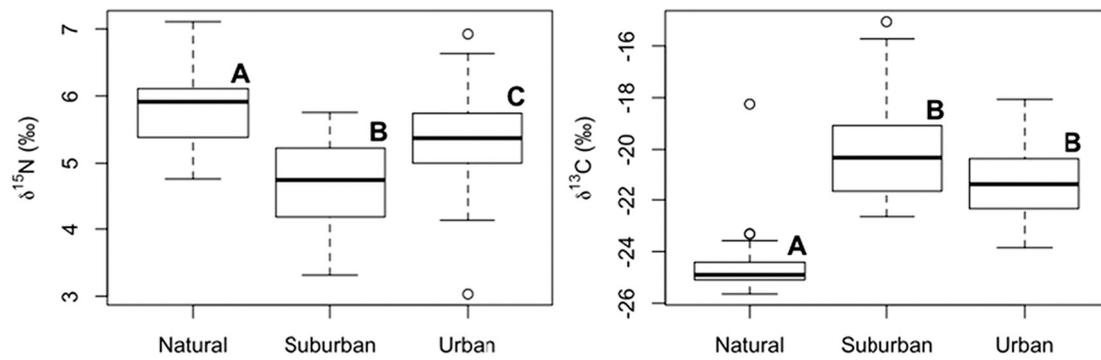


Fig. 2. Differences in δN^{15} and δC^{13} for brown anoles inhabiting natural forest, suburban and urban habitats. Brown anole δN^{15} values were standardized by subtracting mean δN^{15} values of primary producers from that of brown anoles for each site. δC^{13} values were lipid-corrected according to eq. 3 in Post et al. (2007). Letters denote significant differences among habitat types as indicated from Dunn's test for multiple comparisons with Bonferroni correction.

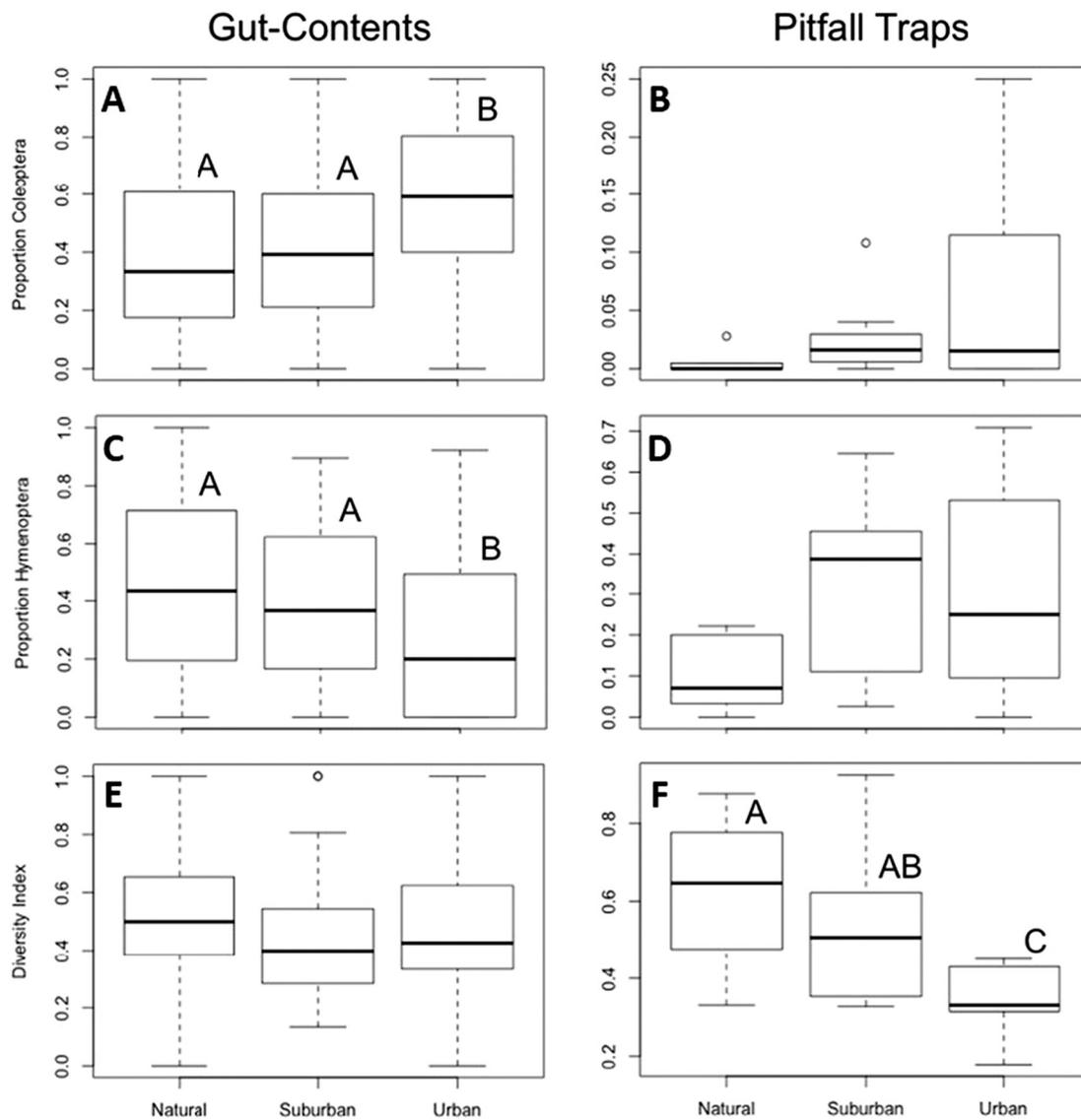


Fig. 3. Proportional consumption (left) and availability (right) of Coleopteran (A–B) and Hymenopteran (C–D) prey among natural forest, suburban, and urban habitats. Also shown are Simpson's Index of Diversity calculated from brown anole gut-contents (E) and pitfall traps (F) for the three habitats. Letters denote significant differences among habitat types as indicated from Dunn's test for multiple comparisons with Bonferroni correction. Note, lower values of Simpson's Index of Diversity indicate higher species richness.

as a measure of isotopic niche width, which we compared among sites and habitat types.

3. Results

3.1. Nutritional subsidies

We observed small, but significant differences in the mean values for all pairwise comparisons among the three habitat types for $\delta^{15}\text{N}$ of anoles ($X^2 = 42.73$, $df = 2$, $p < 0.05$ for all comparisons using Dunn's test). $\delta^{15}\text{N}$ values among habitat types indicated that natural forest anoles occupy higher trophic levels, followed by urban, and then suburban brown anoles (Fig. 2). $\delta^{13}\text{C}$ values were also significantly different among habitat types ($X^2 = 74.64$, $df = 2$, $p < 0.05$), except between urban and suburban habitats ($p = 0.09$), which both had higher $\delta^{13}\text{C}$ values compared to natural forest anoles (Fig. 2). Additionally, IsoError mixing models showed a substantial contribution of grass-based carbon to the diet of both suburban and urban anoles (61% and 49%, respectively).

3.2. Population niche width

On average, isotopic niche widths were widest in urban habitats (mean standard ellipse area = 2.42, $SD = 0.45$), intermediate in suburban habitats (mean standard ellipse area = 1.99, $SD = 0.57$) and narrowest in natural forest (mean standard ellipse area = 1.45, $SD = 1.34$) habitats (also see Fig. S2 in Supplementary Materials). In contrast, we found no differences in the mean prey diversity consumed by individual lizards among habitat types ($X^2 = 4.24$, $df = 2$, $p = 0.12$; Fig. 3C), as well as no difference in diversity when consumed taxa were pooled by site ($X^2 = 0.29$, $df = 2$, $p = 0.87$). However, urban habitats had higher arthropod diversity available compared to natural forest and suburban habitats ($X^2 = 8.32$, $df = 2$, $p = 0.02$), but natural forest and suburban habitats did not differ in diversity (Fig. 3F).

Coleopterans were consumed by brown anoles in greater proportions than were available in all sites ($p < 0.001$ for all comparisons using Welch's two-sample t -test). Hymenopterans were consumed in greater proportions than were available only in natural forest sites (Fern Forest: $t = 4.11$, $df = 8.13$, $p = 0.003$; Markham: $t = 4.53$, $df = 20.89$, $p = 0.0002$), but urban and suburban brown anoles consumed them in proportion to their availability. Urban lizards consumed proportionately more Coleopterans when compared to natural forest and suburban lizards (Dunn's test for multiple comparisons; $X^2 = 10.90$, $df = 2$, $p < 0.01$), which did not differ from each other (Fig. 3A). Urban brown anoles also consumed proportionately fewer Hymenopterans compared to anoles from natural forest habitats ($X^2 = 6.62$, $df = 2$, $p = 0.02$; Fig. 3B). Dipterans were consumed in similar proportions across habitat types ($X^2 = 3.18$, $df = 2$, $p = 0.20$). Spiders were consumed in larger proportions by brown anoles in natural forest (mean = 0.08, $SD = 0.18$) compared to those from urban habitats (mean = 0.01, $SD = 0.03$; $X^2 = 5.07$, $df = 2$, $p = 0.046$), but suburban anoles (mean = 0.05, $SD = 0.11$) were similar to those from both urban and natural forest habitats. The proportional availability of Coleopteran, Hymenopteran and Dipteran taxa did not differ among habitat types ($X^2 = 2.40$, $df = 2$, $p = 0.30$; $X^2 = 3.01$, $df = 2$, $p = 0.22$; $X^2 = 4.05$, $df = 2$, $p = 0.13$, respectively; Fig. 3D–E, Dipteran data not shown due to low proportional values). All numerical values of arthropod consumption and availability are also reported in Table S2 in supplementary materials.

4. Discussion

We compared the trophic ecology of six brown anole populations to examine how food web structure varies along a gradient of urbanization. Our analysis revealed substantial variation in food web structure among habitats. However, our findings did not match our expectations. Specifically, we found little evidence that anthropogenic food subsidies

supported anoles in urban food webs. Further, a tendency for trophic niche widths to increase (isotopic niche width) or remain similar (dietary niche width) across the urbanization gradient was contrary to our overall expectation of narrow trophic niches in urban habitats. Below we discuss these results in greater detail and elaborate on our primary finding—that variation in food web structure is largely described by a shift towards grass-based food webs with increasing urbanization.

Our overall expectation that utilization of anthropogenic resource subsidies would be high in urban areas was not supported. Human food should contain elevated concentrations of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotopes. Thus, if anoles were consuming substantial numbers of arthropods that fed on human foods, we would expect higher concentrations of both isotopes. But $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ levels were not substantially elevated in urban lizards—suggesting that anthropogenic food subsidies are not a major part of the anole resource base. Instead, significant variation among habitats in stable isotopes appeared to arise from variation in food chain length ($\delta^{15}\text{N}$) and the composition of the plant community ($\delta^{13}\text{C}$).

Using $\delta^{15}\text{N}$ (corrected for basal resource signature) as a measure of trophic position, we found that $\delta^{15}\text{N}$ was depleted (lower $\delta^{15}\text{N}$ values) in urban and suburban lizards compared to forested sites (Fig. 2). While this variation could result from a number of factors, we suspect that brown anoles occupy lower trophic levels in urban and suburban habitats. This is supported by our gut content data showing lower frequency of predators, specifically spiders, in the diet of brown anoles from urban and suburban habitats (1 and 5%, respectively) compared to those inhabiting natural forest habitats (8%). The response of spiders to urbanization can be mixed. However, most studies indicate that body size, fecundity, and abundance of spiders decreases with urbanization (Miyashita et al., 1998; Dahirel et al., 2019). Thus, it seems likely that higher rates of spider consumption could generate the slight increase in trophic position in natural forest habitats.

The major source of inter-habitat variation in our isotope dataset appears to be in $\delta^{13}\text{C}$, with clear and significant increases in $\delta^{13}\text{C}$ observed in suburban and urban habitats (Fig. 2). This finding is consistent with a shift in the identity of the basal resource pool across the urbanization gradient. IsoError mixing model estimates show that approximately half or more of the carbon in suburban and urban brown anoles is grass-derived, whereas none of the carbon in forest brown anoles comes from C_4 grasses because this habitat type lacks grasses. Given that most of the C_4 grass cover in urbanized South Florida consists of St. Augustine grass, *Stenotaphrum secundatum*, it appears that a single species supports a majority of brown anole food resources. This fraction is larger than, but similar in magnitude to, an earlier finding of 22–33% grass-based (again, largely St. Augustine grass) carbon for an anole community inhabiting a park-like habitat nearby in North Miami, Florida (Giery et al., 2013). In the latter case, a series of insect pests of St. Augustine grass such as southern chinch bug, *Blissus insularis*, and tropical sod webworm, *Herpetogramma phaeopteralis*, formed a key trophic linkage between St. Augustine grass and anoles. We suspect that a similar set of lawn and turf pests form the same trophic linkages in the suburban and urban habitats studied here. Thus, it appears that food webs at the upper end of the urbanization gradient are supported by a strong trophic linkage with a narrow resource pool—lawns. Turfgrass monocultures (e.g., lawns and golf courses) are widespread and expanding in the United States (Robbins and Birkenholtz, 2003), thus the potential for strong trophic interactions in these novel food webs warrants further investigation.

Our hypothesis that urban anoles would have narrower trophic niches was also not supported. In fact, the isotopic niche of urban anoles was wider compared to those inhabiting natural forest or suburban habitats (see Results and Supplementary Materials). Further, prey diversity of gut contents did not differ between habitats despite the increase in the diversity of arthropods in our pitfall traps with increasing urbanization (Fig. 3E, F). One explanation for this unexpected pattern is that while alpha diversity tends to be lower in urban areas, beta diversity can be greater (e.g., Aronson et al., 2015). This inverse relationship

between alpha and beta diversity is well known for forested ecosystems and may describe variation along urbanization gradients as well. Here, we suspect that species-poor communities coupled with increasing resource patchiness may underpin the increase in intra-population isotopic niche variation along the urbanization gradient. We speculate that the small territories and high site fidelity of male brown anoles (Losos, 2009) would reveal this increased beta diversity in urban areas, even if it expresses at fine spatial scales. Further, a variety of factors influence the dietary niches of individual anoles (e.g., Ingram et al., 2022). Uncovering what factors can decouple linkages between resource use and availability needs additional study. However, our prey selectivity results suggest that anoles are not consuming prey taxa in proportion to their availability (Fig. 3). We speculate that these taxonomic biases in prey consumption dampened the influence of prey availability and could explain why the dietary niche breadth of brown anoles does not vary with urbanization.

Although our study failed to detect a significant contribution of anthropogenic food subsidies to urban anoles, two caveats are worth brief discussion. First, detection of human-derived food subsidies using $\delta^{13}\text{C}$ is confounded by the fact that urbanization in South Florida covaries with coverage by St. Augustine grass—a C_4 plant native to Florida. This confound arises because corn, a major component of human foods that gives it a distinctly elevated $\delta^{13}\text{C}$ signature, is also a C_4 plant with a similar $\delta^{13}\text{C}$ signature to St. Augustine grass (Jahren and Kraft, 2008). Without better accounting of the relative contribution of natural C_4 plant inputs, from St. Augustine grass for instance, $\delta^{13}\text{C}$ will remain of limited use in this context. Second, lawns and turfgrass are a dominant and highly productive landcover in urbanized landscapes (Falk, 1976, 1980; Milesi et al., 2005). As our results show, these highly managed habitats support urban food webs—presumably due to high productivity and robust arthropod pest populations. Some of this productivity is derived from massive and direct inputs of water, nitrogen, and phosphorus often with the intention of increasing or maintaining lawn productivity (Law et al., 2004; Milesi et al., 2005; Fissore et al., 2012). These inputs represent indirect subsidies—routed to consumers through increased primary productivity. We suspect that irrigation and fertilization have substantial effects on urban food web structure. But without additional information on the magnitude of these indirect subsidies, we cannot parse their effects on urban food webs. Nevertheless, it is likely that urban food webs are particularly sensitive to anthropogenic management regimes that alter the productivity and cover of grasses, and we suggest that indirect subsidies such as water and fertilizers make large contributions to urban food web structure.

5. Conclusion

Studies that utilize urban to rural gradients are often constrained by the limited number of species that occur across the entire gradient (McKinney and Lockwood, 1999). Even the use of closely related species along such gradients is likely to introduce variation that obscures habitat-specific patterns. However, when a single species can be found in both urbanized and natural habitats, this enables a more robust assessment of how the trophic niche of that species, and food web structure in general, varies in response to urbanization. The area of urban land cover is projected to triple by 2030 (Seto et al., 2012), and thus over time our results are likely apply to an increasing number of insectivorous and herbivorous taxa inhabiting or foraging in urban areas. It is therefore important that future work considers the consequences of such alterations in basal resources for urban taxa and the food webs they comprise.

Statement of authorship

All authors contributed to generation and writing of the manuscript.

Declaration of interest

We have no conflicts of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.fooweb.2022.e00257>.

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