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Resource niche partitioning and overlap among native and non-native lizards in an urban environment

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Abstract

Non-native species must overcome a number of abiotic and biotic filters to successfully establish and spread into novel ecosystems. Their establishment and spread depend on the ability to acquire resources while avoiding or outcompeting native species. The Mediterranean House Gecko (*Hemidactylus turcicus* Linnaeus, 1758) has been widely introduced into urban areas across tropical and temperate regions, yet studies documenting their resource use relative to native lizard species are still lacking. We examined patterns of resource use between *Hemidactylus turcicus* and a recipient lizard assemblage comprised of Green Anole (*Anolis carolinensis* Voigt, 1832), Little Brown Skink (*Scincella lateralis* Say, 1823), and Five-lined Skink (*Plestiodon fasciatus* Linnaeus, 1758) in an urban ecosystem of eastern Texas. We used functional traits to investigate resource partitioning between *Hemidactylus turcicus* and native lizards regarding habitat, diet, and isotopic niche dimensions. Differences in resource use between *Hemidactylus turcicus* and native lizards were observed, as they utilized a greater array of arboreal perch types at lower temperatures, had generalist diet, and occupied a broader isotopic niche space compared to the native lizards. Overall, *Hemidactylus turcicus* appears a functionally unique species capable of exploiting novel resources along multiple niche axes possibly facilitating their establishment and spread into urban ecosystems.

Key words: Five-lined Skink *Plestiodon fasciatus* (Linnaeus, 1758), functional traits, Green Anole *Anolis carolinensis* (Voigt, 1832), Little Brown Skink *Scincella lateralis* (Say, 1823), Mediterranean House Gecko *Hemidactylus turcicus* (Linnaeus, 1758), emptyche hypothesis

1. Introduction

The introduction of non-native species into novel ecosystems (i.e., outside the natural range of an introduced species) is considered one of the greatest threats to global biodiversity (Elton 1958; Early et al. 2016; Fitzgerald et al. 2016). Establishment of invasive species can result in novel interspecific interactions as well as alter resource availability, that in turn, can reorganize ecological communities due to shifts in resource gradients (Gidoin et al. 2015). Outcomes of invasion may result in co-occurrence between invasive species and resident species, competitive displacement of resident species, or the exclusion of resident species (Reitz and Trumble 2002). As increasing globalization continues to facilitate the spread of invasive species, investigating patterns of species co-occurrence in the context of invasion ecology is a useful framework to understand the potential mechanisms underlying successful invasions and their ecological impacts (Ricciardi et al. 2013).

Non-native species must overcome multiple biotic and abiotic factors to enable them to become establish within a given recipient community (Moyle and Light 1996; Malcicka et al. 2015). Even when the abiotic environment is tolerable for a non-native species, its persistence within a recipient community is greatly influenced by the ability to minimize or avoid antagonistic interactions, such as predation, and to acquire adequate resources for survival, reproduction, and growth. Ecological niche complementarity (i.e., co-occurring species use different forms of a resource; Elton 1958; Levine and HilleRisLambers 2009) is an important mechanism that may increase invasion success and promote co-occurrence in new environments (Byers and Noonburg 2003). Species differences (e.g., traits or resource demands) that allow invaders to either exploit unused resources (i.e., empty niche hypothesis), or be more competitive in exploiting shared, limited resources (i.e., niche replacement hypothesis) underlie invasion success, and potential impact recipient species (Ricciardi et al. 2013). The invasion success of the Tropical House Gecko (*Hemidactylus mabouia* Moreau de Jonnes, 1818) in a Brazilian coastal environment was attributed to its plasticity to use different types of substrates and forest heights (i.e., spatial niche), consequently influencing its daily activity (i.e., behavioral niche) and prey consumption (i.e., trophic niche) compared to the native lizard assemblage (Winck et al. 2017). Behavioral plasticity in activity patterns and habitat use enables invaders to track and exploit the diversity of food resources available within each environment, leading to greater niche breath (i.e., generalist) (Figueira et al. 2023). In a study of resource use of a non-native lizard assemblage, Carranza (2022) found differences in foraging behavior, habitat use, and diet among all three species. These divergent patterns of behavior and resource use were mechanisms permitting co-occurrence of the three lizard species in the recipient ecosystem.

The processes that drive the outcomes of invasion success can be complex, particularly in urban ecosystems (Parris 2016). Propagule pressure may be intensified in urban ecosystems due to accidental or intentional releases, but the occurrence of strong filters (e.g., elevated ambient temperatures, increased traffic volume) can present hardships or opportunities to establishment (Padayachee et al. 2017; Cassey et al. 2018). In urban environments, habitat complexity can range from homogenous to highly complex, with anthropogenic activities (e.g., mowing, construction) influencing the spatial arrangement of these habitat gradients (Byrne 2007; Ossola et al. 2015). In turn, species may exhibit adaptive responses to exploit this patchwork of available habitats (Ossola et al. 2015). Although empirical research suggests that urban ecosystems are beneficial environments to establishment of non-native species, it is not widely understood how non-native species are able to establish and expand in urban habitats that contain native species that are functionally or ecologically similar (Cadotte et al. 2017).

The Mediterranean House Gecko (*Hemidactylus turcicus* Linnaeus, 1758), a gekkonid lizard native to southern Europe and Northern Africa, has been introduced into many tropical and temperate environments worldwide (Kloepfer et al. 2006; Weterings and Vetter 2018). Originally introduced into Key West, Florida, over a century ago, *H. turcicus* has expanded in range across the southeastern United States, though its establishment has largely been confined to more urban ecosystems (Stejneger 1922; Meshaka et al. 2006). Within these novel environments, *H. turcicus* typically occurs in the immediate vicinity of humans and anthropogenic structures, utilizing the vertical surfaces of buildings (Punzo 2001; Gomez-Zlatar et al. 2006). Previous studies focusing on aspects of autecology (e.g., diet, habitat use, and behavior) suggest that *H. turcicus* is a highly adaptable non-native species capable of persisting in dense populations (Klawinski et al. 1994; Saenz 1996; Gomez-Zlatar et al. 2006; Williams and McBrayer 2009; Warren 2018). Despite this apparent adaptivity and supposed restriction to urban ecosystems, the potential effects of *H. turcicus* on native lizard assemblages is not well understood (Wessels et al. 2018). Given that populations of *H. turcicus* are expected to expand with increasing urbanization and shifting climates, defining the ecological niche of this widely established species can benefit our understanding of how *H. turcicus* might affect the organization of native species assemblages in urbanized landscapes (Weterings and Vetter 2018).

Variation in morphological traits related to body size and locomotion is known to play an important role in trophic ecology of vertebrates. In lizards, for example, limb lengths have been associated with feeding tactics and modes (Vitt 1983). The Tropical House Gecko (*Hemidactylus mabouia*) is one of the most successful invasive lizards across tropical urban environments (Agarwal et al. 2021) and its success has been attributed to its morphological advantages associated with larger sizes in feeding traits and limb proportions which allows exploitation of different heights of vertical urban surfaces (Lamb et al. 2021). Across its non-native range in the southern United States, *H. turcicus* populations vary in traits related to sexual selection and resource defense (Granatosky and Krysko 2014). Morphological traits of species may influence multidimensional niche dynamics, therefore, trait-based studies that reflect species' interactions with the biotic and abiotic environment can be informative to the study of biological invasions (McGill et al. 2006; Schalk et al. 2018; Shepta et al. 2023). Organismal functional trait approaches have become a widely used tool by ecologists to demonstrate the functional properties of successful invaders and the assembly of novel communities in the wake of non-native introductions (Cadotte et al. 2015; Schalk et al. 2018; Shepta et al. 2023).

In this study, we investigated the resource use of *H. turcicus* along multiple resource axes in a lizard assemblage comprised of three native species. The study was conducted in an urban setting in east Texas, USA. Specifically, we explored the partitioning of temporal, habitat, diet, and isotopic niches between *H. turcicus* and the native lizard species: Green Anole (*Anolis carolinensis* Voigt, 1832), Little Brown Skink (*Scincella lateralis* Say, 1823), and Five-lined Skink (*Plestiodon fasciatus* Linnaeus, 1758), in the context of their functional traits. Given its success establishing in urban environments, we hypothesized that the invader would have a more generalized diet (i.e., broader niche breath) resulting from exploitation of more urban microhabitats compared to the native lizard species. Likewise, a broader isotopic niche was expected in the invader which would track the diversity of available food items (e.g., arthropods) across surveyed microhabitats. Differences in morphological traits associated with habitat use and prey capture could help to explain establishment advantages of the invader over the native lizards in these urban environments. Finally, given their differences in activity period (nocturnal invader (*H. turcicus*) vs. native, diurnal species), we hypothesized low overlap in resource use, with *Hemidactylus turcicus* exploiting unused resources (i.e., filling an empty niche) compared to the diurnal, native lizard species.

2. Materials and methods

2.1. Lizard surveys

To examine lizard temporal niche partitioning on a daily time scale, visual encounter surveys were conducted from 22 May 2019 to 10 July 2019 at Stephen F. Austin State University's (SFASU's) campus in Nacogdoches, Texas, USA (31°37′29.397″N, 94°38′47.899″W). Surveys consisted of 1–2 observers actively searching for lizards (both adults and juveniles) that coincided with periods of high lizard activity (i.e., typically 1000 h for diurnal surveys and 2100 h for nocturnal surveys). Each survey (diurnal, $n = 11$; nocturnal, $n = 11$; 22 total) lasted between 2 and 3 h and was conducted within 11 h of one another and within the same vicinity. The total area surveyed included approximately 1 km^2 of the SFASU campus, and two primary habitat types (SFASU gardens and campus buildings or structures) were surveyed during both day

Table 1. Functional morphological traits associated with lizard feeding ecology and habitat use measured on each specimen.

Functional trait	Trait code	Definition of trait
Snout-vent length	SVL	Maximum distance from tip of the snout to behind the vent
Total length	TL	Maximum distance from tip of snout to the tip of tail
Jaw length	JL	Maximum distance from tip of snout to the posterior margin of the jaw
Head depth	HD	Vertical distance measured through the eye
Eye diameter	ED	Horizontal distance from eye margin to eye margin
Forelimb length	FL	Maximum distance of the ulna/radius to the tip of the third digit on the hand
Thigh length	TH	Maximum distance of femur while leg is held in a Z pattern at a perpendicular angle to vertebral column
Shank length	SL	Maximum distance of tibia/fibula while leg is held in a Z pattern
Tarsus-and-foot length	TFL	Maximum distance from beginning of tarsus to the tip of the third digit on the foot while leg is held on a Z pattern
Body depth	BD	Maximum distance from the lumbar vertebrae to the ventral abdomen
Stomach length	SL	Maximum distance from the esophagus to the pyloric sphincter

Note: Body mass was also measured in addition to the linear morphological traits below.

and night. The SFASU gardens (~0.5 km^2 surveyed) contained the arboretum area, which comprised a mixed hardwood forest with sparse anthropogenic structures (buildings, gazebos, bridges, etc.). The second habitat type was represented by multiple structures containing dormitories, academic buildings, among others, and were located across SFASU campus (~0.5 km^2 surveyed). This second site also contained ornamental shrubs and trees planted throughout the campus. During both diurnal and nocturnal surveys, ground cover and debris (e.g., rocks, fallen logs or wooden boards, leaf litter, etc.) were searched or turned over when encountered along the survey route. Lizards were captured by hand or using a fishing-line lasso attached to a pole. During the 22 visual encounter surveys, we captured a total of 166 lizards (*H. turcicus* ($N = 92$), *A. carolinensis* ($N = 34$), *P. fasciatus* ($N = 9$), *S. lateralis* ($N = 31$)).

2.2. Functional traits

We measured 10 continuous morphological traits associated with lizard habitat use and trophic ecology using digital calipers (precision = 0.01 mm; Table 1; Granatosky and Krysko 2014; Leavitt and Schalk 2018). Mass (g) was measured using a digital scale (Gemini-20 Portable Milligram Scale; precision = 0.001 g). As we were interested in quantifying patterns of interspecific niche partitioning, for each species, we pooled all individuals (e.g., adults/juveniles, males/females) together in our analyses of their functional traits and resource use. Captures of juveniles were uncommon for every species we sampled. Range and average snout-to-vent length (SVL) measurements for the species (*A. carolinensis*, minimum = 47 mm, maximum = 69, mean = 58.7 mm; *H. turcicus*, minimum = 29 mm, maximum = 59 mm, mean = 46.7 mm; *P. fasciatus* minimum = 26 mm, maximum = 72 mm, mean = 48.3 mm; *S. lateralis*, minimum = 18 mm, maximum = 49 mm, mean = 43.9 mm) were consistent with reported SVL in the literature (Hibbitts and Hibbitts 2015). Prior to analysis, raw measurements of trait values were natural log-transformed and adjusted for the effects of body size by calculating residuals for each trait with linear regression of trait values against SVL (Schalk et al. 2015). Functional trait space of species was described using Principal Components Analysis (PCA). Species loadings on the first two principal components (PCA 1 and 2) were used for interpretation of species distribution in morphospace as they accounted for greater than 50% of the overall variance explained (sensu Montaña and Winemiller 2010). To test for differences between *H. turcicus* and native lizard functional traits, we used PERMANOVA with 9999 unrestricted permutations of the species scores (i.e., Euclidean distance dissimilarity) obtained from PCA (Anderson 2006; Schalk et al. 2018). All data transformations and statistical analyses of functional traits and microhabitat use (see below) were performed using the statistical software Paleontological Statistics (PAST) version 4.0 (Hammer et al. 2001).

2.3. Microhabitat use

Microhabitat use of lizards was determined by measuring five microhabitat variables at the initial location of individual observations including: ambient temperature (°C) and percent relative humidity using a Kestrel 5500 Weather Meter (Nielsen-Kellerman Company, Boothwyn (ambient temperature accuracy: ±0.5 °C, humidity accuracy ±2%), perch temperature (°C) with an Extech 42512 Dual Laser Infrared Thermometer (Transcat, Rochester, accuracy ±1 °C) perch height (cm) with a metric ruler, and perch type. Perch type was subcategorized across five different substrate types: (0) bare soil, (1) glass, (2) metal, (3) painted concrete, (4) unpainted processed wood, leaves, and smooth bark trees (e.g., Crepe Myrtle *Lagerstroemia indica*, Linnaeus), and (5) thick bark trees (e.g., southern red oak *Quercus falcata* Michx and mockernut hickory *Carya tomentosa* Nutt), and (6) unpainted or weathered concrete (Winchell et al. 2018). We described variation in microhabitat use among species by performing a nonmetric multidimensional scaling (NMDS) analysis using the presence or absence of species according to the measured microhabitat variables. The NMDS constructs two-dimensional ordination in the manner that best represents the relationships among samples and a similarity matrix (Field et al. 1982). We used

PERMANOVA with 9999 unrestricted permutations to test for differences between *H. turcicus* and native lizard microhabitats based on the NMDS scores.

2.4. Dietary analysis

Collected lizards were placed in a cooler to slow metabolism and prevent digestion of stomach contents before they could be processed in the lab (van Marken Lichtenbelt 1992). Due to the potential for inhaled or injectable chemical euthanasia agents to affect the isotopic signature of their tissues, lizards were euthanized via physical methods in the lab (blunt force trauma to the head; Underwood et al. 2020). Animals were then stored in a freezer and thawed before processing. Specimens were fixed in 10% formalin and stored in 70% ethanol. We then dissected the stomach contents of lizards and measured stomach length using a metric ruler (mm). Stomachs were stored in a solution of 70% ethanol until dissection. Using a dissecting microscope, we removed stomach contents and all invertebrate prey were identified to the lowest taxonomic level possible (i.e., order). Prey items were dried/blotted with Kimwipes to remove as much alcohol as possible and the wet mass of each prey item was weighed using a digital scale (Gemini-20 Portable Milligram Scale, Cumming, precision: 0.001 g). Animals were collected with a state Scientific Research Permit No. SPR-0519-087, and specimens were handled and preserved following the guidelines of the Institutional Animal Care and Use Committee #2019-005 approved by SFASU.

For dietary analysis, we aggregated prey items into 19 taxonomic orders to calculate the frequency of occurrence (FO) and relative occurrence (RO) of dietary contents (Hutton et al. 2018). FO was calculated as the percentage of lizard specimens that consumed a specific prey type: FO = $(S^{*}100)/N$, where S is the number of stomachs with that prey type and N represents the total number of stomachs examined. RO was calculated as the percentage of each prey type's occurrence relative to the prey items using the formula: RO = $(P^{*}100)/T$, where P is the total number of occurrences for that prey type and T is the total number of prey items found within the stomach (Hutton et al. 2018). Diet diversity was estimated using the Levin's (1968) index of niche breadth (also called niche width or niche size $[\mathrm{B}' = \left(\sum_{i=1}^{n} Pi2\right)^{-1}]$, where B' is niche breadth, Pi is the volumetric proportion of food item i in the diet, and n is the total number of food items in the diet. Values closer to 1 represent a wide (generalist) niche breath (Montaña and Winemiller 2009):

Diet similarities were calculated using Pianka's (1973) symmetrical measure of niche overlap $(\theta jk = \left(\sum_{i=1}^{n} Pij * Pik\right) / \left(\sum_{i=1}^{n} Pij2 * Pik2\right)^{1/2})$, where θ_{jk} is symmetrical niche overlap between species j and k, P_{ij} is the proportion of the resource i used by species j, and P_{ik} is the proportion of resource i used by species k, and n is the total number of resource categories. Proportion of resource was based on mass of the prey item. In this index, values range from 0 (no overlap) to 1 (complete overlap). A threshold of 0.60 was used to determine significant overlap (Wallace 1991).

2.5. Stable isotope analysis

Prior to their fixation in formalin, we removed the tails of lizard specimens for stable isotope analysis of carbon ($\delta^{13}\mathrm{C}/\delta^{12}\mathrm{C}$) and nitrogen ($^{15}\mathrm{N}/^{14}\mathrm{N}$). The heavy to light ratios carbon (denoted as $\delta^{13}\mathrm{C}$) allows definition of the basal production pathways supporting consumers biomass (e.g., C3 vs. C4 photosynthetic pathways; Peterson and Fry 1987) and can be a useful proxy to help define habitat use variation and movement ability among organisms (Layman et al. 2012; McCauley et al. 2012). The heavy to light ratios of nitrogen (denoted as $\delta^{15}\mathrm{N}$) are used as a proxy to estimate an organism's trophic position within a food web (Post 2002). Tail samples were rinsed with distilled water to avoid contamination and then dried in a drying oven at 60 °C for 48 h (Arrington and Winemiller 2002). Once dried, samples were ground to a fine powder using a mortar and pestle and stored in clean glass vials. Subsamples of each ground sample were then weighed (1–2 mg) and packaged into Ultra-Pure tin capsules (Costech Analytical, Valencia). Samples were sent to the Stable Isotope Ecology Laboratory at the University of Georgia for analysis of stable isotope ratios of carbon ($^{13}\mathrm{C}/^{12}\mathrm{C}$) and nitrogen ($^{15}\mathrm{N}/^{14}\mathrm{N}$). Isotopic ratios are reported in parts per thousand (‰) relative to standards in delta (δ) notation, as expressed according to the equation: $\delta\mathrm{X} = ((\mathrm{R}_{\text{sample}}/\mathrm{R}_{\text{standard}}) - 1) \times 10^{3}$, where $\mathrm{R} = {}^{13}\mathrm{C}/{}^{12}\mathrm{C}$ or $^{15}\mathrm{N}/^{14}\mathrm{N}$.

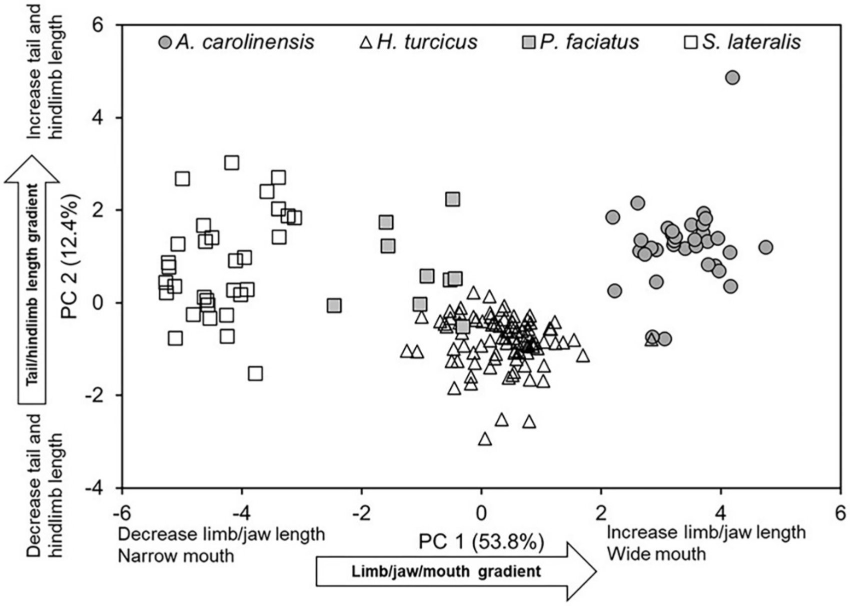
Biplots of $\delta^{13}\mathrm{C}$ and $\delta^{15}\mathrm{N}$ values of lizards were used to depict the isotopic structure of *H. turcicus* in relation to native lizard species, in which $\delta^{13}\mathrm{C}$ ratios reflect how materials from various carbon production sources are assimilated into consumer tissue, while $\delta^{15}\mathrm{N}$ ratios help to explain the vertical trophic position of consumers (Peterson and Fry 1987). We estimated isotopic niches of lizard species using standard ellipses areas (SEAs) based on Bayesian inference (Jackson et al. 2011). Similar to bootstrapping techniques, this approach generates a posterior SEA distribution that accounts for uncertainty within the sampling process that may influence ellipse size, shape, and location in isotopic space. Given the disparity of sample sizes across species within the assemblage, we corrected for sample size following Jackson et al. (2011) to estimate corrected standard ellipse area ($\mathrm{SEA}_{\mathrm{C}}$). Statistical analyses of isotopic data were conducted using the Stable Isotope Bayesian Ellipses "SIBER" extension of the Sable Isotope Analysis "SIAR" package and base statistical functions in R (Parnell and Jackson 2013; R Core Team 2019).

3. Results

3.1. Functional traits

Lizards were differentiated on the basis of jaw length, mouth width, limb, and tail length. The PCA resulted in two main axes that explained 66.2% of the total morphological variation (PC1 = 53.8%, PC2 = 12.4%). Positive loadings on PC1 were associated with lizards having larger jaws, longer limbs, and wider mouths (e.g., *A. carolinensis*), while negative loadings were associated with lizards having shorter and narrower mouths and shorter limbs (e.g., *S. lateralis*). PC2 separated lizards with shorter tails and hindlimbs (negative loadings) from those lizards having larger tails and

Fig. 1. Principal components analysis (PCA) of the functional position of the three native lizard species and *Hemidactylus turcicus* based on size-adjusted functional morphological traits. Each point represents a single individual of each species captured during the lizard surveys.

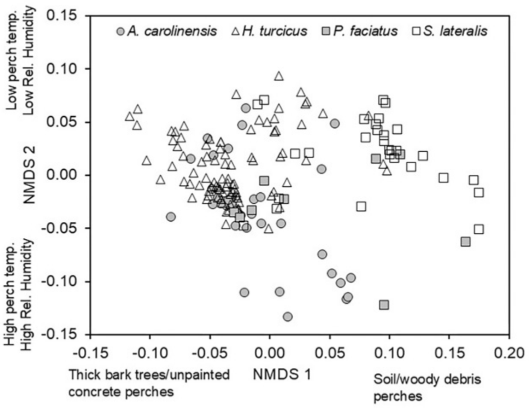


hindlimbs (positive loadings) (Fig. 1). *Hemidactylus turcicus* were significantly different in their functional traits compared to the native lizard assemblage (PERMANOVA; df = 166, F = 16.93; P [perm] = 0.0001; Fig. 1). *Hemidactylus turcicus* and *P. fasciatus* occupied an intermediate position in a gradient explained by jaw and mouth lengths/widths. In comparison, *A. carolinensis* and *S. lateralis* were positioned on opposite ends of this gradient. Specifically, *H. turcicus* and the native lizards separated slightly along PC2, with *H. turcicus* possessing shorter tails and hind limbs compared to the native species. Such position in morphological space likely suggests separation of species based on traits that make them more specialist (e.g., *Anolis* and *Scincella* in extremes of the PCA) or generalist (e.g., *Hemidactylus* and *Plestiodon*, intermediate position of the PCA) for exploiting resources.

3.2. Microhabitat niche partitioning

During our microhabitat surveys, we encountered native species only during diurnal surveys, while *H. turcicus* were only encountered during nocturnal surveys. The NMDS analysis identified two gradients in microhabitat use between the lizard species. The NMDS 1 contrasted a thicker barked tree/unpainted concrete perch type versus a more soil/woody debris perch type. NMDS 2 axis contrasted increasing versus decreasing perch temperature and relative humidity. Compared to native lizards, *H. turcicus* exploited novel microhabitats that consisted of high perches typically on unpainted concrete that were lower in temperature and relative humidity (PERMANOVA; df = 165, F = 34.66; P [perm] = 0.0001; Fig. 2). Native species used warmer perches (*A. carolinensis*) or lower perches associated with more terrestrial substrates (*S. lateralis* and *P. fasciatus*; Fig. 2).

Fig. 2. Nonmetric multidimensional scaling (NMDS) ordination of microhabitat use of the non-native *Hemidactylus turcicus* and the three native lizards.



3.3. Dietary niche partitioning

Overall, 715 food items were identified in the stomach contents of the four lizards, which represented two invertebrate phyla, Arthropoda and Mollusca, containing 19 orders. The most abundant prey taxa for all lizards were Araneae (spiders), Orthoptera (crickets and grasshoppers), and Dermaptera (earwigs). For *H. turcicus*, the most abundant prey taxa were Araneae, Diptera (flies), and Hemiptera (true bugs). Using FO of the prey taxa, the six orders frequently found in the stomachs of *H. turcicus* were Araneae (35.8%), Diptera (25.0%), Hemiptera (22.8%), Orthoptera (15%), Dermaptera (13.0%), and Coleoptera (beetles; 12.0%) (Table 2). When the RO of the prey taxa was used, the six orders most frequently found in the stomachs of *H. turcicus*

Table 2. The frequency of occurrence (FO), relative occurrence (RO), and standardized niche breadth (B_A) of prey taxa found in stomach content analysis of four lizard species.

Prey taxon	Lizard species			
	Hemidactylus turcicus	*Anolis carolinensis*	*Plestiodon fasciatus*	*Scincella lateralis*
	(n = 92)	(n = 34)	(n = 9)	(n = 31)
	FO/RO	FO/RO	FO/RO	FO/RO
Mollusca				
Gastropoda				
Stylommatophora	2.17/0.67	0.00/0.00	22.22/6.67	0.00/0.00
Arthropoda				
Crustacea				
Isopoda	5.43/6.06	0.00/0.00	11.11/3.33	6.45/1.09
Arachnida				
Acari	3.26/1.35	0.00/0.00	11.11/3.33	0.00/0.00
Araneae	35.87/15.15	35.29/12.25	44.44/20.00	45.16/10.87
Chilopoda				
Scutigeromorpha	2.17/0.67	0.00/0.00	11.11/3.33	6.45/1.09
Diplopoda				
Polydesmida	1.09/0.34	0.00/0.00	0.00/0.00	0.00/0.00
Insecta				
Lepidoptera	4.35/1.35	23.53/3.92	11.11/3.33	6.45/1.09
Hemiptera	22.83/9.43	35.29/11.76	0.00/0.00	12.90/2.72
Orthoptera	15.22/12.46	14.71/8.33	11.11/3.33	9.68/1.63
Diptera	25.00/12.12	29.41/11.27	0.00/0.00	9.68/2.17
Dermaptera	13.04/4.38	11.76/2.45	33.33/13.33	6.45/2.17
Coleoptera	11.96/6.06	61.76/23.53	33.33/13.33	3.23/0.54
Neuroptera	0.00/0.00	8.82/1.47	0.00/0.00	6.45/1.09
Hymenoptera	14.13/11.11	23.53/5.39	0.00/0.00	22.58/10.33
Ephemeroptera	1.09/0.67	0.00/0.00	0.00/0.00	0.00/0.00
Trichoptera	2.17/0.67	0.00/0.00	0.00/0.00	0.00/0.00
Nematoda*	0.00/0.00	0.00/0.00	0.00/0.00	41.94/19.57
Zygentoma	1.09/0.34	0.00/0.00	0.00/0.00	9.68/1.63
Collembola				
Collembola	0.00/0.00	0.00/0.00	11.11/3.33	29.03/30.98
Unidentified arthropods	54.38/17.17	85.29/19.61	77.78/26.67	74.19/13.04
B_A (standardized)	0.641	0.324	0.505	0.323

Note: The FO and RO metrics reported were based on counts of individual prey items. The B_A metric was based on prey mass. Taxon designated with an asterisk (*) were likely parasites.

included Araneae (15%), Orthoptera (12%), Diptera (12%), Hymenoptera (ants, bees, and wasps 11%), Hemiptera (9%), and Isopoda (woodlice; 6%) (Table 2). Of the 166 stomachs dissected, only 7 were empty. When compared to the three native lizard species, *H. turcicus* had the broadest dietary niche breadth and was slightly wider than *P. fasciatus*, and nearly double the size of both *A. carolinensis* and *S. lateralis* (Table 2). Even though *H. turcicus* had the widest dietary niche breadth, it exhibited relatively low to intermediate levels of dietary niche overlap with the two native lizards, *P. fasciatus* ($O_{jk} = 0.049$) and *A. carolinensis* ($O_{jk} = 0.077$), respectively. *Hemidactylus turcicus* did exhibit high niche overlap with *S. lateralis* ($O_{jk} = 0.927$), which was due to the high abundance of unidentified invertebrates found in the stomachs of each species.

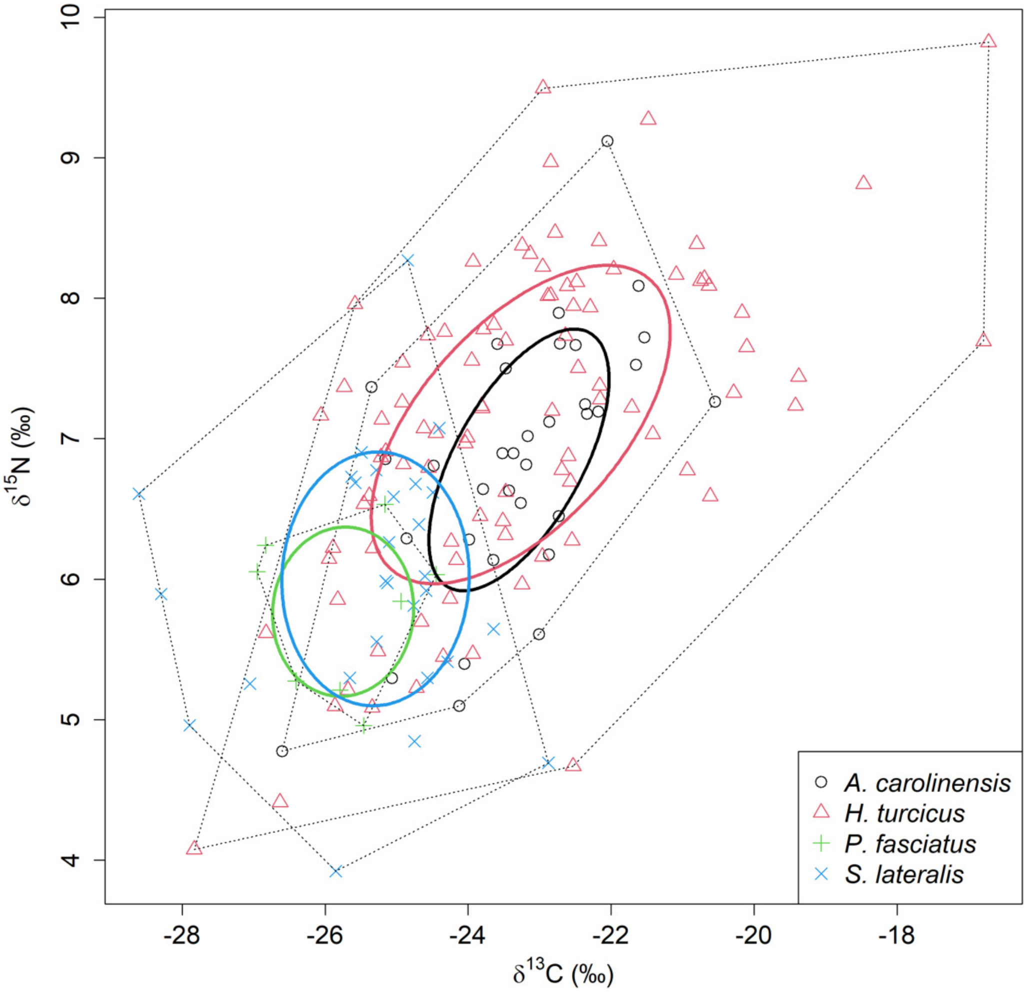
3.4. Isotopic niche partitioning

Tissues from 161 individuals were used in isotopic analyses (*H. turcicus* $n = 91$; *A. carolinensis* $n = 34$; *P. fasciatus* $n = 8$; *S. lateralis* $n = 28$). *Hemidactylus turcicus* occupied a significantly greater SEA_C of isotopic niche space compared to native lizards (Table 3; Fig. 3). Additionally, the wide isotopic niche breadth observed in *H. turcicus* was reflected in the isotopic ranges of both $\delta^{13}C$ and $\delta^{15}N$, suggesting utilization of a greater diversity of dietary sources of carbon and a broader trophic range compared to native species (Table 3; Fig. 3). SEA_C estimates showed almost complete isotopic niche overlap of *H. turcicus* with the native lizard *A. carolinensis* (98.2%). However, there was substantially less overlap in the isotopic niches between *H. turcicus* and the native skink species *S. lateralis* and *P. fasciatus* (1% and 11.3%, respectively).

Table 3. Number of individuals used in isotopic analysis (*N*), δ13C range, δ15N range, total area of occupied isotopic space (TA), and estimated corrected standard ellipse area (SEA_C) of isotopic niche space of lizard species within the sampled assemblage.

Species	*N*	δ^{13}C range	δ^{15}N range	TA	SEA_C
Hemidactylus turcicus	91	11.11	5.75	37.44	6.07
Anolis carolinensis	34	6.06	4.39	13.08	2.90
Plestiodon fasciatus	8	2.51	1.58	2.10	1.87
Scincella lateralis	28	5.73	4.35	14.73	3.72

Fig. 3. Bi-plot of $^{13}\delta$C and $^{15}\delta$N representing the sampled lizard assemblage in isotopic niche space. Total areas of occupied isotopic space are represented with dotted grey lines. Standard area ellipses corrected for sample size are represented by color coded ellipses.



4. Discussion

Compared to the native lizard species, *H. turcicus* exploited novel resources along multiple niche axes which may be attributed to, in part, its functionally unique traits (e.g., moderate jaw length and mouth width and shorter hindlimb length), a pattern that supports our first hypothesis. Though it functioned as a generalist in many aspects of its niche dimensions, *H. turcicus* exhibited no niche overlap with native species with respect to their temporal activity, and depending on the specific native species and niche axis, low to high overlap in habitat, diet, and isotopic niche axes. For instance, *H. turcicus* exhibited high overlap with *S. lateralis* with regards to their dietary niche, but low overlap was observed in their isotopic and microhabitat niches. Additionally, *H. turcicus* showed high overlap with *A. carolinensis* in their isotopic niche, but low overlap in regards to dietary and microhabitat niches. Taken together, the complete lack of temporal overlap with native species, the low overlap on most other niche dimensions, and its generalist habits enables *H. turcicus* to occupy an empty niche in this urban ecosystem, supporting our second hypothesis. Furthermore, these results highlight why this gecko species is a successful invader in this region and other areas where it has been introduced. Below, we discuss the ecological context in which niche partitioning between *H. turcicus* and a recipient lizard assemblage may occur, the implications of our findings to the future establishment of *H. turcicus* populations, and the potential effects of this invader on native lizards in light of these findings.

Hemidactylus turcicus possess several traits (e.g., adhesive toe pads, reduced limb length) that allow them to perform well in their natural range of habitats that includes rocky cliffs, cracks, and crevices. These same traits allow for exploitation of urban habitats with an abundance of vertical structures with hard exterior surfaces (Stabler et al. 2012). In this urban population of *H. turcicus*, we found this species occupying an intermediate functional trait space compared to other native lizard species. This observation is likely linked to life-history characteristics of *H. turcicus*, which is known for the use of a broader range of human-associated microhabitats and food resources not accessible to native species (Saenz 1996; Williams and McBrayer 2009; Dallas et al. 2022). Furthermore, *H. turcicus* was found to exploit higher perching sites on concrete surfaces at lower temperatures and relative humidity. The combination of intermediate limb lengths and large sticky toe-pads in *H. turcicus* may help facilitate the exploitation of this microhabitat type (Powell and Henderson 2008). While not measured in our functional trait analyses for this assemblage, the uniqueness of this trait in *H. turcicus* underlies the ability to exploit vertical structures that other species cannot, and the use of such habitats likely allows for the exploitation of a number of resources that are unavailable to native species (Yang et al. 2012). In addition, these unused microhabitats may provide refuge and suitable thermoregulatory environments for *H. turcicus*, consequently, minimizing resource overlap with native lizards (Hitchcock and McBrayer 2006). Cracks and crevices in the sides of climate-controlled buildings can provide thermoregulatory refuges that allow *H. turcicus* to be more active at lower ambient temperatures and allow for the survival of the species in regions colder than their native habitat (Locey and Stone 2009). Although there was some overlap with the native, semi-arboreal species (i.e., *A. carolinensis*) in terms of habitat use, *A. carolinensis* is likely to only exploit lower perches in trees and shrubs in which they can thermoregulate at higher temperatures (Jenssen et al. 1998). Neither one of these habitats could be exploited by the two native skink species, which possessed shorter limbs better suited for terrestrial environments with abundant leaf litter or woody debris (Hibbitts and Hibbitts 2015).

Hemidactylus turcicus may also be able to temporally exploit habitats and other resources used by native lizards when heterospecifics are less active (sensu Barbault and Maury 1981; Kronfeld-Schor and Dayan 2003). *Hemidactylus turcicus* is a nocturnal species while the native species have diurnal activity patterns. The differences in activity patterns, coupled with the differences in functional traits and habitat use, may underlie the increased dietary generalization in *Hemidactylus turcicus*. Like other gekkonids, *H. turcicus* are generalist predators that have been documented feeding on a wide variety of prey (Saenz 1996; Punzo 2001). However, urban environments have features that may create temporally available, and spatially abundant, food resources that are not accessible to native species. First, *H. turcicus* can easily traverse up and down walls, and previous research on this species has suggested that a broader dietary niche may be due to lizards exploiting resources at lower perches or on ground (Saenz 1996). Second, artificial lights on the external walls of buildings attract an abundance of insects that *H. turcicus* may exploit (Williams and McBrayer 2009; Owens and Lewis 2018). For example, Thawley and Kolbe (2020) found that artificial light at night increased the growth and reproduction of another non-native lizard, the brown anole (*Anolis sagrei* Duméril and Bibron, 1837) in urban habitats. Other invasive gekkonids in urban environments, that possess similar life-history traits to *H. turcicus* have been shown to increase time spent foraging around artificial light (Baxter-Gilbert et al. 2021). The ability to feed on spatially or temporally abundant prey in multiple ways could explain the greater habitat and dietary niche breadth we observed in *H. turcicus* compared to the recipient lizard assemblage.

Artificial lights attract a great diversity of both herbivorous and carnivorous arthropods that may forage in other urbanized habitats (Owens and Lewis 2018). The broader isotopic niche we observed in *H. turcicus* compared to native lizards may reflect this pattern, as these artificial light sources attract both diurnal and nocturnal arthropods (Owens and Lewis 2018). The ability of *H. turcicus* to forage at artificial lights may lead to a broader isotopic niche breadth in terms of both resource diversity and trophic position. Likewise, the ability to forage in multiple microhabitats may also lead to the occupation of a broader isotopic niche as resources from other energetic pathways in the terrestrial environment are being exploited. For example, the isotopic niches of *H. turcicus* and *A. carolinensis* overlapped considerably, despite temporal differences in activity. Temporal partitioning of activity has been proposed as a mechanism of coexistence in other lizard assemblages (Pianka and Huey 1978; Gordon et al. 2010). Despite their high overlap in isotopic niche space, differences in temporal activity in foraging between *H. turcicus* and *A. carolinensis* likely facilitates their co-occurrence. Additionally, overlap in isotopic signature does not mean these two species are consuming the same prey, but they are being supported by similar energetic pathways in this system. *Hemidactylus turcicus* also exploited resources with isotopic signatures representative of a C4-based energetic pathway and had a broader trophic range.

The functional traits possessed by *H. turcicus* likely allow for the utilization of resources occurring in multiple microhabitats at different spatial and temporal scales than native lizard species in urban ecosystems. This allows *H. turcicus* to reduce the resource overlap that may limit their growth or reproduction. Because *H. turcicus* exploits resources not utilized by native lizards, they may not experience strong biotic barriers to establishment, which suggests the species may fulfill an empty niche in this urban system. In an urbanized setting, predators and competitors are few because intense and long-term anthropogenic pressures have completely altered habitats and dismantled natural communities (Gaertner et al. 2017). Urban environments are also particularly susceptible to biological invasions because, as major centers of trade and transportation, propagule pressure is intensified (Gaertner et al. 2017). For invaders that possess unique traits from the native assemblages that do persist within these environments, human-associated habitats provide ample opportunities for establishment. These aforementioned traits of *H. turcicus* also facilitate their spread via jump dispersal (Locey and Stone 2006). Once established, functional traits of invaders can reflect the mechanisms in which they are able to adapt to novel environments, become superior competitors, or avoid competition entirely (Cadotte et al. 2017). The ability to use resources not used by native species (e.g., thermoregulatory refuges, food hotspots) provides an advantage for establishment of *H. turcicus*. In urbanized areas, where *H. turcicus* has been introduced alongside other functionally similar non-native species, only the superior competitor persists (Klawinski et al. 1994; Dame and Petren 2006; Short and Petren 2012). Klawinski et al. (1994), for example, found that a long-established population of *H. turcicus* at the port of Galveston was replaced by the introduction and establishment of the competitively superior rough-tailed gecko (*Cyrtopodion scabrum* Heyden, 1827). Nonetheless, the functional uniqueness of *H. turcicus* likely facilitates their establishment and spread in urban ecosystems where only native lizards exist.

Non-native species may be prone to establishment in urban environments because they happen to have traits that may be advantageous to altered environmental conditions and the loss, or conversion, of native habitats (Cadotte et al. 2017; Stroud et al. 2019). Alternatively, natural, intact ecosystems appear to be more resistant to invasion due to the diversity of predators and competitors that can provide biotic resistance to invasion (Levine and D'Antonio 1999). Urban areas feature unique combinations of environmental conditions not readily found in natural systems, and species must be flexible or pre-adapted to these conditions to persist (Gaertner et al. 2017; Stroud et al. 2019). While most native species are limited in urban environments due to the patchiness of preferred habitat, many non-native species are able to thrive in urban areas, especially those in which anthropogenic structures may represent habitats similar to those found in their native range (McKinney 2006). For example, our search effort for diurnal and nocturnal surveys was consistent across our study, yet our sample sizes differed for each species. The disparity in sample size may reflect their relative abundance within this urban area due to differences in available habitat preferred by each species. The two native skinks, for example, prefer habitats with high leaf litter and downed woody debris (Hibbitts and Hibbitts 2015), which are often removed from urban environments (McCleery et al. 2020). Indeed, depending on the species, lizards exhibit either positive or negative shifts in their abundance due to urbanization (French et al. 2018; de Andrade 2020).

Introductions of *H. turcicus* may not displace native lizards through antagonistic interactions in the urban habitats they occupy. However, factors that could contribute to increased overlap of shared resources that are not well understood. For example, artificial light has been shown to influence the behavior and physiology of organisms in urban ecosystems (Gaynor et al. 2018; Maurer et al. 2019). Taylor et al. (2022) found that artificial light led to increases in the nocturnal activity of *A. carolinensis*. This would suggest that in urban habitats occupied by *H. turcicus* and *A. carolinensis* there could be increased temporal overlap which could result in overlap of shared resources. Thus, greater overlap in their functional and isotopic niche dimensions may increase the strength of antagonistic interactions between these species (Figueira et al. 2023). Although we did not observe diurnal lizards active during our nocturnal surveys, we were not able to sample across each species' entire activity period (i.e., 24 h period). Artificial light has been shown to reduce temporal niche partitioning between diurnal and nocturnal insects (Avalon et al. 2020). This could then alter food-web dynamics in urbanized environments, influence availability and abundance of shared resources among predators, and could lead to increased resource overlap despite differences in foraging activity (McMunn et al. 2019; Grubisic and van Grunsven 2021). However, the impacts this species might have on resource availability in these systems are not yet known. The true impact of established non-native species, if occupying empty niches, may ultimately rely on a robust understanding of the viability and dispersal of introduced populations (Wessels et al. 2018). Non-native species introduced via multiple long-distance and jump dispersals over broad geographic areas may exhibit context dependent resource use and niche differentiation over time in response to local environmental gradients. Some non-native species that appear to have no negative effects may eventually become a nuisance or invasive if localized adaptations lead to novel traits in populations by specializing or expanding their realized niche (Nania et al. 2020). With urbanization and other anthropogenic threats increasing dramatically worldwide, predicting future introductions and the impacts of these introductions will have on recipient ecosystems is critical for maintaining diversity.

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Data availability

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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