Disentangling the Influence of Urbanization and Invasion on Endemic Geckos in Tropical Biodiversity Hot Spots: A Case Study of *Phyllodactylus martini* (Squamata: Phyllodactylidae) along an Urban Gradient in Curaçao

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ABSTRACT

Predicting the response of endemic species to urbanization has emerged as a fundamental challenge in 21st century conservation biology. The factors that underlie population declines of reptiles are particularly nebulous, as these are often the least understood class of vertebrates in a given community. In this study, we assess correlations between feeding ecology and phenotypic traits of the Lesser Antillean endemic Dutch leaf-toed gecko, *Phyllodactylus martini*, along an urban gradient in the Caribbean island of Curaçao. There has been a marked decline of this species in developed habitats associated with the invasive tropical house gecko *Hemidactylus mabouia*. We find a correlation between aspects of locomotor morphology and prey in undeveloped habitats that is absent in developed habitats. Analyses of stomach contents further suggest that *Phyllodactylus martini* alters primary prey items in developed areas. However, changes in prey promote the overlap in foraging niches between *Phyllodactylus martini* and *Hemidactylus mabouia*, suggesting that direct resource competition is contributing to the decline of *Phyllodactylus martini*. In addition to competitive exclusion, we suggest that the urban extirpation of *Phyllodactylus martini* could also be attributed to a top-down control on population growth by *Hemidactylus mabouia*. Colonizations of walls put *Phyllodactylus martini* in direct contact with *Hemidactylus mabouia* increasing the chances for predation events, as evidenced by our observation of a predation event on a *Phyllodactylus martini* juvenile by an adult *Hemidactylus mabuoia*. In total, our results add to a growing body of literature demonstrating the threat that invasive synanthropic reptiles pose to endemics that might otherwise be able to cope with increased urbanization pressures.

KEYWORDS

Urbanization, Caribbean biodiversity hot spot, conservation, invasive species, *Hemidactylus mabouia*, predation, Anthropocene, extinction, functional morphology, sexual dimorphism

Introduction

Understanding the effect of anthropogenic change on native species is a topic of considerable priority for long-term conservation efforts in biodiversity hot spots, which contain at least 44% of all living plant and 35% of all living vertebrate taxa, yet only comprise approximately 1.4% of the planet's total land area (Myers et al. 2000). Tropical hot spots are of particular concern as these regions are experiencing some of the world's highest rates of human population growth (Cincotta et al. 2000) and habitat loss (Myers et al. 2000; Sodhi et al. 2004; Seto et al. 2012). There is substantial evidence documenting population declines of native taxa in these regions, which has led to the hypothesis that tropical species are at disproportionate extinction risk relative to temperate species (Brook et al. 2008). Although this pattern of extinction risk is found across all major vertebrate clades (Gibbons et al. 2000; Brooks et al. 2002; Brook et al. 2008), studies of reptile declines are perhaps the most limited (Gibbons et al. 2000; Garden et al. 2007). In many cases, population declines or local extinctions of reptile species go unnoticed for extended periods of time (Gibbons et al. 2000; Zavaleta et al. 2001; Kraus 2008; Fisher and Ineich 2012). Even when population declines are observed, we often lack the empirical data necessary to assess what factors drive changes in reptile population dynamics (Echternacht 1999; Gibbons et al. 2000).

Over the past several decades, there has been a documented decline in reptile species endemic to the islands of Aruba, Bonaire and Curaçao (ABC). Together these islands represent the most southwestern component of the Caribbean biodiversity hot spot (Myers et al. 2000) with a reptilian fauna that is approximately 50% endemic (Van Buurt 2005, 2006). These arid islands are considered biogeographically isolated from the Caribbean West Indies, with over-water dispersal from the South American mainland hypothesized as the primary pathway for terrestrial colonization (Koopman 1958, 1959; Staton and Dixon 1977; McFarlane and Lundberg 2002; Debrot 2003; Wüster et al. 2005; Zijlstra et al. 2010; Muñoz-Garay and Mantilla-Meluk 2012; Rivas et al. 2013). Despite the close geographic distance and taxonomic affinity between the ABC islands and the mainland, high rates of endemism have led to

the hypothesis that these islands comprise a distinct biogeographic province (Van Buurt 2006). However, the long-term persistence of ABC endemic reptile species is of concern, as they are under increasing pressure from not only human population growth and urban development, but also the spread of invasive reptile species (Van Buurt 2005, 2006).

The continual arrival and establishment of nonnative reptiles has resulted in a 30% increase in reptile species richness across the ABC islands (Van Buurt 2005, 2006). Modeling the effect that these new colonizers will have on native species is rendered difficult by gaps in our knowledge of the ecology and natural history of ABC island endemics and the association of several invasive species with the urban landscape. The endemic Dutch leaf-toed gecko *Phyllodactylus martini* (Lidth de Jeude 1887) seems particularly vulnerable to urban growth patterns and is notably absent from many portions of its former range (Van Buurt 2005, 2006). Although this toe pad–bearing gecko will readily colonize human dwellings (Van Buurt 2005, 2006), there is a notable decrease of *P. martini* abundance as distance from natural habitats increases (Hughes et al. 2015). Displacement by the nonnative tropical house gecko, *Hemidactylus mabouia* (Moreau de Jonnès, 1818), is hypothesized to underlie this population decline of *P. martini* (Hughes et al. 2015).

Hemidactylus geckos are often deemed "weedy" species (Kluge 1969; Carranza and Arnold 2006) and have been linked to the displacement of various gecko species through the New World (Meshaka et al. 2006; Reynolds and Niemiller 2010). Disentangling how much of this displacement is because of direct prey resource competition in contrast to other factors is often challenging, as there is little documentation concerning the natural history of *Phyllodactylus martini*. For example, although *P. martini* will readily colonize walls and other human structures (Van Buurt 2005, 2006; Hughes et al. 2015), it remains unknown whether this habitat shift corresponds with a shift in prey resource availability. Urban development often corresponds with substantial changes in arthropod communities (Gibbs and Stanton 2001; Shochat et al. 2004), and the continual pace of development on the island raises the question of how changes at lower trophic levels

influence the feeding ecology of *P. martini*. Can *P. martini* shift its diet in response to changes in the prey resource community? If the diet of *P. martini* should change, would it then overlap with that of *H. mabouia*, which primarily consumes arthropods associated with urban habitats (Iturriaga and Marrero 2013)?

Here we examine the trophic ecology, ecomorphology and dispersal opportunities of *Phyllodactylus martini* along an urban gradient, with the goal of identifying factors potentially affecting the persistence of this species in the face of anthropogenic pressures and species competition. We provide the first detailed analysis of the diet of *P. martini* based on specimens collected from around the island of Curaçao and test whether transitions to suburban habitats lead to a shift in dietary resources indicating dietary flexibility. Because many geckos are sexually dimorphic (Kratochvíl and Frynta 2002; Werner and Seifan 2006; Starostová et al. 2010), including other species of *Phyllodactylus* (Ramírez-Sandoval et al. 2006), we compare feeding habits between sexes to account for the possibility of males and females utilizing different prey resources. We contrast this data with a morphometric data set of limb and cranial elements in *P. martini* to test for the potential for sexual dimorphism as well as correlations between phenotype and diet. Using spatial analyses, we further test for dispersal abilities between existing natural parks and developed areas sampled in this study to quantify the degree of habitat fragmentation experienced by *P. martini*. Finally, we provide a detailed account of the first observation of the invasive gecko *Hemidactylus mabouia* preying on *P. martini*.

Materials and Methods

Data Collection

Sixty-nine adult *Phyllodactylus martini* individuals were collected and prepared as research specimens between July 2009 and September 2011 from three locations across northern Curaçao that represent both developed (Westpunt and Lagun) and undeveloped (vicinity of Shete Boca) habitats (Figure 1). Three additional *P. martini* individuals were collected opportunistically at the Caribbean Research and Management of Biodiversity (CARMABI) research station and used to supplement the morphological data set. The low sample size and distance to the other areas render these samples inadequate for meaningful comparison of dietary differences between sites. Specimens and stomach contents were deposited in the Division of Vertebrate Zoology Herpetology Collection (Reptiles), Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA (YPM HERR; Appendix 1). Geckos were collected by hand at least 1 hour after complete sunset to increase the probability of stomachs containing freshly ingested prey. To test for differences in ecomorphology between sexes and correlations with ecomorphology and diet, we used calipers to measure a total of 10 morphological traits for each specimen at a precision of 0.01 mm: (1) snout-vent length (SVL), (2) postorbital width, (3) temporalis width, (4) head length, (5) jaw length, (6) head height, (7) upper forelimb, (8) lower forelimb, (9) upper hind limb and (10) lower hind limb.

Stomach Content Analyses

For each individual specimen, the stomach was removed and preserved in 10% formalin for later analysis. All stomach contents were identified and enumerated under a dissecting MVX10 microscope (Olympus Corp.; http://www.olympus-lifescience.com/). Prey items were identified to the lowest taxonomic grouping possible, with categories largely overlapping with other studies of Caribbean lizards (Perry 1996). Preliminary observations indicated a high frequency of prey item fragments in stomach contents, suggesting that volume or size analyses of individual prey items would not provide representative metrics across the uneven distribution of prey preservation in our specimens (Perry 1996). Thus, we restricted quantification of gut contents to the number of identified prey taxa found in each stomach.

Percent frequency of stomach content items was calculated for each individual within each sampling locality. Differences in gut contents were visualized using nonmetric multidimensional scaling (NMDS) in the vegan software package in R, v. 2.4 (Oksanen et al. 2007; Oksanen 2011) using sex or sampling locality as groups. We quantified stress values to assess whether NMDS ordination is a viable indicator of the dissimilarity between groups, with stress values less than 0.1 indicating good representation of the dissimilari-

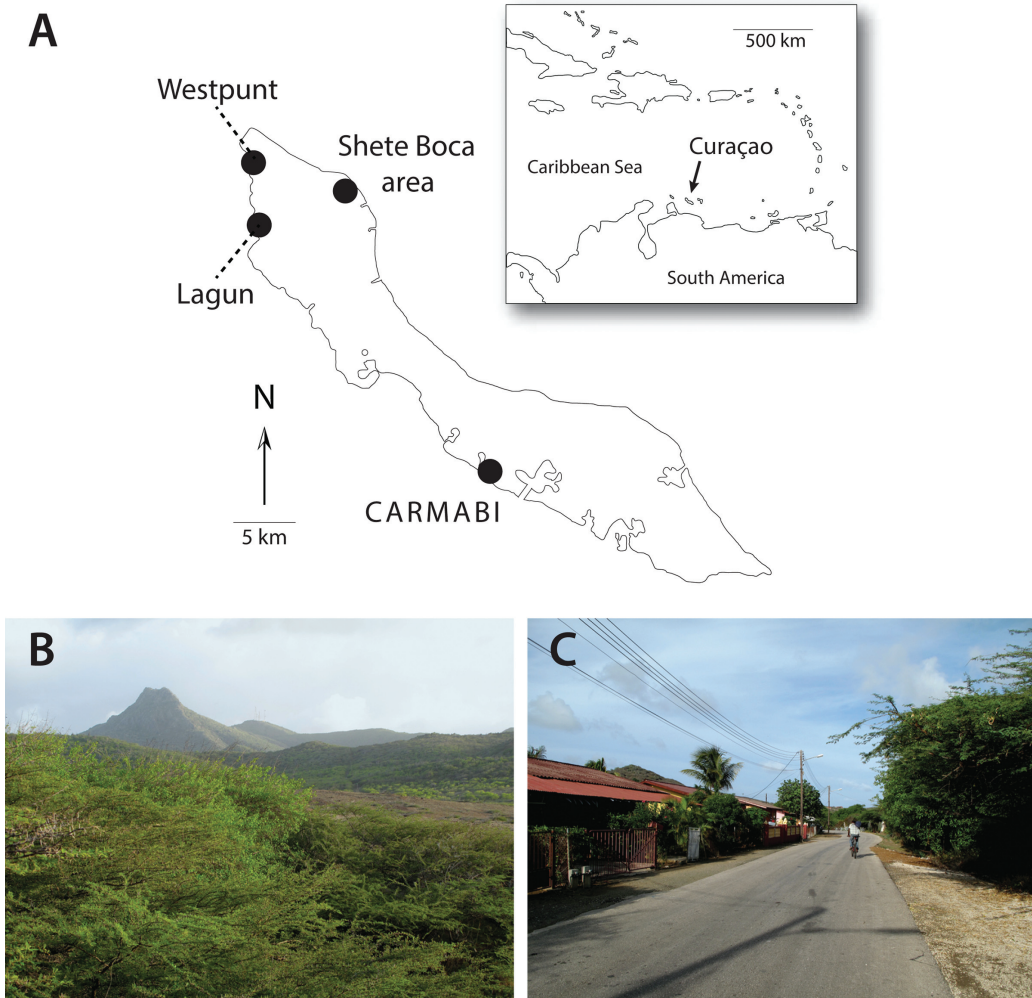FIGURE 1. Overview of study area. **A,** Map of sites sampled in this study (redrawn from Dornburg et al. 2011). **B,** Photograph characterizing the habitat in undeveloped sites. **C,** Photograph characterizing the habitat in developed sites. *Abbreviation:* CARMABI, Caribbean Research and Management of Biodiversity.

ties (Clarke 1993). We tested for significant differences between these groupings by subjecting stomach contents to an analysis of similarity (ANOSIM; Clarke 1993; Chapman and Underwood 1999) using Bray-Curtis distances and 999 permutations in the vegan software package (Oksanen et al. 2007; Oksanen 2011). Differences in mean ranks were quantified using the R statistic, with values close to zero indicating high similarity and values close to one indicating high dissimilarity (Chapman and Underwood 1999).

Because this analysis can potentially mask whether a small subset of prey items occurs at a higher or lower frequency than expected by chance, we also conducted a series of simulations to assess if differences in percent frequency are outside of the expectations of stochastic sampling. For each site, we simulated a data set with identical numbers of individuals and randomly assigned between one and three stomach content items to mirror the variance of prey items in a given stomach from our empirical samples. Items were also randomly drawn from a candidate pool of all stomach contents. This simulation was repeated 5,000 times per population, and the distribution of each stomach item's percent frequency was com-

pared to the empirically calculated frequency to assess significance. Because of the low sample size collected at Lagun ($n = 7$), ANOSIM and simulation analyses were limited to comparisons between samples collected in Westpunt and the vicinity of Shete Boca.

Morphometric Analyses

To test for sexual dimorphism in *Phyllodactylus martini*, we followed the procedure used by Manicom et al. (2014). Briefly, we used an iterative analysis of covariance with each morphometric measurement as a factor, keeping SVL as the covariate. Data were $\log_{10}$ transformed, and assumptions of normality were tested using a Shapiro-Wilk test (Shapiro and Wilk 1965). This allowed us to simultaneously test for a potential correlation with each measured trait and SVL; whether there are significant differences between male and female trait values when accounting for a potential correlation with SVL; and whether there is a significant interaction between SVL and sex, which would indicate one sex is consistently larger than the other for a given trait.

We further tested for correlations between aspects of diet and phenotype using linear regressions between the $\log_{10}$-transformed morphometric trait values and NMDS axes. Trait values were first regressed against SVL, and the residuals of each trait were used in an iterative series of linear regressions between each size-corrected trait and the two NMDS axes. Because preliminary analyses indicated no differences between the sexes, these were pooled for the regression analysis. Conducting a principal components analysis and removing the axis that correlates with body size is a commonly used alternative to controlling for body size in linear measurements (McCoy et al. 2006), but this approach has recently been criticized as potentially misleading in both simulation and empirical data sets. Regression-based analyses, however, which allow covariance with body size, seem more robust to statistical artifacts (Berner 2011).

Spatial Analyses

To quantify how urbanization may influence the movement of *Phyllodactylus martini* on Curaçao, we constructed a cost surface to infer the probability of dispersal between sites sampled in this study. Resistance-to-movement values were assigned to roads, rivers and percent of urbanized in contrast to natural habitat at a scale of square kilometers to create a cost surface in ArcGIS, v. 10.0 (ESRI 2016) using data layers compiled from the DIVA-GIS database, v. 7.5 (Hijmans et al. 2012) and the 2012 MODIS-based maximum green vegetation fraction from the U.S. Geological Survey Land Cover Institute (http://landcover.usgs.gov/green_veg.php; Broxton et al. 2014). Although this spatial scale is potentially coarse for studies of small organisms, this represents the finest-scale data currently available for the island of Curaçao. Additionally, this scale provides a broad assessment of urbanization that can provide the framework for future studies of areas within the island as data layers with increased resolution become available. Based on the natural history of *P. martini* (Van Buurt 2005), as well as mortality studies of other gecko species (Das et al. 2007; Schutt 2008; Wotherspoon and Burgin 2011), rivers, roads and urbanized areas were weighted as difficult to pass through, whereas the natural arid bush habitat (mondi) of the island was given the lowest resistance (Appendix 2). Although *P. martini* will readily colonize walls, this coding of resistance reflects findings by Hughes et al. (2015), who found this species to be absent in urban areas away from edge habitats. Using the resistance surface, we calculated the shortest cost path distances between all pair localities using the Landscape Genetics toolbox (Etherington 2011), which calculates the pairwise least cost paths among multiple points in ArcGIS. We then tested for a correlation between geographic distance and landscape resistance in limiting potential dispersal between sampled localities, by computing a matrix of the Euclidean distances between points and testing for correlation between this and the resistance matrix using a Mantel test, based on Pearson's product-moment correlation and 999 permutations, in the vegan package of R (Oksanen et al. 2007). To visualize the cost surface and potential dispersal pathways, we used the CIRCUITSCAPE software package, v. 4.0 (McRae and Beier 2007).

Results

Stomach Content Analyses

Seventy-two specimens were dissected, with between 1 and 3 items found per specimen
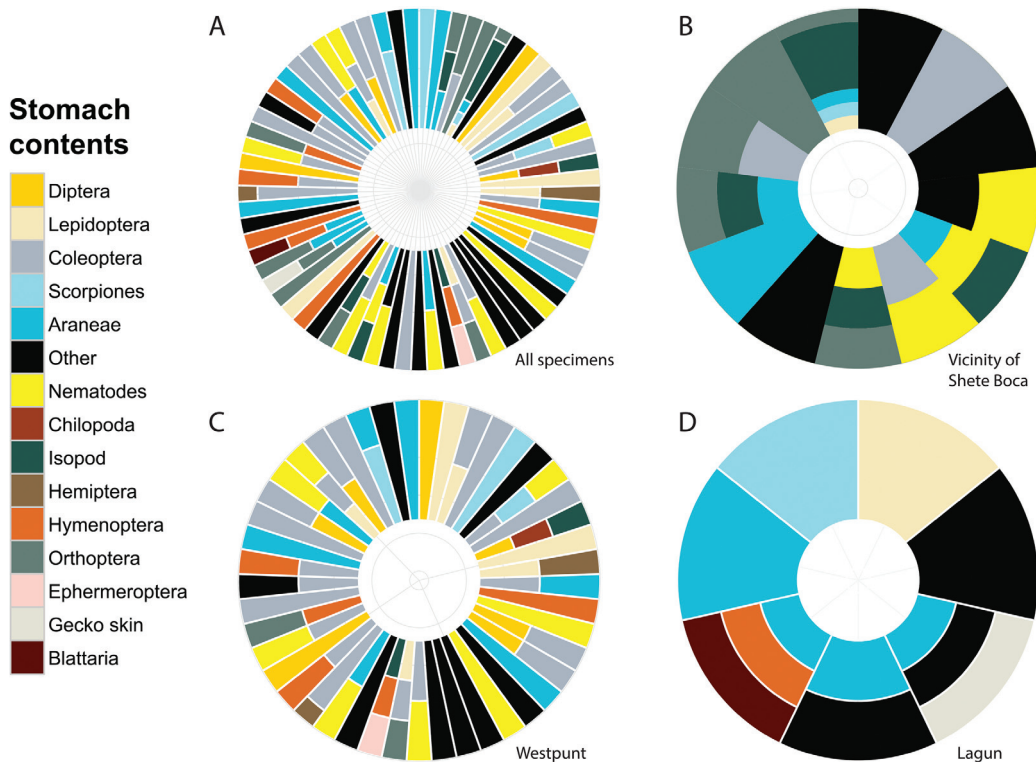
FIGURE 2. Visualizations of the stomach content data. **A,** From all individuals. **B,** Samples collected in the vicinity of Shete Boca (*n* = 13). **C,** Samples collected in Westpunt (*n* = 45). **D,** Samples collected in Lagun (*n* = 7). Colors correspond to prey items in the legend, and slices in each sphere correspond to the stomach contents of an individual specimen.

(Figure 2). In total, 126 items were recovered, suggesting that *Phyllodactylus martini* consumes a broad diversity of prey items, with beetles (Coleoptera, 20%) and spiders (Araneae, 13%; Table 1; Figure 2A) at the highest frequency. Nematodes were observed in high numbers, accounting for 9% of all stomach items. Although this rate of infection is similar to background infection rates of *P. martini* stomach nematodes in Bonaire (approximately 12%; Goldberg et al. 2014) and suggests that parasitic infections are not uncommon, we cannot rule out the possibility that some of these represent parasites from prey items. Comparing samples from Westpunt with those collected in the vicinity of Shete Boca suggests that in developed sites there is a shift toward consumption of more dipterans, lepidopterans, and hemipterans while maintaining a high degree of overlap. In the population near Shete Boca, *P. martini* individuals consumed a high frequency

of orthopterans (17%) and isopods (27%; Table 1; Figure 2B). In contrast, orthopterans and isopods were found at a much lower frequency in the Westpunt population (each approximately 2%; Table 1; Figure 2C), with coleopterans instead accounting for about 30% of all items (Table 1; Figure 1). Isopods were also absent from the samples collected at Lagun, where the stomach contents reflected a high frequency of predation on araneaens (Table 1; Figure 2D). Relative to the vicinity of Shete Boca, Westpunt-collected geckos also contained a higher frequency of dipterans (11% in contrast to 6%) and lepidopterans (11% in contrast to 3%), possibly reflecting the tendency for these groups to aggregate under artificial lighting.

Stress values were below 0.015 for all NMDS analyses, suggesting that dissimilarities between groups were adequately captured. NMDS-based visualizations of the gut contents between male

TABLE 1. Percentage of frequency occurrence of stomach contents found in *Phyllodactylus martini* across three sites. *Abbreviations:* μ, number of total items found in all guts at a sampling locality; *n*, number of individuals captured.

Item	All specimens	Vicinity of Shete Boca ($n = 13$; μ = 30)	Westpunt ($n = 45$, μ = 82)	Lagun ($n = 7$, μ = 14)
Araneae	0.13	0.13	0.09	0.43
Blattaria	>0.01	—	—	0.07
Chilopoda	>0.01	—	0.01	—
Coleoptera	0.20	0.1	0.29	—
Diptera	0.06	—	0.11	—
Ephermeroptera	>0.01	—	0.01	—
Gecko skin	>0.01	—	—	0.07
Hemiptera	0.015	—	0.02	—
Hymenoptera	0.06	—	0.02	0.07
Isopod	0.07	0.27	0.02	—
Lepidoptera	0.08	0.03	0.11	0.07
Nematodes	0.09	0.13	0.10	—
Scorpiones	0.04	0.03	0.05	0.07
Orthoptera	0.07	0.17	0.02	0.21
Other	0.10	0.13	0.10	—

and female *Phyllodactylus martini* in the vicinity of Shete Boca suggests a large degree of overlap, with slightly larger resource use for females (Figure 3A). This trend is reversed in the NMDS visualizations of *P. martini* in Westpunt, where there is considerably more overlap and males exhibit a wider resource use (Figure 3A). However, results of ANOSIM analyses did not support significant dissimilarity in diet between sexes for either population (Shete Boca: $R = 0.043$, $p = 0.51$; Westpunt: $R = 0.01592$, $p = 0.254$).

NMDS-based visualizations of stomach contents between developed and undeveloped sites provide evidence for a much wider resource use in developed sites (Figure 3B). This overlap is supported by an ANOSIM analysis that fails to recover significant dissimilarity between these sites ($R = 0.02341$, $p = 0.258$). This pattern is also evident when adding the samples from Lagun to the visualizations (Figure 3B).

Our simulations demonstrate that several prey items are sampled at a higher frequency than would be expected by chance alone. The frequency of isopods and orthopterans in specimens from the Shete Boca area is significantly elevated ($0.0001 < p < 0.03$; Figure 4A). In contrast, the simulations detected significantly fewer consumed isopods and orthopterans in Westpunt ($0.012 < p < 0.011$; Figure 4) and more coleopterans ($p < 0.0001$; Figure 4B). Although this analysis cannot determine whether shifts in feeding ecology are primarily driven by prey preference or changes in availability, our combined results detect a shift in feeding ecology when these animals transition from the mondi to more developed areas.

Morphometric Analyses

We found a strong correlation between size and all other measured morphometric traits (Table 2). However, our results provide no evidence for sexual dimorphism. We did not find a significant relationship between size-corrected traits and the sex of the specimen or evidence of size differences between the sexes (Table 2). Linear regressions instead revealed two different patterns of correlation between phenotype and diet in the Westpunt and Shete Boca area populations (Figure 5). Within the Westpunt population, we found no significant correlation between phenotype and either of the two NMDS axes (Table 3). In contrast, within the Shete Boca area we found a significant correlation between both femur and fibula length and the first NMDS axis (Table 4), and a significant correlation between head length and the second NMDS axis (Table 4).
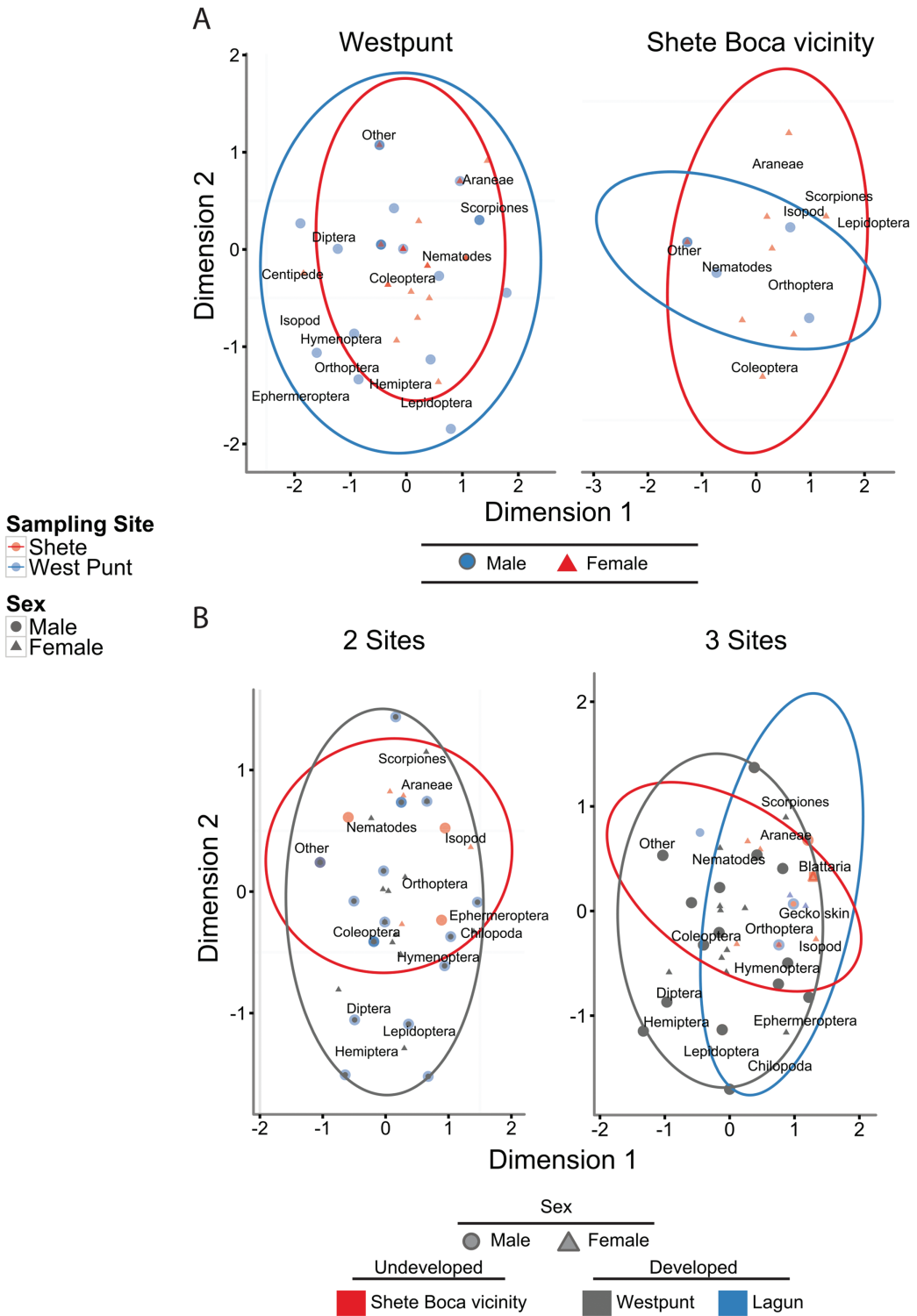
FIGURE 3. Nonmetric multidimensional scaling-based visualizations of stomach contents. **A,** Comparisons between males and females captured within sites. **B,** Comparisons between developed and undeveloped sites.
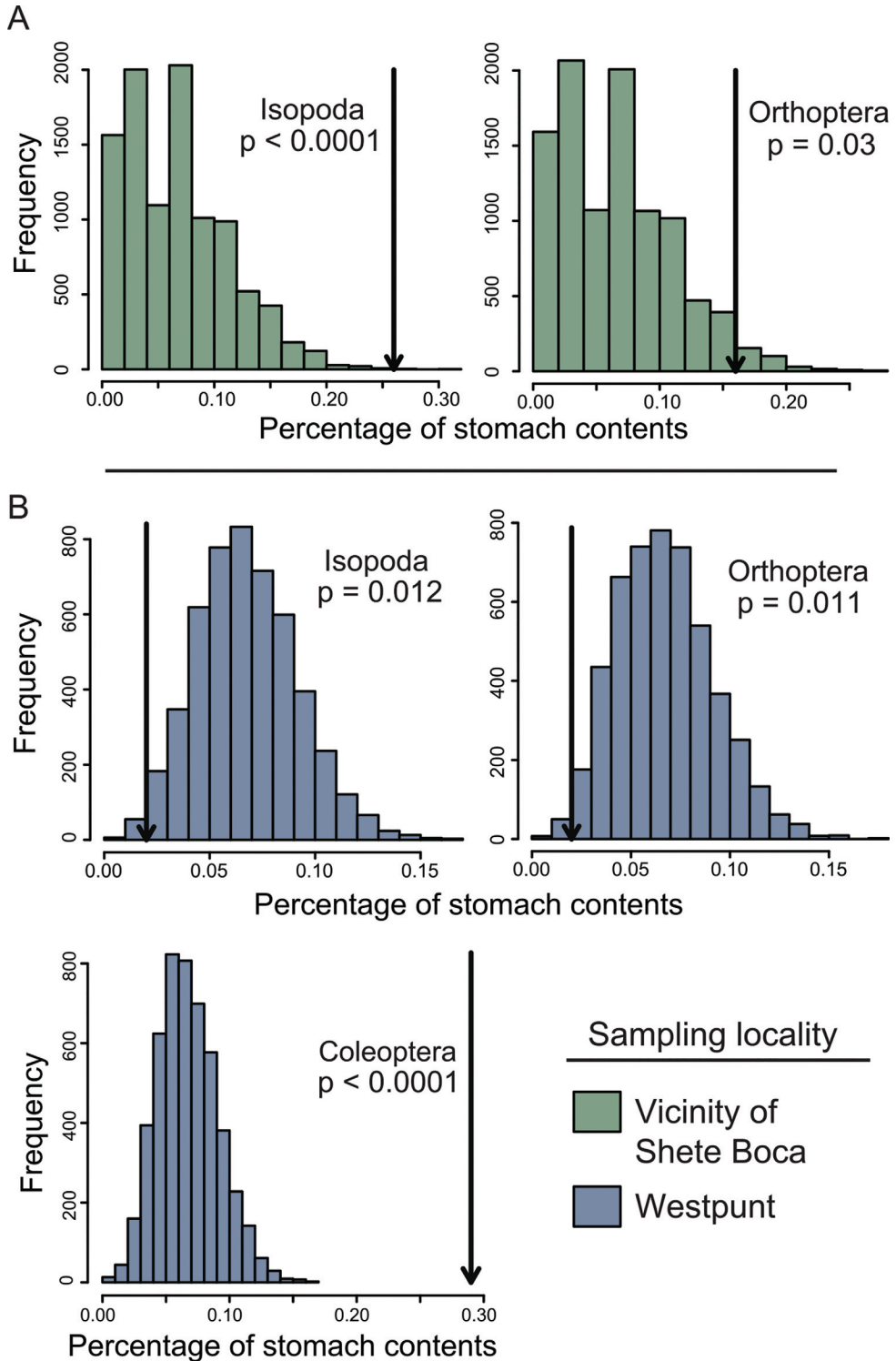
FIGURE 4. Visualizations of stomach content simulations comparing the expected percentage versus empirical percentage. **A,** For isopods and orthopterans in the vicinity of Shete Boca. **B,** For isopods, orthopterans and coleopterans in Westpunt. Arrows indicate the percentage of each prey item in the empirical data.

TABLE 2. Results from an analysis of covariance testing the effect of snout-vent length (SVL), sex and their interaction on measured ecomorphological characters. Values in bold indicate significant effects.

Trait	SVL (F, p)	Sex (F, p)	Sex:SVL (F, p)
Postorbital width	**45.7, 1.7e-8**	0.026, 0.87	2.97, 0.09
Temporalis width	**237.3, <2.0e-16**	1.54, 0.22	0.31, 0.58
Head length	**207.2, <2.0e-16**	0.26, 0.611	0.07, 0.79
Jaw length	**64.1, 2.15-15**	0.015, 0.82	0.37, 0.54
Head height	**62.1, 3.2e-10**	0.011, 0.91	0.08, 0.77
Humerus length	**5.5, 0.023**	0.69, 0.41	0.04, 0.84
Ulna length	**66.2, 1.38e-10**	0.56, 0.45	0.008, 0.93
Femur length	**38.6, 1.2e-7**	0.06, 0.81	0.80, 0.37
Tibia length	**15.94, 0.00023**	0.54, 0.46	1.179, 0.28

Spatial Analyses

Quantification of a resistance surface at a scale of square kilometers suggests the potential for high population connectivity between the Shete Boca area and the northern towns of Lagun and Westpunt (Figure 6). Likewise, dispersal between the areas at the western outskirts of Willemstad near CARMABI research station and the Shete Boca area also requires only a small amount of movement through the high-resistance area (Figure 6). The results of the Mantel test strongly support landscape resistance to be significantly different from Euclidian distances (Mantel statistic 0.9974; $p = 0.034$), suggesting that distance is a greater factor than landscape resistance in limiting dispersal between the sampled areas.

An Observation of Predation on *Phyllodactylus martini* by *Hemidactylus mabouia*

At approximately 23:00 h on 11 September 2011, five of the authors (A.D., A.J., D.L.W., M.C.B. and T.L.I.) observed a juvenile *Phyllodactylus martini* running across the wall of our laboratory setup on the second floor of Curaçao Sunshine Getaways in Westpunt. This area was open to the outside, and geckos were commonly observed just outside of the window openings or on the living room walls. As the juvenile reached an area above a framed poster hanging on the wall, another gecko rapidly emerged and engulfed the juvenile *P. martini*. We immediately caught this second gecko and identified it as a large (55.7 mm SVL) *Hemidactylus mabouia*. The tail of the *P. martini* juvenile was still protruding from the mouth of the captured *H. mabouia*. We extracted the deceased (31.7 mm SVL) *P. martini* (YPM HERR 108620) from the *H. mabouia* (YPM HERR 018631), and both were preserved in formalin and subsequently deposited in the collections of the Yale Peabody Museum. Although *H. mabouia* has been documented as an opportunistic predator of *Gonatodes antillensis* on Curaçao (Dornburg et al. 2011), this represents the first documented instance of *H. mabouia* preying on *P. martini*.

Discussion

Our study suggests that in *Phyllodactylus martini*, population decline is not the direct effect of habitat alteration or development but is instead driven by interspecific conflict with the invasive *Hemidactylus mabouia*. We find that *P. martini* can switch its feeding and foraging behavior in developed habitats and is able to disperse between developed and undeveloped habitats. Although developed habitats may represent new ecological opportunities for *P. martini*, this opportunity is limited by the presence of the invasive synanthropic gecko *H. mabouia*. Our observation of predation provides additional evidence that the rapid decline of *P. martini* is linked to a combination of competition (exploitative and interference) and predation. Extrapolating from our results suggests that the presence of *Hemidactylus* geckos, which are among the most common invasive urban and suburban tropical lizards, enhances the pace of local extinction for toe pad–bearing geckos that would otherwise be able to adapt to at least some level of urban development.
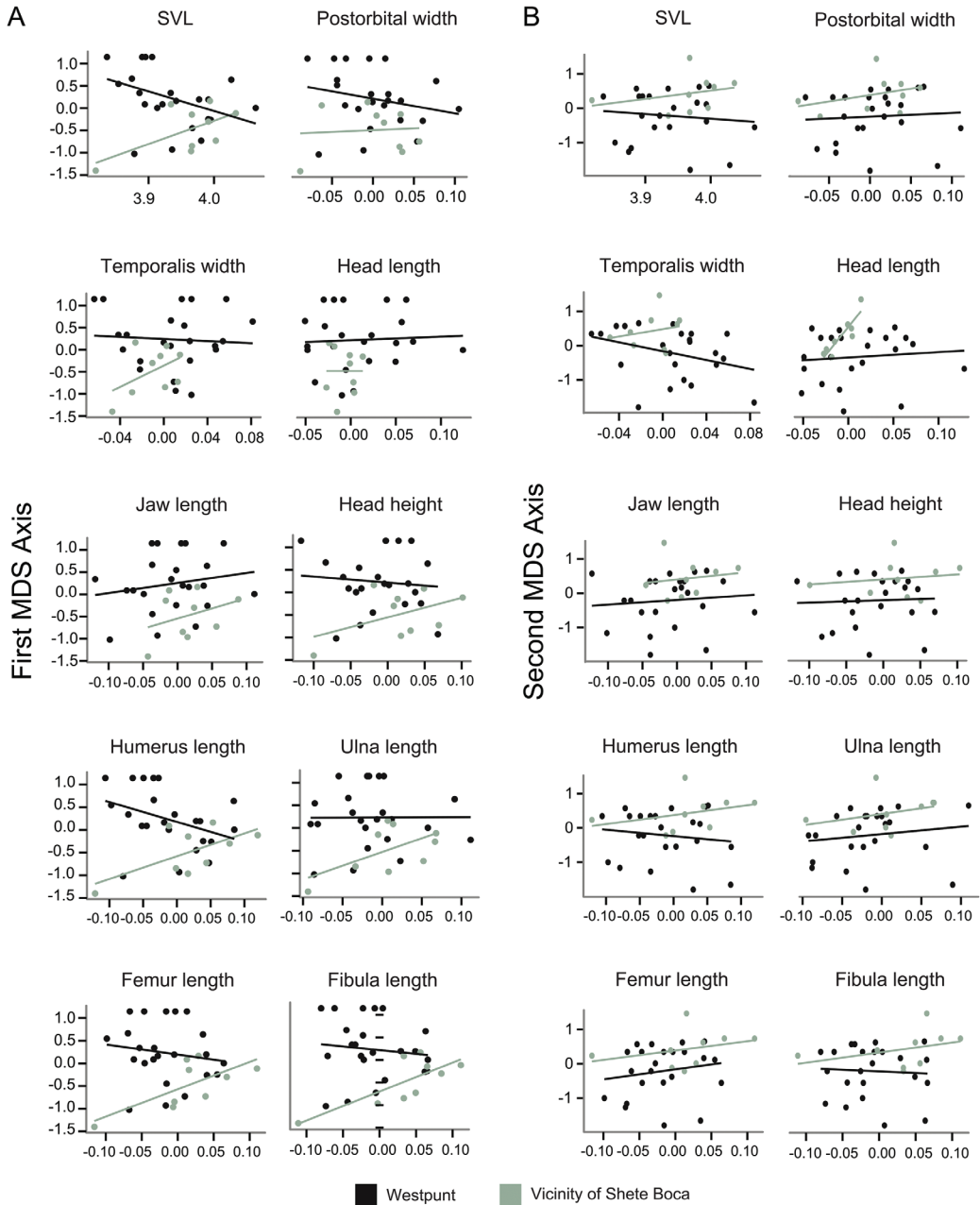
FIGURE 5. Visualizations of regressions between nonmetric multidimensional scaling (NMDS) axes of diet and phenotype in Westpunt (dark) and Shete Boca (light). **A,** First NMDS axis. **B,** Second NMDS axis. *Abbreviation:* SVL, snout-vent length.

Feeding Plasticity and Opportunity along an Urban Gradient

The persistence of native wildlife species in urbanizing habitats (synurbanization) often corresponds with major ecological and behavioral shifts (Luniak 2004; McKinney 2006; Pattishall

and Cundall 2009; Wang et al. 2015). Our analyses reveal that *Phyllodactylus martini* portrays a significant shift in consumed prey resources in developed as opposed to undeveloped environments (Figures 2, 3 and 4). Although our sample size encompasses only a small number of individ-

TABLE 3. Testing for correlations between phenotype and the nonmetric multidimensional scaling (NMDS) axes of stomach contents within the Westpunt population.

Trait	NMDS1 (F, p)	NMDS2 (F, p)
Snout-vent length	3.638, 0.070	0.2417, 0.628
Postorbital width	1.186, 0.288	0.0977, 0.757
Temporalis width	0.096, 0.759	2.709, 0.114
Head length	0.064, 0.801	0.2064, 0.654
Jaw length	0.728, 0.403	0.2092, 0.652
Head height	0.193, 0.664	0.0423, 0.838
Humerus length	3.259, 0.085	0.4041, 0.531
Ulna length	0.8e-3, 0.97	0.487 1, 0.492
Femur length	0.4814, 0.495	0.6487, 0.429
Fibula length	0.2861, 0.598	0.0721, 0.790

TABLE 4. Testing for correlations between phenotype and the nonmetric multidimensional scaling (NMDS) axes of stomach contents within the population residing in the vicinity of Shete Boca. Bold text indicates p values below 0.05.

Trait	NMDS1 (F, p)	NMDS2 (F, p)
Snout-vent length	3.851, 0.090	0.6108, 0.460
Postorbital width	0.0369, 0.853	0.9736, 0.356
Temporalis width	1.978, 0.2024	0.3558, 0.569
Head length	1.6e-6, 0.999	**28, 0.001**
Jaw length	0.8961, 0.375	0.1889, 0.677
Head height	1.881, 0.212	0.1850, 0.680
Humerus length	4.691, 0.067	0.8822, 0.378
Ulna length	3.604, 0.099	0.8183, 0.395
Femur length	**6.58, 0.037**	0.7920, 0.403
Fibula length	**9.9, 0.0162**	1.01, 0.348

uals in a small portion of the island, the shift in resources coupled with the observation that this species readily colonizes walls (Van Buurt 2005, 2006; Hughes et al. 2015) suggests that feeding and foraging behavior in *P. martini* is quite plastic. Low to moderate levels of development may in fact be providing *P. martini* with novel ecological opportunities.

Urban development often results in a fundamental transformation of an environment (Luniak 2004). Although detrimental for many taxa, this resetting of the local ecological stage is also expected to create novel niches and ecological opportunities (Gloor et al. 2001; Luniak 2004) in a fashion similar to natural processes such as the colonization of islands or movements of glaciers (Harmon et al. 2008; Parent and Crespi 2009; Near et al. 2012; Federman et al. 2015). Toe pad–bearing gecko species like *Phyllodactylus martini* can readily invade the smooth vertical surfaces of human dwellings (Autumn et al. 2002; Autumn et al. 2006; Tian et al. 2006); however, it is unclear how the urban and rural invertebrate communities that provide their prey base differ. Urbanization is generally associated with a restructuring of the invertebrate community (Frankie and Ehler 1978; McIntyre 2000; Shochat et al. 2004; Raupp et al. 2010; Sattler et al. 2010). The study of prey resources along urban gradients, and how they change selective pressures on the feeding ecology of predators, therefore, represents an exciting frontier in the urban ecology of the southern Caribbean.

In *Phyllodactylus martini*, transitions to foraging on anthropogenic walls correlated with a shift away from prey items such as isopods and orthopterans in developed habitats (Figure 4). This shift suggests that *P. martini* spends less time foraging terrestrially or that terrestrial prey resources in urbanized habitats are more limited. Although it is difficult to determine whether one, or both, of these hypotheses explains the abundance of terrestrial arthropods in the diet of urbanized *P. martini*, this raises the question of whether resource use is correlated with phenotypic variation in ecomorphologically relevant traits. Hind limb morphology and diet for geckos at Shete Boca were significantly related (Table 4); however, no such association was found in Westpunt (Table 3). Longer hind limbs are associated with increased terrestrial sprint speeds in geckos (Zaaf and Van Damme 2001; Cameron et al. 2013). Longer-limbed geckos at Shete Boca seem to frequently prey on terrestrial isopods, suggesting that foraging behaviors may change in response to urbanization. However, long limbs decrease locomotor performance for wall-foraging geckos (Zaaf and Van Damme 2001). The increased locomotor performance of shorter limbs on walls suggests that urbanized *P. martini* may be under selective pressures that limit the natural range of ecomor-

phological variation in the species. As urbanization has been found to drive rapid evolution in other species (Winchell et al. 2016), further research is clearly warranted.

Are Suburban Invasions Promoting the Decline of Phyllodactylus martini?

For many reptile species, competition with non-native reptiles has been found to drive population declines (Case and Bolger 1991; Case et al. 1994; Petren and Case 1996; Gibbons et al. 2000; Cole et al. 2005). In particular, exploitative competition has been demonstrated to be a major driver of population declines of native geckos in other areas facing *Hemidactylus* invasions. It is possible that the shift in diet by *Phyllodactylus martini* in developed habitats (Figures 2, 3 and 4) overlaps with the diet of *H. mabouia*, which is largely composed of arthropod prey items in the orders Diptera, Hemiptera and Araneae in urban environments throughout the world (Zamprogno and Teixeira 1998; Meshaka 2000; Bonfiglio et al. 2006; Iturriaga and Marrero 2013). *Hemidactylus* geckos seem to be particularly efficient at harvesting spatially aggregated resources (Petren and Case 1996), and in areas of Curaçao where both *H. mabouia* and *P. martini* occur, *H. mabouia* has been found to be more abundant near light sources that aggregate arthropods (Hughes et al. 2015). In addition to being potentially more efficient at harvesting spatially aggregated resources, *H. mabouia* may also be limiting access to food resources through territorial interactions.

Hemidactylus mabouia is highly aggressive, and the defense of territories by this species has been linked to the decline of other gecko species in Florida (Meshaka et al 2006; Short and Petren 2012). Following the colonization of *H. mabouia* on structures previously colonized by *Phyllodactylus martini* in Curaçao, the latter species becomes noticeably absent (Van Buurt 2010; Hughes et al. 2015). This suggests that interference competition may also be limiting the persistence of *P. martini* in developed habitats. As we demonstrate that *P. martini* exhibits no sexual size dimorphism or dimorphism of ecomorphological traits associated with territoriality or foraging (Table 2), this implies that interference competition is likely to affect both sexes equally. Although we cannot rule out the hypothesis that *H. mabouia* may promote sex-specific differences in foraging behavior, nei-
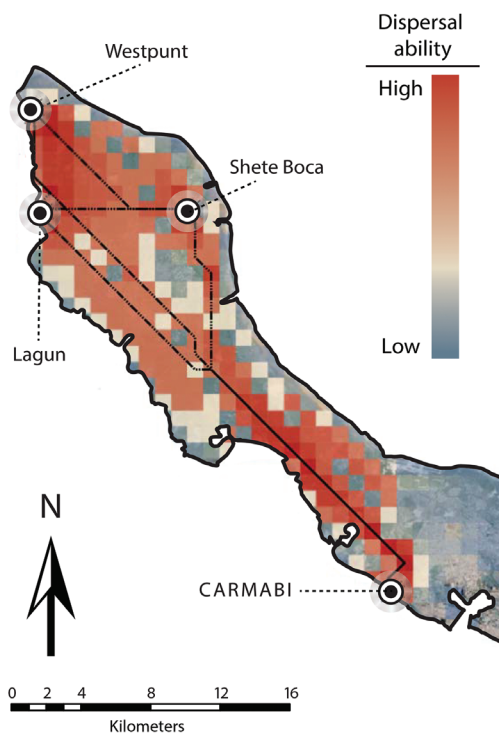

FIGURE 6. A satellite image of Curaçao depicting predicted *Phyllodactylus martini* dispersal abilities through the study area. Black labeled circles are collection sites; black dotted lines show the least cost pathways among localities; colors represent a resistance gradient of dispersal ability with red being high dispersal probability and blue being low. Areas of least resistance and shortest least cost path correspond to those areas experiencing the least urbanization. *Abbreviation:* CARMABI, Caribbean Research and Management of Biodiversity.

ther our study nor others documenting the decline of *P. martini* have provided sufficient evidence in favor of this hypothesis (Hughes et al. 2015). Although the combination of interference and exploitative competition may explain the decline of *P. martini* in urban areas, the rate at which *H. mabouia* displaces other gecko species exceeds the theoretical expectations of displacement by competition alone (Short and Petren 2012).

Our observation of predation on a juvenile *Phyllodactylus martini* by *Hemidactylus mabouia* suggests another factor influencing the decline of *P. martini* on Curaçao. Predation on native juvenile lizards by an invading lizard has been repeat-

edly documented across several species. For example, within *Anolis* lizards, *A. sagrei* has been shown to prey on juvenile *A. carolinensis* in Florida and *A. conspersus* in the Grand Cayman (Gerber and Echternacht 2000). Within geckos, predation on juvenile *Lepidodactylus lugubris* by *H. frenatus* has been demonstrated experimentally and has been proposed as a potential factor contributing to displacement of *L. lugubris* (Frogner 1967; Bolger and Case 1992; Case et al. 1994). However, gut content analysis of *H. frenatus* could not verify that this behavior was occurring in the wild (Bolger and Case 1992). Our observation coupled with a documented instance of predation by *H. mabouia* on *Gonatodes antillensis* (Dornburg et al. 2011) raises the possibility that *H. mabouia* is opportunistically saurophagous. Therefore, in addition to both exploitative and interference competition, predation is likely at least partially contributing to the displacement of *P. martini*.

Although *Hemidactylus mabouia* cannot survive in the harsh arid habitat that characterizes the island, the species is ubiquitous in urban and semiurban habitats (Van Buurt 2005). This geographic pattern raises the potential that, as in other biological invasions, suburban landscapes provide invasion "stepping stones" across the landscape for *H. mabouia* (McKinney and Lockwood 1999). Integrating our spatial and ecomorphological results with this finding, we can speculate that the continued connectivity of native habitat throughout the northern two-thirds of the island will be critical to ensuring gene flow between populations of *Phyllodactylus martini*. However, this is based on both a coarse analysis of connectivity and the assumption that these reptiles readily disperse to new areas. A recent study in another species of *Phyllodactylus* inhabiting the dry forests of Mexico suggests that the presence of *H. mabouia* in developed habitats may dramatically alter dispersal pathways and hasten population fragmentation (Blair et al. 2015). Although our spatial analyses suggest high connectivity between undisturbed habitats north of CARMABI research station and the western portion of Willemstad (Figure 6), further study of *H. mabouia* using landscape genetic approaches and sampling from across its range will be fundamental in illuminating the conservation needs of this species.

Conclusions

Predicting the effect of urbanization on the persistence of native, cryptic animals in biodiversity hot spots presents a major challenge to conservation biology in the 21st century. Our study suggests that moderate levels of urbanization may not promote the decline of *Phyllodactylus martini* as both male and females of this gecko species seem to alter their diet and foraging behavior in urban habitats. However, our findings posit that the invasive *Hemidactylus mabouia* in semiurbanized and urbanized areas may drive the decline of *P. martini* through competition and predation. *Hemidactylus* geckos have invaded suburban habitats in the tropics and subtropics globally, and our findings may be illustrative of a global conservation concern for toe pad–bearing geckos. Despite the potential ecological opportunities in suburban habitats for wall-climbing geckos, these habitats may in fact serve as points of invasion for nonnative species and set the stage for homogenization of the urban reptile community (e.g., With 2004; Blair and Johnson 2008). Given the increased anthropogenic pressures on many of the world's tropical biodiversity hot spots, further investigating the ecological and population dynamics of these less commonly observed species in semideveloped habitats will be critical in understanding their conservation needs.

Appendix 1
Specimens of Curaçao
Phyllodactylus martini

Specimens of Curaçao *Phyllodactylus martini* examined for stomach contents and morphometric analysis, by locality. *Abbreviations:* CARMABI, Caribbean Research and Management of Biodiversity; YPM HERR, Division of Vertebrate Zoology Herpetology Collection (Reptiles), Peabody Museum of Natural History, Yale University.

CARMABI
YPM HERR 018435, 018436, 018437

Lagun
YPM HERR 018461, 018462, 018463, 018466, 018467, 018468

Shete Boca
YPM HERR 018342, 018343, 018344, 018345, 018346, 018347, 018348, 018349, 018624, 018625, 018626, 018627, 018628, 018629

Westpunt
YPM HERR 017585, 017586, 017587, 017588, 017589, 017590, 017591, 017592, 017593, 017594, 017595, 017596, 017597, 017598, 017599, 017600, 017601, 017602, 017605, 017607, 018141, 018165, 018166, 018167, 018168, 018169, 018170, 018171, 018172, 018173, 018174, 018175, 018176, 018177, 018178, 018179, 018180, 018181, 018183, 018184, 018185, 018186, 018187, 018611, 018612, 018613, 018614, 018615, 018616, 018617, 018618, 018619, 018620, 018621, 018622, 018623, 018645, 018646

Appendix 2
Resistance Values Used for
Spatial Analyses

	Land cover class	Resistance [b]
Forest cover (%) [a]	89–100	1
	73–89	2
	53–73	4
	31–53	6
	10–31	8
	0–10	10
Road	Present	10
	Absent	1
River	Present	10
	Absent	1

[a] Forest cover was divided according to natural breaks into six categories using ArcGIS, v. 10.0.

[b] Resistance to movement across a surface, where high numbers represent difficulty of movement and low numbers represent ease of movement.

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