Phenotypic response to a major hurricane in *Anolis* lizards in urban and forest habitats

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Little is known about the synergistic impacts of urbanization and hurricanes on synanthropes. We compared morphological traits of the lizard *Anolis cristatellus* on Puerto Rico sampled before the 2017 category 5 Hurricane Maria and 4 and 11 months after the hurricane. We measured limb lengths, toepad size and the number of subdigital scales, termed lamellae, that facilitate adhesion. We hypothesized that the hurricane should have selected for longer limbs and larger toepads with more lamellae, which are traits that other research has suggested to increase clinging performance. Given prior work demonstrating that urban lizards of this species tend to share this phenotype, we also predicted increased phenotypic overlap between post-hurricane urban–forest pairs. Instead, we found that forest and urban populations alike had smaller body sizes, along with a small size-adjusted decrease in most traits, at 4 months after the hurricane event. Many traits returned to prehurricane values by 11 months post-hurricane. Toe morphology differed in the response to the hurricane between urban and forest populations, with significantly decreased trait values in forest but not in urban populations. This difference could be attributable to the different biomechanical demands of adhesion to anthropogenic substrates compared with natural substrates during intense winds. Overall, more research will be required to understand the impacts of hurricanes on urban species and whether differential natural selection can result.

ADDITIONAL KEYWORDS: anole – Hurricane Maria – morphological adaptation – Puerto Rico – synanthrope – toepad – urbanization.

INTRODUCTION

Hurricanes are powerful weather events that affect ecosystems by altering species composition, transforming habitats, changing species demographics and disrupting dispersal patterns (Lugo, 2008; Sergio *et al.*, 2018). Studies of long-term responses to hurricanes are common in plants and show that species in hurricane-prone areas tend to possess traits enabling them to withstand powerful winds or to colonize the resulting forest gaps (Griffith *et al.*, 2008; Zimmerman *et al.*, 2014; Hogan *et al.*, 2018). There are fewer examples in the literature of animal adaptations to hurricanes, with most studies focused instead on population dynamics and ecological consequences (see Spiller *et al.*, 1998; Schoener *et al.*, 2004; Gannon & Willig, 2009). However, recent research on lizards has suggested that selection might favour traits that minimize dislodgement by winds (Donihue *et al.*, 2018, 2020). Some simulations indicate that regimes of high disturbance intensity and frequency can result in increased genetic differentiation, especially when widespread site-level extinction disrupts patterns of gene flow (Davies *et al.*, 2016).

These effects, however, are likely to vary across space and time, even with respect to a single hurricane, owing to variation in wind and rainfall across the path of a given hurricane. For example, the effects of a hurricane within a given forest are often heterogeneous, with some patches losing considerably more canopy and/or mature trees than others (Brokaw & Grear, 1991). Likewise, mortality and phenotypic adaptations to hurricanes can also vary with the historical frequency of hurricanes (Griffith *et al.*, 2008;

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Donihue *et al.*, 2020). If this is true, the effects of a hurricane seem likely also to differ between different types of habitats, such as between forest and anthropogenic areas, including urbanization.

Urbanization is characterized by a high abundance of impervious surfaces, such as roads and pavements, artificial substrates and reduced vegetation (Forman, 2014). These attributes undoubtedly modify how meteorological disturbances, such as hurricanes, interact with the structural features of the habitat. Additionally, the direct effect of hurricanes on organisms that reside in urban spaces will be mediated by properties of the urban habitat such as the availability of artificial refuges during storms. Storm-related mortality might be mitigated in urban populations owing to access to artificial sheltering sites (e.g. concrete buildings, metal structures) if they are more robust to the hurricane than shelters typifying forest sites. In forest habitats, tree mortality and canopy shearing influence post-hurricane species dynamics greatly through changes in food abundance and the microclimate of the forest floor (Secrest *et al.*, 1996; Angulo-Sandoval *et al.*, 2004; Spiller & Schoener, 2007). Urban areas typically have reduced forest cover (Foley *et al.*, 2005; Walton *et al.*, 2008), which might, in turn, decrease the impact of hurricanes via forest disturbance. If so, the post-storm natural selection could be relatively weak in urban habitats compared with forest environments. Changes to the microclimate after a hurricane, driven primarily by the reduction in the tree canopy (Fernandez & Fetcher, 1991), might be less dramatic in urban environments owing to diminished urban canopy in compared with forests or to the alternative cover provided by artificial structures (Winchell *et al.*, 2018a; Avilés-Rodríguez & Kolbe, 2019).

Nonetheless, it is difficult to predict how the considerable human alteration of the environment associated with urbanization might interact with strong tropical storms to affect synanthropic organisms that live and breed in urban habitats. It is possible that the intense disturbance wrought by hurricanes could compound the negative aspects of urbanization. Mortality could be higher in urban habitats if wind speeds are exacerbated as a result of downdraughts caused by buildings and impervious surfaces (Zhu, 2008). Urban species with reduced effective population size might lack the genetic variation to adapt or persist in the face of an intense storm event (Lande, 1998; Benson *et al.*, 2016). In coyotes, for example, anthropogenic structures are effective barriers to gene flow, but the same features can also function as conduits for movement in other taxa (Zhang *et al.*, 2013; Miles *et al.*, 2019; Adducci II *et al.*, 2020; Maigret *et al.*, 2020). As such, it is largely unknown whether urbanization will tend to exaggerate or mitigate the effect of catastrophic weather events on the synanthropic taxa of cities.

Our research will attempt to address this question by contrasting the phenotypic response to Hurricane Maria in the synanthropic lizard species, *Anolis cristatellus*, between three pairs of urban and forest sites. Given that the majority of ecological and evolutionary research on *Anolis* has taken place in a hurricane-prone region (the Caribbean; see Losos 2009), a large body of literature has accumulated on the effects of tropical storms on *Anolis* population biology, ecology, evolution, behaviour and biogeography (Reagan, 1991; Schoener *et al.*, 2001, 2004). Hurricanes can cause mortality directly, owing to the kinetic wind forces, and by indirect changes to the structural habitat (Rodríguez-Durán & Vázquez, 2001; Lugo, 2008; Donihue *et al.*, 2018). For example, after Hurricane Floyd many island populations of *Anolis sagrei* in the Bahamas experienced massive mortality (including total population extinction on the smallest islands; Schoener *et al.*, 2001). Additionally, hurricane-caused changes to the habitat structure can impact the availability of important resources, such as shelter and food. After Hurricane Hugo, for instance, *Anolis stratulus*, which typically perch on tree trunks and often use tree canopies, were found more frequently perching near or at the ground level of the forest (Reagan, 1991). After canopy regrowth, this species was rarely seen near or on the forest floor because it recolonized the perches that it had typically used before the hurricane (Reagan, 1991).

More recently, some researchers have also begun to investigate the ecological and evolutionary effects of urbanization on anoles (e.g. Marnocha *et al.*, 2011; Winchell *et al.*, 2016; Chejanovski *et al.*, 2017; Avilés-Rodríguez & Kolbe, 2019. In *A. cristatellus*, urban lizards tend to have more toepad lamellae and exhibit longer limbs and larger toepads relative to their body size than lizards in nearby forest habitats (Winchell *et al.*, 2016, 2018b). In theory, these urban lizard traits should also increase clinging performance in the context of hurricanes. Specifically, greater toepad area is correlated with increased adhesion force (Irschick *et al.*, 2006), and longer limbs increase the ability of a lizard to grip their perch via adductive force (Kolbe, 2015). On the contrary, recent research has also suggested that longer hindlimb lengths can increase the probability of dislodgement by strong unidirectional wind (Donihue *et al.*, 2018). So far, however, no research has examined the ecological and evolutionary effects of tropical storms on *Anolis* (or any type of lizard) in urban environments.

Here, we measured phenotypic traits that are known to underlie clinging and running performance of anoles in both natural (Losos & Sinervo, 1989; Foster & Higham, 2012) and urban (Winchell *et al.*, 2018b) environments and that we thought could be relevant to survival in the context of hurricanes (Donihue *et al.*,

2018, 2020) to evaluate three questions regarding the effects of Hurricane Maria on urban populations of *A. cristatellus*. First, we used a multivariate approach to ask whether either urban or forest populations (or both) exhibited any evidence of a phenotypic response to the hurricane. Second, we asked whether the phenotypic response (to the extent that one was found) differed between forest and urban environments. Third, we investigated whether any resulting morphological shifts occurred in traits that tend to be associated with greater clinging performance by analysing each trait one by one. We predicted a phenotypic response to the hurricane in traits associated with clinging ability and that the magnitude of change in traits should differ between urban and forest habitats. Specifically, we hypothesized that urban populations would exhibit smaller changes in traits in response to the hurricane owing to the higher availability of robust refuges in urbanized areas compared with forest and owing to pre-existing differences in limb lengths and toepad areas between forest and urban sites (Winchell *et al.*, 2016). Lastly, we hypothesized that natural selection owing to the hurricane might reduce phenotypic dissimilarity between urban and forest *A. cristatellus* identified in prior research (Winchell *et al.*, 2016).

MATERIAL AND METHODS

ECOLOGICAL CONTEXT

Hurricane Maria was one of the most devastating hurricanes to make landfall on the island of Puerto Rico during recorded history. It produced the highest amount of total rainfall attributed to any previous hurricane in Puerto Rico since 1956 (Keellings & Hernández Ayala, 2019), although exact measurements of rainfall are slightly uncertain owing to storm damage sustained by island weather instruments (US Geological Survey, 2017). These heavy rains triggered > 70 000 landslides across the island (Bessette-Kirton *et al.*, 2020). The combined effects of rainfall and category 5 strength winds resulted in severe, widespread damage to forest across the island (Hall *et al.*, 2020).

SAMPLING

We sampled three pairs of urban–forest sites across the island of Puerto Rico before (first between 2012 and 2014 and again during 2016) and after (all sites at 4 and 11 months) the landfall of category 5 Hurricane Maria, which occurred in September 2017. At each time point, urban and forest sites within each municipality were sampled in the same 2 week period. We chose sites for our post-hurricane sampling that we had also sampled before Hurricane Maria as part

of other unrelated studies on the ecology and evolution of anoles in urban areas. These sites were distributed across the island, including the areas most affected by the hurricane (Fig. 1). After Hurricane Maria, K.J.A.-R. revisited the sites and sampled ≥ 50 adult male lizards per site. In total, we captured 569 animals post-hurricane to complement our pre-hurricane sample of 234 across the three pairs of sites, for a total of 803 lizards across all sampling periods. We used a handheld GPS instrument to record the location of capture, and all lizards were returned as close as possible to their original perch.

Our paired sites are in three different municipalities of Puerto Rico (San Juan, Arecibo and Mayagüez; Fig. 1), and span a range of urbanization intensity. San Juan, sampled initially in 2012, represents the largest extent of urban development on the island of Puerto Rico. Mayagüez, sampled initially in 2013, and Arecibo, in 2014, are developed to a similar extent, but Mayagüez is more densely populated. Our sampling sites experienced varied impacts from the hurricane. San Juan, in the north-east, is close to the entry point of the hurricane and thus experienced among the strongest winds on the island. Arecibo is located near the exit point of the hurricane and experienced intermediate wind speeds. Mayagüez experienced the weakest wind intensity owing to its location in the far west of the island and west of the hurricane path (Fig. 1).

MORPHOLOGICAL DATA COLLECTION

For each captured lizard, we first measured mass using a digital scale (mass +/- 0.01 g). We then anesthetized lizards using an oral ingestion of isoflurane and used a Kodex portable X-ray system to obtain a digital X-ray image of skeletal morphology (Fig. 1). From each image, we collected the following 15 linear measurements (in centimetres): head length, jaw length, jaw width, metacarpal length on the third digit, radius length, ulna length, humerus length, pectoral girdle width, pelvic girdle width, femur length, tibia length, fibula length, metatarsal length of the fourth rear toe, first phalangeal bone length of the fourth rear toe, and snout–vent length (SVL, measured by tracing the length of the vertebral column from the base of the skull to the cloaca).

Next, we used an Epson flatbed scanner to obtain high-resolution images (2100 dpi) of the ventral toepads on the third and fourth digits of each fore- and hindfoot, respectively (Fig. 1). From the images, we counted the number of lamellar scales on each toepad (counting from the next distal lamella that is wider than the previous subdigital scale to the end of the toepad, following Yuan *et al.*, 2019), the total length of the toepad (defined in a similar manner), and the toepad area. To
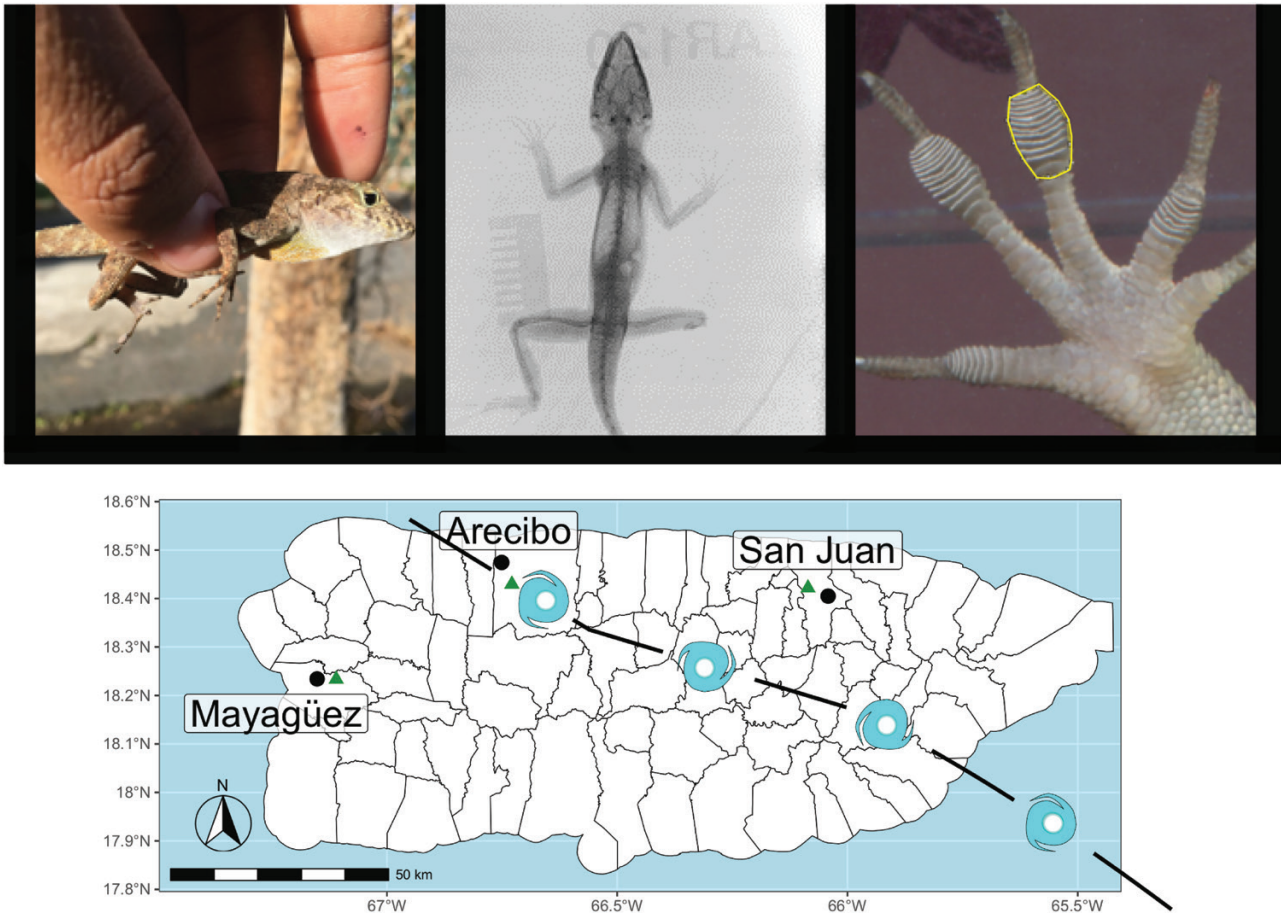
Figure 1. General morphological data collection methods and paired urban and forest sites relative to the path of the hurricane. The top panels show the same individual (captured 4 months after Hurricane Maria and missing the right hindlimb) as it was captured, then X-rayed and subsequently scanned for collection of body and toepad morphological data. The bottom panel shows the path of the hurricane relative to our paired sites. Forest sites are shown as green triangles and urban sites as black circles.

ensure consistency, a single investigator (K.J.A.-R.) re-measured all 234 pre-hurricane sets of X-ray and toepad images from the studies by Winchell *et al.* (2016; 2018b) in addition to all post-hurricane images.

Finally, to reduce the total number of variables in our analysis, we combined the measurements of several traits as follows. First, we computed forelimb length as the sum of the length of the humerus, the ulna and the metacarpal of the third digit. Second, we computed hindlimb length as the sum of the lengths of the femur, the tibia and the metatarsal of the fourth digit of the hindfoot. We also analysed pectoral girdle width, pelvic girdle width, toe length on the third digit of the forefoot, toe length of the fourth digit of the hindfoot, total number of lamellae on the third digit of the forefoot, total number of lamellae on the fourth digit of the hindfoot, and toepad areas for the third forefoot and fourth hindfoot digit. Thhird, for bilaterally symmetrical traits, we averaged across

both sides to obtain a single measure for each trait. If the left or right bilaterally symmetrical trait was missing or damaged, we used the measure from the undamaged side. In total, we analysed morphological traits (the 12 listed above, plus SVL) for each lizard.

STATISTICAL ANALYSIS

Our main goal in this study was to examine whether and how morphological traits of *A. cristatellus* responded to the drastic environmental changes wrought by Hurricane Maria and how this response might have been mediated by habitat type (urban or forest). To evaluate which traits differed by habitat in response to the hurricane, we first calculated the residuals of each trait against size (i.e. snout–vent length). We then reduced the overall dimensionality of our data by using principal components analysis (PCA) on the correlation matrix of the 12 size-corrected traits to extract scores for

principal components (PCs). We also performed PCAs without correcting for size and including size (SVL) as a covariate. Although the results were comparable (see Supporting Information, Tables S1–S5), our size-corrected analyses were easier to interpret and *more easily comparable to previous research* on phenotypic shifts in relationship to urban habitats by Winchell *et al.* (2016) and Gómez-Benitez *et al.* (2020).

We then assessed how this phenotypic variation was partitioned among our factors (hurricane context, habitat and municipality) using mixed effect models. We treated hurricane (before/after) and habitat (forest/urban) as fixed effects in our model, with municipality as a random effect. Specifically, we fitted every variant of the model of morphology explained by the fixed effects of habitat, hurricane context, and their interaction, with municipality as a random effect. A significant effect of habitat would indicate a difference in morphology between urban and forest sites across all municipalities. A significant effect of hurricane would indicate a shift in morphology between time points before and after the hurricane. A significant interaction effect of hurricane and habitat would indicate that morphological responses to the hurricane differ between urban and forest habitats. We used the Akaike information criterion to identify the best-supported model.

We also computed the contrast (difference) between the marginal means for each factor at each treatment level, in addition to its standard error. Given that the ratio of this difference and its standard error should have a Student's *t*-distribution under the null hypothesis, we used these contrasts to identify the significant factors for each response variable. We adjusted our *P*-values for multiple testing using the false discovery rate method (Benjamini & Hochberg, 1995). Lastly we evaluated changes in univariate traits by fitting separate linear mixed effect models to each trait, following the same structure as for our PCs, above. For all univariate traits, we included overall size (SVL) as a covariate.

We performed all our statistical analyses in the scientific computing environment R (R Core Team, 2019), v.3.6.3, using the R packages *lme4* (Bates *et al.*, 2015) and *emmeans* (Lenth, 2019).

DATA AVAILABILITY

Data are available on the Dryad Digital Repository (https://doi.org/10.5061/dryad.r7sqv9sbk).

RESULTS

CHANGES IN SHAPE AND SIZE AFTER HURRICANE MARIA

The first five PCs explained 73.8% of the total variation in our dataset (Table 1). For PCs 1, 2 and 4, the best linear mixed effect model included hurricane, habitat and the interaction of hurricane and habitat (Supporting Information, Tables S6–S10). For PC 3, the best model included the fixed effects hurricane and habitat, but not their interaction. For PC 5, the model with the lowest Akaike information criterion included the fixed effects of hurricane, habitat and their interaction; however, this model was not significantly different from a model that included only the fixed effect

Table 1. Loadings for the first five components from principal components analysis on the correlation matrix of *Anolis cristatellus* morphological traits

Trait	PCl	PC2	PC3	PC4	PC5
Head width	0.168	0.113	0.344	0.251	0.138
Head length	0.110	0.017	−0.127	−0.315	0.171
Forelimb length	0.034	0.020	0.263	**0.449**	0.379
Hindlimb length	0.176	−0.018	−0.004	0.265	**0.420**
Pectoral girdle width	0.172	0.001	0.304	**0.468**	0.002
Pelvic girdle width	0.024	0.023	**0.560**	**0.753**	−0.097
Front toepad area	**0.891**	**0.437**	0.070	−0.051	−0.066
Rear toepad area	**0.875**	**−0.465**	0.079	−0.057	−0.031
Number of front lamellae	**0.428**	0.145	**−0.656**	0.390	−0.193
Number of rear lamellae	0.377	−0.217	**−0.597**	**0.407**	−0.338
Front toe length	**0.782**	0.264	−0.259	0.117	**0.414**
Rear toe length	**0.763**	**−0.408**	−0.162	0.128	0.167
Proportion of variance	29.52	16.39	10.5	8.99	7.79
Cumulative variance	59.52	45.95	56.42	65.41	73.84

Loadings are defined as the correlation between each component and the original variable. Correlations approaching an R^2 of 0.50 are shown in bold. Abbreviation: PC, principal component.

of hurricane (ANOVA: χ^2 = 7.716, d.f. = 3, P = 0.052). Thus, for PC 5 we selected the model with the lowest number of parameters for downstream analyses.

Principal component 1 was strongly correlated with toepad area and toe lengths (for both fore- and hindfeet; Table 1). Our contrast analysis showed that forest populations had smaller trait values of PC 1 (e.g. positively correlated with toepad area) at 4 and 11 months after the hurricane compared with pre-hurricane forest populations (Table 2; Fig. 2). Urban populations had smaller PC 1 scores at 4 but not at 11 months after the hurricane when compared with pre-hurricane urban populations.

Principal component 2 was weakly correlated with front and rear toe morphology, with positive correlations for front toe traits and negative correlations for rear toe traits. Forest and urban lizards had smaller values for PC 2 at 4 and 11 months after the hurricane compared with prehurricane populations within their respective habitats (Table 2); however, the magnitude of this difference was larger in forest populations.

Principal component 3 was negatively correlated with counts of lamellae. Values for PC 3 for forest lizards were not different from pre-hurricane forest populations at 4 months after the hurricane (Table 2), but they were significantly smaller 11 months after. In contrast, values for PC 3 in post-hurricane populations were significantly smaller than those in pre-hurricane urban populations at both 4 and 11 months.

Principal component 4 was strongly correlated with pelvic girdle width. Forest populations had significantly larger values for PC 4 at 4 but not at 11 months after the hurricane compared with pre-hurricane forest populations. Urban populations, in contrast, had significantly larger values for PC 4 at 4 and 11 months after the hurricane compared with pre-hurricane urban populations (Table 2).

Principal component 5 showed weak correlations with limb lengths and front toe lengths. For PC 5, we did not identify a significant interaction between hurricane and habitat; however, we did find that post-hurricane populations had larger values at all sampling dates (Table 2).

Univariate trait analyses

We next examined which univariate traits differed between habitats in response to the hurricane. We found a significant effect of the hurricane on overall body size (i.e. SVL; χ^2 = 175.833, P < 0.001), but no interaction with habitat (ANOVA: hurricane × habitat: χ^2 = 1.37, P = 0.50). Contrast differences showed that post-hurricane lizards were smaller than pre-hurricane lizards at 4 but not 11 months post-hurricane (Supporting Information, Table S11).

Furthermore, urban lizards were larger than forest lizards at all sampling dates (Fig. 3).

Non-parallel shifts in response to the hurricane

Our mixed effect models showed that six of the 12 traits evaluated had a significant interaction between hurricane and habitat, indicating differing trait responses to the hurricane between urban and forest populations. Four of the six traits with non-parallel responses were associated with toe morphology (front and rear toepad areas, rear toe length and rear lamellae count), whereas the two others were the head and pectoral girdle widths. The remaining six traits (SVL, head length, hindlimb length, pelvic girdle width, front toe length and front lamellae counts; Supporting Information, Table S11) responded in a similar manner to the hurricane in both urban and forest habitats (i.e. they showed no significant interaction of hurricane and habitat in our mixed effect models).

Forest populations had toepad areas (front and rear) that were significantly smaller 4 months after the hurricane than pre-hurricane (Fig. 4A, D; Supporting Information, Table S11). At 11 months, front toepad area in forest populations remained smaller than pre-hurricane values, but rear toepad area recovered to pre-hurricane values. In contrast, front toepad area in urban populations did not differ before and after the hurricane. As in the forest populations, rear toepad area in urban populations was significantly smaller at 4 but not at 11 months post-hurricane compared with pre-hurricane values. When contrasting toepad areas between habitats, we found that urban populations had larger toepad areas (front and rear) than forest populations at both sampling dates after the hurricane, but not beforehand.

We found a significant interaction between habitat and hurricane for rear but not front toe lengths (Fig. 4 C, F). Rear toe lengths were shorter in post-hurricane forest populations at both sampling dates. In contrast, post-hurricane urban populations had longer toe lengths at 11 but not 4 months after the hurricane (Supporting Information, Table S11). Likewise, we found a significant interaction between habitat and hurricane for the number of rear lamellae but not front lamellae. In forest habitats, populations had fewer lamellae on their rear toes after the hurricane compared with pre-hurricane populations, at both post-hurricane sampling dates (Fig. 4 B, E). In contrast, urban populations had fewer lamellae at 4 but not at 11 months after the hurricane. At 11 months after the hurricane, urban populations had more lamellae on their rear toes than pre-hurricane populations (Supporting Information, Table S11).

The pectoral girdle width increased after the hurricane, but this response lagged in urban populations. Urban populations had wider pectoral girdles at 11 but not

Table 2. Contrasts for factor difference for mixed effect models for principal component axes 1–5

Fixed effects	β	SE	*t*-ratio	*P*-value
Principal component 1				
Forest				
Before–4 months after	1.931	0.219	8.806	< 0.001
Before–11 months after	0.995	0.219	4.534	< 0.001
4–11 months after	−0.936	0.206	−4.553	< 0.001
Urban				
Before–4 months after	0.645	0.216	2.987	0.008
Before–11 months after	−0.541	0.214	−2.531	0.031
4–11 months after	−1.187	0.207	−5.741	< 0.001
Forest–urban interaction				
Before–4 months after	0.350	0.227	1.538	0.124
Before–11 months after	−0.936	0.207	−4.522	< 0.001
4–11 months after	−1.186	0.205	−5.783	< 0.001
Principal component 2				
Forest				
Before–4 months after	1.153	0.166	6.934	< 0.001
Before–11 months after	1.146	0.166	6.887	< 0.001
4–11 months after	−0.007	0.156	−0.047	0.443
Urban				
Before–4 months after	0.456	0.160	2.785	0.015
Before–11 months after	0.882	0.159	5.438	< 0.001
4–11 months after	0.426	0.110	2.717	0.018
Forest–urban interaction				
Before–4 months after	0.305	0.173	1.766	0.078
Before–11 months after	−0.392	0.157	−2.499	0.013
4–11 months after	0.041	0.156	0.263	0.793
Principal component 3				
Forest				
Before–4 months after	0.064	0.126	0.505	0.869
Before–11 months after	0.875	0.126	6.947	< 0.001
4–11 months after	0.812	0.118	6.876	< 0.001
Urban				
Before–4 months after	0.557	0.124	4.488	< 0.001
Before–11 months after	1.086	0.123	8.839	< 0.001
4–11 months after	0.529	0.119	4.456	< 0.001
Forest–urban interaction				
Before–4 months after	0.011	0.131	0.085	0.932
Before–11 months after	0.504	0.119	4.243	< 0.001
4–11 months after	0.221	0.118	1.880	0.061
Principal component 4				
Forest				
Before–4 months after	−0.449	0.121	−3.721	0.001
Before–11 months after	−0.190	0.121	−1.576	0.257
4–11 months after	0.259	0.113	2.287	0.058
Urban				
Before–4 months after	−0.754	0.119	−6.344	< 0.001
Before–11 months after	−0.889	0.118	−7.546	< 0.001
4–11 months after	−0.134	0.114	−1.179	0.466
Forest–urban interaction				
Before–4 months after	0.345	0.125	2.752	0.006
Before–11 months after	0.039	0.114	0.346	0.730
4–11 months after	−0.354	0.113	−3.131	0.002

Table 2. Continued

Fixed effects	β	SE	*t*-ratio	*P*-value
Principal component 5 (additive model shown)				
Before–4 months after	−0.338	0.085	−3.981	< 0.001
Before–11 months after	−0.226	0.084	−2.679	0.021
4–11 months after	0.112	0.080	1.391	0.346
Forest–urban interaction	0.140	0.068	2.071	0.039

The coefficients B shows the degree of change in the outcome variable and the t ratio is the difference in means over the standard error.
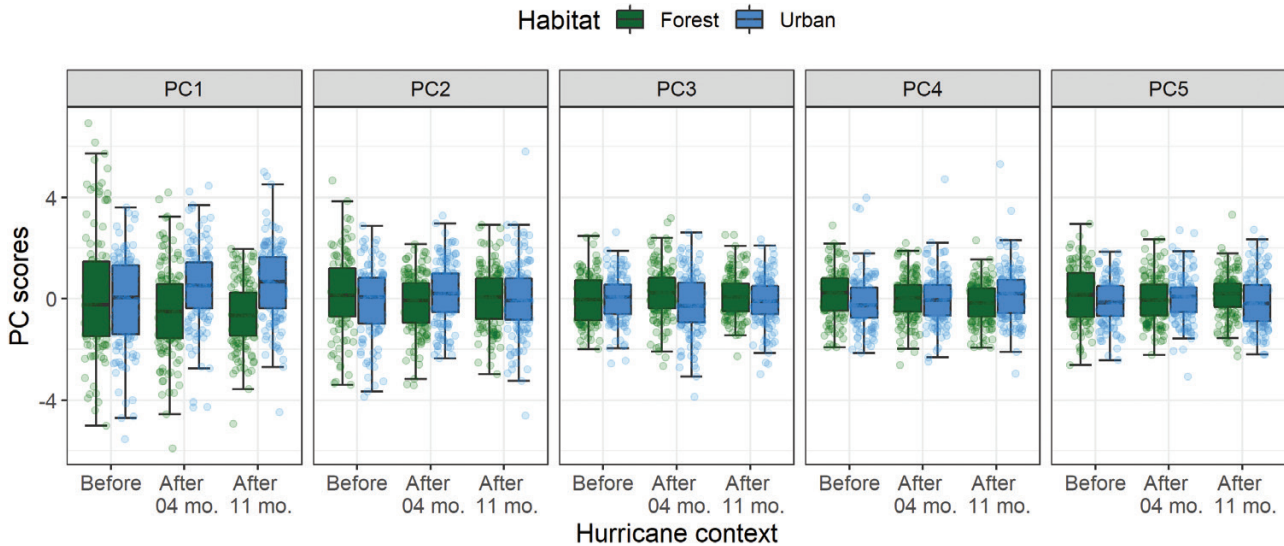
Figure 2. Principal components (PC) analysis of morphological traits of lizards. Different colours indicate urban and forest populations through time in the context of Hurricane Maria. Eigenvectors have been centred around the municipality mean for each hurricane context.

4 months after the hurricane (Supporting Information, Table S11). In contrast, forest populations had wider pectoral girdles widths at both post-hurricane sampling dates (Supporting Information, Table S11).

Head width was significantly larger in post-hurricane populations in both habitats. However, urban lizards had significantly wider heads at 11 but not at 4 months after the hurricane compared with pre-hurricane urban populations. We found the opposite pattern for head length, with post-hurricane lizards having shorter head lengths irrespective of habitat and post-hurricane sampling date (Supporting Information, Table S11).

Changes in traits associated with clinging performance

We found mostly non-significant differences between pre- and post-hurricane samples (Fig. 3 B, C). Specifically, neither habitat nor hurricane context was a significant factor in explaining variation in forelimb length (habitat: $\chi^2 = 0$, $P = 0.992$; hurricane context $\chi^2 = 1.395$, $P = 0.49$).

In contrast, hindlimb lengths showed parallel decreases in trait values at 4 months after the hurricane in both forest and urban populations. By 11 months after the hurricane, however, hindlimb lengths had returned to pre-hurricane values (Supporting Information, Table S11). Likewise, we found parallel decreases in the number of lamellae in the forefeet at 4 but not at 11 months after the hurricane (Supporting Information, Table S11).

Finally, we found that several toe traits showed non-parallel responses to the hurricane. Specifically, although most toe-related traits decreased in forest populations, for some traits we detect a lagged shift in the opposite direction of the change in forests among our urban populations.

DISCUSSION

Hurricanes are severe weather events that can drive drastic ecological changes (Lugo *et al.*, 2000; Lugo, 2008). However, the evolutionary consequences of hurricanes have only begun to be explored (Griffith
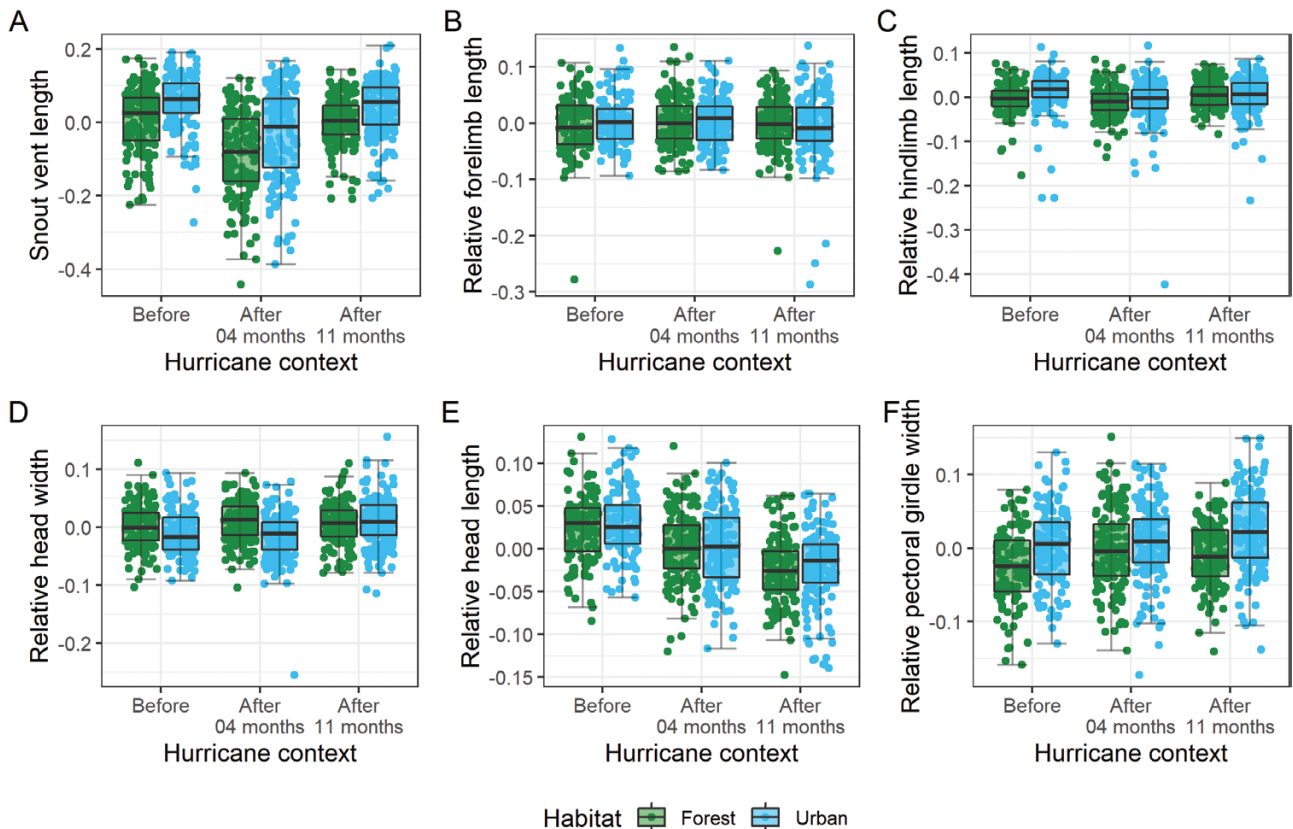
Figure 3. Values of traits sampled in urban and forest lizard populations across our sampling dates. A, snout–vent length (SVL) on a logarithmic scale. The other panels show the values relative to size calculated from the residuals of the logarithmic model of trait regressed against SVL. Data points were centred by the municipality. Many traits, including SVL, were reduced at 4 months after the hurricane and then increased to pre-hurricane values. F, pectoral girdle width increased with the hurricane.

et al., 2008). As such, we still have an in complete picture of how the increases of severity and frequency of extreme hurricanes that are predicted by many climate change scenarios will impact plant and animal species (Zhao *et al.*, 2009; Bender *et al.*, 2010). Likewise, we already know that human-induced environmental changes of different types (climate change, habitat destruction and invasive species) can act synergistically to increase the likelihood of local extinction (Johnstone *et al.*, 2016; Seidl *et al.*, 2016). Nonetheless, we do not yet understand fully how urbanization might interact with severe weather events to affect ecological and evolutionary dynamics.

We began this study primed with the notion that hurricanes can act as events of natural selection and that the survivors of an extreme weather event, such as an intense hurricane, could be a phenotypically non-random subset of the individuals alive at its onset. In the wake of the passage of the category 5 Hurricane Maria over the island of Puerto Rico in 2017, we thus set out, first, to explore whether populations of *A. cristatellus* differed in their morphology

as a response to the hurricane regardless of the habitat they occupy. Second, we evaluated whether anthropogenic populations differed in their phenotypic responses from forest populations. Finally, because prior research has shown that some traits associated with improved clinging performance are already prevalent in urban populations, we evaluated whether post-hurricane forest populations might converge on the urban phenotype of longer limbs and larger toepad areas with more adhesive lamellae.

A recent study found evidence of phenotypic natural selection in populations of the closely related species *Anolis scriptus*, which had longer forelimb, larger toepad area and shorter hindlimb after Hurricane Maria in the Turks and Caicos archipelago (Donihue *et al.*, 2018). Furthermore, experimental trials using *A. scriptus* showed that lizards with shorter hindlimb were more likely to resist being dislodged by strong unidirectional winds (Donihue *et al.*, 2018). Our results from Puerto Rico do not, in general, recapitulate the findings of Donihue *et al.* (2018). We found that (even after controlling
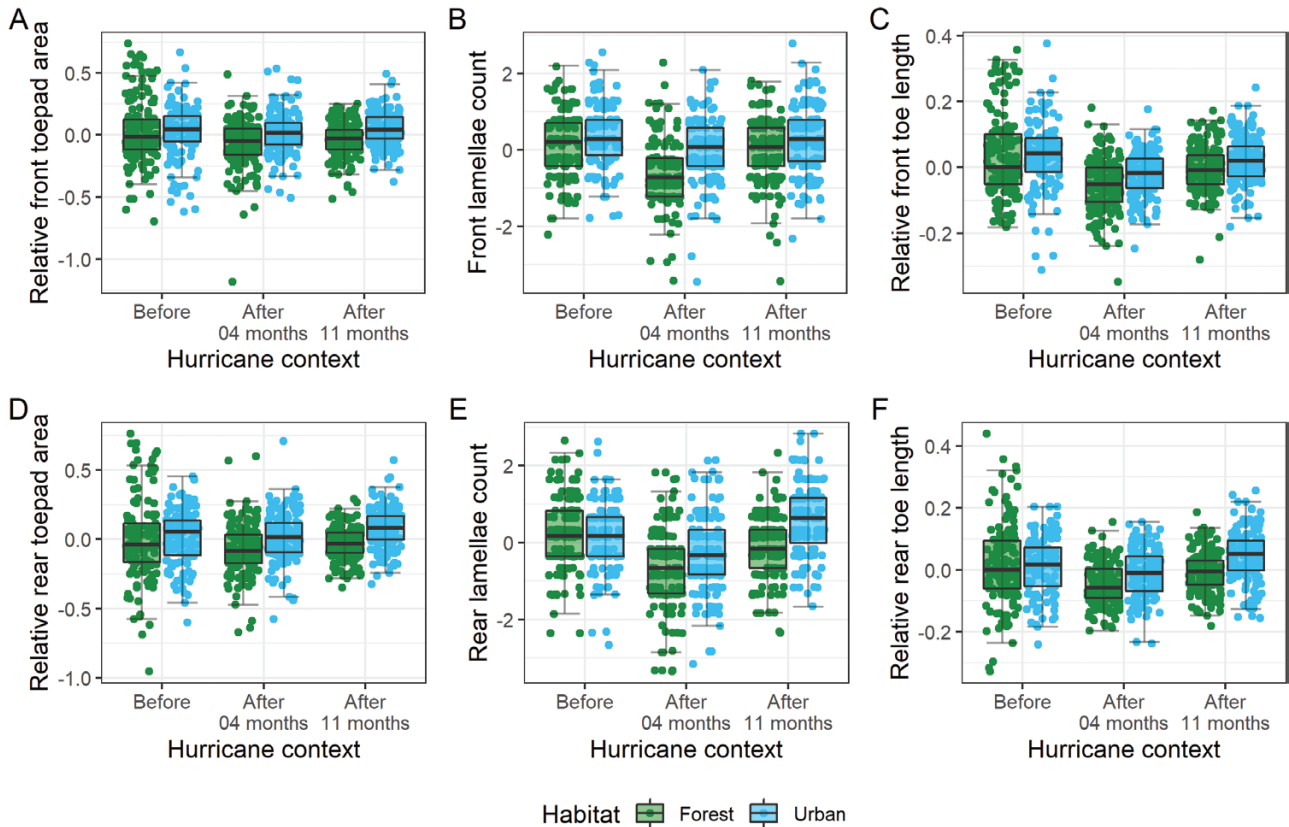
Figure 4. Relative trait values of toe morphology in urban and forest lizard populations across our sampling dates. The relative values are the residuals of the logarithmic model of trait regressed against body size [snout–vent length (SVL)]. Data points were centred by the municipality. Lizards sampled 4 months after the hurricane were significantly smaller than those sampled pre-hurricane.

for overall size) most of the traits that we measured decreased in the aftermath of the hurricane, and that this shift was similar in both urban and forest sites. Furthermore, the majority of the phenotypic change that we observed was followed by a quick recovery to pre-hurricane values.

One explanation for this pattern might be linked to differential mortality between large and small lizards during and after the storm event. During our post-hurricane surveys, we noted a remarkable scarcity of the larger males that would typically be easiest to find in urban and forest sites alike (because of their larger size and conspicuous perching behaviour; KJA-R and KMW, personal observation; Fig. 3). Unfortunately, our study was not designed to measure agespecific mortality, and thus it is not possible to rule out the alternative hypothesis of uniform mortality across age and size classes. However, we found that many size-relative trait values were smaller following the hurricane, indicating trait shifts irrespective of the observed shift in body size. Furthermore, some traits responded differently to the hurricane in urban and forest populations. Specifically, toe morphology in urban populations did not decrease at 4 months after

the hurricane, and some traits were significantly larger at 11 months after the hurricane compared with pre-hurricane urban populations. However, attribution of a mechanism behind changes in trait values relative to body size is complicated by our lack of understanding of how these traits affect survival during hurricanes. Thus, the selective effects of hurricanes appear, at least sometimes, to favour traits that impede dislodgement by winds through both an increase in clinging performance and a decrease in exposed surface area. We postulate that our findings are explained by a combination of increased mortality in larger-bodied males and differential survival of individuals with smaller traits relative to their body, which presumably enabled them to resist dislodgement by wind through a reduction of their overall body size or through another, as yet unknown, phenotype and habitat interaction.

ARE URBAN LIZARDS PRE-ADAPTED TO HURRICANES?

Ample examples in the literature show how shifts in habitat structure and use can induce rapid morphological divergence in anoles (Losos, 1990, 2009; Yuan *et al.*,

2019). At the population level, changes in vegetation can drive phenotypic divergence within one or two generations after transplantation of breeding pairs into extremely divergent habitats (Kolbe *et al.*, 2012). Likewise, some prior research indicates that divergence between urban and forest habitats can be driven, in part, by the adaptive response to urban habitat structure (including artificial structures; Winchell *et al.*, 2016, 2018b). Specifically, urban populations of *A. cristatellus*, the focal species of our study, have relatively longer limb lengths and larger toepad areas relative to their forest counterparts (Winchell *et al.*, 2016). These traits have been associated with increased clinging performance and differential selection after a hurricane (Kolbe, 2015; Donihue *et al.*, 2018).

In addition, larger toepad area was recently associated with species and populations that inhabit islands with higher hurricane frequency (Donihue *et al.*, 2020). This suggests that, over macroevolutionary time, hurricanes might impose regular bursts of strong and consistent directional selection on the toepad area of anole species, presumably driven by differential mortality during hurricanes. If so, we might expect that urban adaptations might function as pre-adaptations to decrease mortality associated with hurricanes. Such decreased mortality in urban populations could, in turn, result in convergence on the urban phenotype across habitat types. Instead, we found that toe morphology, captured by PC 1 in our PCA, was smaller at 4 months after the hurricane for forest populations but not for urban populations (Fig. 2). The significant interaction with habitat suggests that these morphological shifts were non-parallel between urban and forest populations (Fig. 2; Supporting Information, Table S11). Likewise, our univariate models for rear toepad area showed a positive interaction between urban habitat and the hurricane event. These models suggest that urban lizards had larger trait values than expected based on the marginal effects of the hurricane and urbanization alone. We verified this pattern by examining the contrasts of the marginal means for each term. This analysis revealed that toepad area (front and rear) decreased in forest but not in urban populations at 4 months after the hurricane (Supporting Information, Table S11).

Attributing a mechanism to our finding of morphological shifts associated with toepad morphology requires further examination. Prior studies comparing traits measured before and after Hurricanes Maria and Irma reported increases in trait values associated with clinging performance (Donihue *et al.*, 2018; Rabe *et al.*, 2020). However, Huey & Grant (2020) observed that the proposed agents of selection attributed to hurricanes remain untested, and they questioned whether increased toepad area

can increase survival in the wet and complex wind patterns typical of hurricanes. For example, after Hurricane Maria the surviving anole populations on the island of Dominica had relatively smaller toepad areas but greater clinging performance, suggesting an uncoupling of toepad area with greater clinging ability (Dufour *et al.*, 2019). Dufour *et al.* (2019) postulated that perhaps selection on clinging performance could be occurring on unmeasured aspects of the toepad, e.g. at the microscopic level, in the density and/or structure of the setae (the hairs covering lamellae that create toepad adhesion through Van der Waals forces). Each of these studies was conducted on different species and in different environmental contexts, which could account for the different results uncovered. Claws also appear to contribute to clinging ability (Song *et al.*, 2016; Yuan *et al.*, 2019), and claw morphology is related to structural differences in urban vs. forest habitats across several anole species (Falvey *et al.*, 2020). Specifically, urban claws tend to be shorter, perhaps owing to a decreased functional ability to interlock with smooth anthropogenic surfaces or to decrease obstruction of claws with the contact of toepads on surfaces (Naylor & Higham, 2019; Falvey *et al.*, 2020). Hence, we speculate cautiously that the biomechanical demands on adhesion from using smooth urban substrates (Kolbe, 2015; Winchell *et al.*, 2016, 2018b) might explain why toepad area did not decrease in urban areas as it did in our forest sites. We also highlight two additional important aspects for consideration in evaluating the findings of the present study: ontogeny and plasticity.

Ontogenetic variation can lead to different patterns of traits as an organism matures. If we sampled primarily subadult individuals immediately after the hurricane, and if our procedure to size correct our morphological data was insufficient to account for this effect, then our observed results could simply reflect trait values of individuals still undergoing ontogenetic change and not representative of the adult population. We believe that ontogeny is unlikely to explain our findings fully, for two reasons.

First, we sampled only sexually mature adult males (SVL > 40 mm; Andrews 1976). Although the generation time of *A. cristatellus* has not been measured explicitly in any prior study, our own research indicates that it is likely to be significantly > 1 year. For instance, Revell *et al.* (2010) recaptured nearly 25% of marked, fully grown males (> 55 mm on initial capture) a full 9 months after marking. Likewise, *A. cristatellus* reared in the laboratory do not reach the cut-off minimum size for this study until close to 1 year after hatching. As such, we consider it to be unlikely that lizards hatched post-hurricane would have been included in our sample taken 4 months after the hurricane; and few, if any,

of our sampled males at 11 months are likely to have hatched after the hurricane. Nonetheless, 4 months after the hurricane ~20% of our sample consisted of younger adult males (SVL from 40–50 mm) compared with samples from before and 11 months after the hurricane, for which ~95% of the sampled lizards had SVL > 50 mm. Although, we suspect that the effects of allometry over the size classes we sampled are relatively small, we nonetheless repeated all analyses, excluding the smallest lizards (SVL < 50 mm) from our sample at 4 months after the hurricane. Our results are qualitatively unchanged (Supporting Information, Table S12). To the extent that we found any evidence of phenotypic shifts (and excluding other factors, such as ontogeny or phenotypic plasticity), this could be attributable to differential survival of lizards during or after the hurricane, i.e. natural selection. It would not constitute evidence of evolution, because the lizards in our sample are almost certainly all survivors of the hurricane, not the progeny of survivors.

Second, some of the phenotypic differences that we have reported could also be explained by plasticity. Prior experiments conducted on other anole species have shown significant plasticity in the limb length of lizards reared from hatching on perches with different widths (Losos *et al.*, 2000; Kolbe & Losos, 2005; Langford *et al.*, 2014; Feiner *et al.*, 2020). Thus, plasticity arising in response to a modified post-hurricane environment could account for some of the differences we observed. Although plasticity in limb lengths cannot be ruled out, squamation is fixed at hatching and is not thought to be influenced by plasticity (Collette, 1961). Moreover, we believe it is unlikely that post-hurricane environmental change would yield the same plastic response for both forest and urban populations, given the structural and environmental differences between these habitats (Winchell *et al.*, 2018a; Avilés-Rodríguez & Kolbe, 2019).

Overall, our work adds to an increasing body of literature documenting phenotypic responses in lizards after major hurricanes (Donihue *et al.*, 2018, 2020; Dufour *et al.*, 2019; Rabe *et al.*, 2020). We expand on this work by examining how these responses vary between forest and urban populations. Our findings concur with several recent studies showing greater mortality rates of larger-bodied individuals that might be more likely to be dislodged by strong winds. We were not, however able to recapitulate the findings of increases in the size of traits that are associated with greater clinging ability that were documented by Donihue *et al.*, (2018). Interestingly, toe morphology (i.e. toepad area, toe length and number of lamellae) in urban populations either did not differ at all as a function

of the hurricane or showed a lagged shift towards greater trait size nearly 1 year after the event. We hypothesize that these contrasting phenotypic responses between urban and forest lizards might be driven by different biomechanical demands on urban lizards owing to the use of anthropogenic substrates (Winchell *et al.*, 2018a; Falvey *et al.*, 2020). Our results suggest that hurricanes can impose natural selection on *A. cristatellus* and that this selection might differ between urban and forest habitats; however, the direction of the phenotypic response was, in some cases, contrary to our prediction, indicating that the mechanisms underlying differences in response between urban and forest habitats are still unknown.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Linear mixed effect model parameter estimates and fits for principal component (PC) 1. Column headers denote factor levels with respect to time after the hurricane (4 and 11 months after) and habitat (forest or urban). The best-supported model (shown in bold) for PC 1 included the factors habitat and hurricane and their interaction.
Table S2. Linear mixed effect model parameter estimates and fits for principal component (PC) 2. Column headers denote factor levels with respect to time after the hurricane (4 and 11 months after) and habitat (forest or urban). The best-supported model (shown in bold) for PC 2 included the factors habitat and hurricane and their interaction.
Table S3. Linear mixed effect model parameter estimates and fits for principal component (PC) 3. Column headers denote factor levels with respect to time after the hurricane (4 and 11 months after) and habitat (forest or urban). The best-supported model (shown in bold) for PC 3 included the factors habitat and hurricane, but not their interaction.
Table S4. Linear mixed effect model parameter estimates and fits for principal component (PC) 4. Column headers denote factor levels with respect to time after the hurricane (4 and 11 months after) and habitat (forest or urban). The best-supported model (shown in bold) for PC 4 included the factors habitat and hurricane and their interaction.
Table S5. Linear mixed effect model parameter estimates and fits for principal component (PC) 5. Column headers denote factor levels with respect to time after the hurricane (4 and 11 months after) and habitat (forest or urban). The best-supported model (shown in bold) included only the factor hurricane.
Table S6. Results from mixed effect models for each trait evaluated.
Table S7. Loadings for the first five components from principal components analysis on the correlation matrix of *Anolis cristatellus* morphological traits. Loadings are defined as the correlation between each component and the original variable.
Table S8. Linear mixed effect model parameter estimates and fits for principal component (PC) 1. Column headers denote factor levels with respect to time after the hurricane (4 and 11 months after) and habitat (forest or urban). The best-supported model (shown in bold) for PC 1 included the factors habitat and hurricane, but not their interaction.

Table S9. Linear mixed effect model parameter estimates and fits for principal component (PC) 2. Column headers denote factor levels with respect to time after the hurricane (4 and 11 months after) and habitat (forest or urban). The best-supported model (shown in bold) for PC 2 included the factors habitat and hurricane and their interaction.

Table S10. Linear mixed effect model parameter estimates and fits for principal component (PC) 3. Column headers denote factor levels with respect to time after the hurricane (4 and 11 months after) and habitat (forest or urban). The best-supported model (shown in bold) for PC 3 included the factors habitat and hurricane and their interaction.

Table S11. Contrast difference for principal component axes from untransformed dataset.

Table S12. Contrast difference for principal component axes from dataset with lizards > 50 mm snout–vent length (SVL).