Hurricane effects on Neotropical lizards span geographic and phylogenetic scales

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Extreme climate events such as droughts, cold snaps, and hurricanes can be powerful agents of natural selection, producing acute selective pressures very different from the everyday pressures acting on organisms. However, it remains unknown whether these infrequent but severe disruptions are quickly erased by quotidian selective forces, or whether they have the potential to durably shape biodiversity patterns across regions and clades. Here, we show that hurricanes have enduring evolutionary impacts on the morphology of anoles, a diverse Neotropical lizard clade. We first demonstrate a transgenerational effect of extreme selection on toepad area for two populations struck by hurricanes in 2017. Given this short-term effect of hurricanes, we then asked whether populations and species that more frequently experienced hurricanes have larger toepads. Using 70 y of historical hurricane data, we demonstrate that, indeed, toepad area positively correlates with hurricane activity for both 12 island populations of *Anolis sagrei* and 188 *Anolis* species throughout the Neotropics. Extreme climate events are intensifying due to climate change and may represent overlooked drivers of biogeographic and large-scale biodiversity patterns.

cyclones | extreme climate events | rapid evolution | *Anolis*

Extreme climate events can be powerful agents of natural selection, but their consequences for large-scale biodiversity patterns are relatively unknown (1–3). Some theory predicts that infrequent, extreme selection events on ecological timescales will not have long-lasting evolutionary impacts on species (4). Few empirical studies have tested this prediction because extreme climate events are intrinsically rare (1, 5). Testing the long-term evolutionary effects of extreme climate events requires investigating two propositions: first, that extreme events actually impose strong selection and, second, that the evolutionary response to this selection is durable enough to shape large-scale diversity patterns. To date, such data only exist for Darwin's finches on a small, isolated island (6). There, researchers observed that extreme wet or dry years drive strong selection, but that alternating extreme climate events reverse the direction of selection and erase the evolutionary trends on decadal timescales (6). An alternative approach to tracking evolutionary change over time is to compare it over space, with the prediction that if extreme events have long-lasting impact, then populations in areas more often affected by such events will exhibit traits different from those in less affected areas. Here, we pair a cross-generational and spatial approach to investigate the evolutionary impact of hurricane-induced selection.

Immediately following Hurricanes Irma and Maria in 2017, we documented rapid, directional shifts in morphology in two island populations of a Caribbean anole (*Anolis scriptus*) in the Turks and Caicos Islands (TCI) (3). We found that posthurricane populations had larger subdigital toepads—a key trait in anoles responsible for clinging performance (3, 7). However, it remained unclear whether this selection would lead to persistent phenotypic differences in the population through time.

In 2019, we revisited the *A. scriptus* populations on Pine and Water Cays (TCI) to determine whether the hurricane effect had persisted in the 18 mo following the initial selective event. We resurveyed the populations following the same methods used in 2017 (*Methods*) (8). The relative surface areas of the forelimb and hindlimb toepads of the populations measured 18 mo after the hurricanes were statistically indistinguishable from those of

Significance

Extreme climate events can act as agents of natural selection. We demonstrate that lizards hit by Hurricanes Irma and Maria in 2017 passed on their large, strong-gripping toepads to the next generation of lizards. Moreover, we found that across 12 insular populations of *Anolis sagrei*, and 188 *Anolis* species across the Neotropics, those hit by more hurricanes in the last 70 y tended to have proportionately larger toepads. Our study suggests that hurricanes can have long-term and large-scale evolutionary impacts that transcend biogeographic and phylogenetic scales. As hurricanes become more severe due to climate change, these extreme climate events may have a much larger impact on the evolutionary trajectory of the affected ecological communities than previously appreciated.

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the hurricane survivors [forelimb: $\beta \pm$ SE: -0.009 ± 0.006, $t_{(290)} = -1.37$; $P = 0.1709$; hindlimb: $\beta \pm$ SE: -0.007 ± 0.006, $t_{(291)} = -1.278$; $P = 0.2024$], and remained significantly larger than those of the prehurricane populations [forelimb: $\beta \pm$ SE: 0.050 ± 0.007, $t_{(290)} = 7.117$; $P < 0.0001$; hindlimb: $\beta \pm$ SE: 0.038 ± 0.006, $t_{(291)} = 6.074$; $P < 0.0001$; Fig. 1; all analyses corrected for body size]. Moreover, these patterns of selection (3) and persistence (shown here) were parallel across both island populations (see *SI Appendix*, section 1, for full model output).

To test whether these trait shifts transcended generations, we further analyzed these data, restricting the analyses to those individuals measured in 2019 that, based upon estimated growth rates, most likely hatched after the hurricane and thus were offspring of hurricane survivors (*SI Appendix*). Results were unchanged: The relative surface area of the toepads of these next-generation lizards was indistinguishable from that of the hurricane survivors [forelimb: $\beta \pm$ SE: -0.006 ± 0.018, $t_{(267)} = -0.332$; $P = 0.7401$; hindlimb: $\beta \pm$ SE: -0.011 ± 0.015, $t_{(269)} = -0.711$; $P = 0.4774$] and remained significantly larger than the prehurricane populations [forelimb: $\beta \pm$ SE: 0.124 ± 0.020, $t_{(267)} = 6.086$; $P < 0.0001$; hindlimb: $\beta \pm$ SE: 0.093 ± 0.017, $t_{(269)} = 5.246$; $P < 0.0001$; Fig. 1]. The shifts were parallel on the two islands and robust for different growth rate estimates (*SI Appendix*, section 1).

These results demonstrate that changes following a catastrophic selective event were maintained over the short term. To test whether such events have longer-term impacts, we broadened our sampling and investigated whether variation in hurricane history across space correlated with variation in toepad characteristics at two geographical scales: within a single widespread species found on many Caribbean islands, and across the range of the *Anolis* genus.

To do so, we surveyed populations of the brown anole (*Anolis sagrei*), a species that is similar in ecology and morphology to *Anolis scriptus* (9). Across 12 islands that span the natural range of *A. sagrei* from the Bahamas to the Cayman Islands, the number of hurricane events in the preceding 70 y significantly predicted the surface area of an island population's toepads [forelimb: $\beta \pm$ SE: 0.050 ± 0.018, $t_{(9)} = 2.878$; $P = 0.0182$; hindlimb: $\beta \pm$ SE: 0.055 ± 0.014, $t_{(9)} = 3.881$; $P = 0.0037$; Fig. 2; analyses accounted for body size and phylogenetic nonindependence; see *Methods* for hurricane activity calculations and *SI Appendix*, section 2, for full model output]. Island populations of *A. sagrei* that experienced more hurricanes have relatively larger toepads than those that experienced fewer hurricanes.

We next investigated whether the hurricane-driven pattern would hold true across the distribution of the *Anolis* genus as a whole. We measured toepad size for 188 species of *Anolis* lizards across the clade's distribution (Fig. 3). Species that experienced more hurricanes had relatively larger toepads on both forelimbs [$\beta \pm$ SE: 0.061 ± 0.012, $t_{(165)} = 5.031$; $P < 0.0001$] and hindlimbs [$\beta \pm$ SE: 0.050 ± 0.013, $t_{(165)} = 3.90$; $P = 0.0001$; Fig. 3; analyses accounted for body size and phylogenetic nonindependence; *SI Appendix*, section 3]. We tested additional potential explanatory variables across the range of the anoles including local maximum tree height, air temperature, and precipitation and found no significant correlations with toepad area (*SI Appendix*, sections 4 and 5). Eliminating mainland species—which typically experience fewer hurricanes than their insular counterparts—yielded a similar positive relationship [forelimb: $\beta \pm$ SE: 0.056 ± 0.013, $t_{(121)} = 4.467$; $P < 0.0001$; hindlimb: $\beta \pm$ SE: 0.048 ± 0.012, $t_{(121)} = 3.882$; $P = 0.00017$; *SI Appendix*, section 3].

The correlation between toepad surface area and hurricane activity seen among populations of *A. sagrei* and across Neotropical

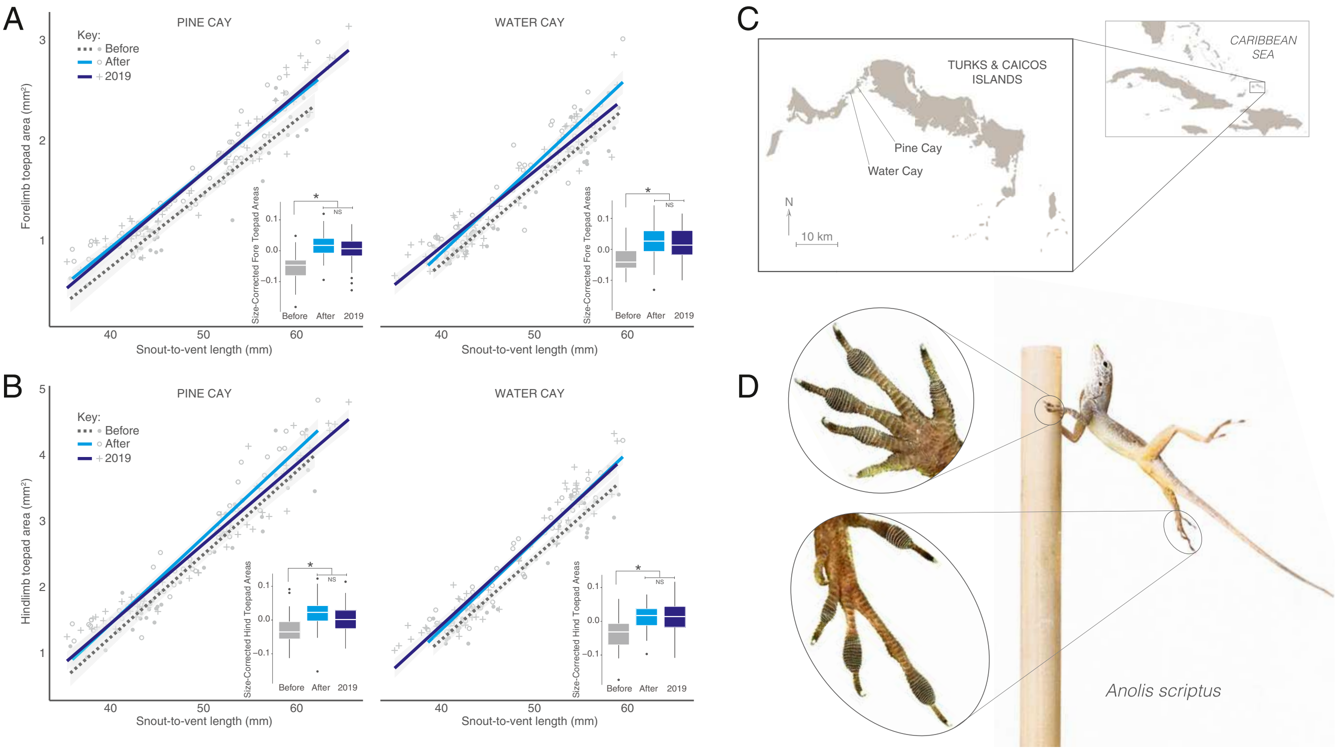

Fig. 1. *Anolis scriptus*, like other anoles, use specialized toepads to cling to surfaces (*D*, *Inset* images: A lizard clings to a perch while experiencing hurricane-force winds in a performance experiment; see ref. 3). Populations of *A. scriptus* on Pine and Water Cays in the TCI (*C*) that survived 2017's Hurricanes Irma and Maria had relatively larger toepads on average than the populations surveyed before the storms (3). When we resurveyed the populations in 2019 (*A* and *B*) following the storms, those body size-corrected differences in toepad area persisted.

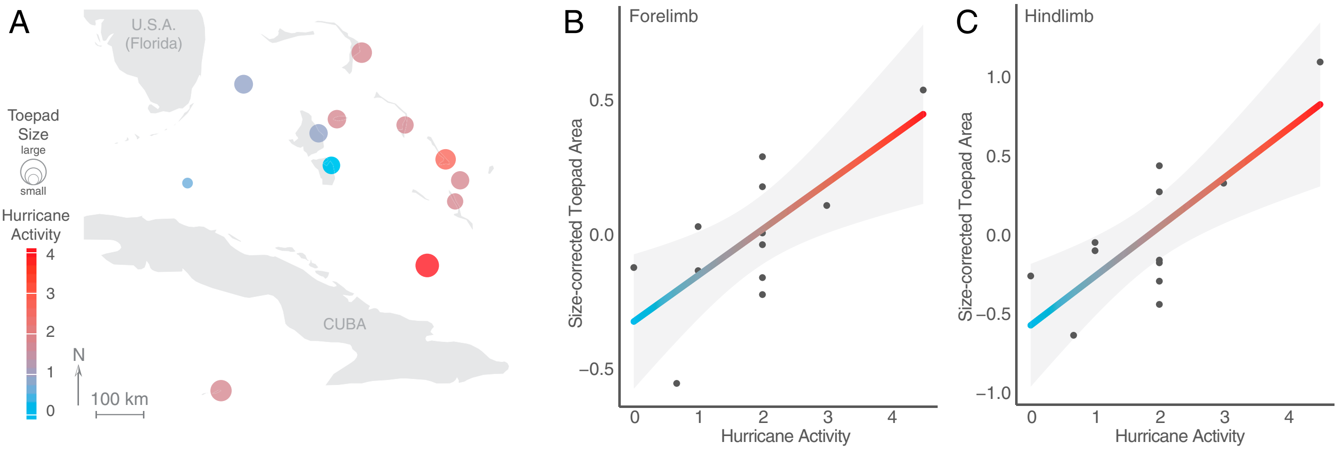

Fig. 2. By measuring toepad areas of individuals from 12 populations of *A. sagrei* (*A*), we found that populations that experienced more hurricanes in the last 70 y (red) had larger toepads than those that were hit less often (blue). In the map, each point corresponds to an island population, the size of the point corresponds to the relative toepad surface area of that population, and the color to the number of hurricanes experienced in the last 70 y. Regressions are of phylogenetically and body size-corrected toepad area residuals for forelimbs (*B*) and hindlimbs (*C*). See *SI Appendix* for additional detail about the hurricane activity calculation.

Anolis could arise in two ways. On one hand, selection for larger toepads, as seen in *A. scriptus* in the Turks and Caicos, may have long-lasting consequences that are not erased by different selection pressures in periods between hurricanes. Alternatively, hurricanes may change the environment in ways that change selection pressures in subsequent years when hurricanes do not occur. However, given that hurricane-prone areas tend to have shorter trees (*SI Appendix*, section 4) and that a general positive correlation between perch height and toepad area exists (9), one might expect hurricane-prone areas to have smaller toepads, the opposite of the trend we observed. More detailed analysis of how hurricanes affect vegetation structure vis-à-vis anole habitat use as well as long-term selection studies are needed to clarify this mechanism.

Our demonstration that rare but extreme events can impact evolution raises the further question of what role such events play in shaping phylogenetic patterns of trait diversity compared to other selective factors. Caribbean anoles are an excellent group in which to investigate this pattern because of the well-documented replicated patterns of adaptive radiation across Greater Antillean islands (9, 10). Anoles have repeatedly diverged into multiple habitat specialist types, termed ecomorphs, that differ in morphological traits related to habitat use. In the context of this adaptive divergence, we can ask what effect hurricane activity has on this variation in relative toepad surface area. For all ecomorphs, species in areas more frequently hit by hurricanes have larger toepads (*SI Appendix*, section 3). One might predict that the effect of hurricanes would differ among habitats—more arboreal species, for example, might be more exposed to the storm's force. Our analyses, however, find that the response to hurricanes was consistent and positive across habitat specialist types (*SI Appendix*, section 3). Moreover, hurricane activity explains a substantial portion of variation in relative toepad area (Table 1), revealing a hitherto-unsuspected driver of anole diversity and demonstrating that extreme events can be a major contributor to phenotypic diversity patterns at large phylogenetic and biogeographic scales.

More remains to be discovered about how variation in hurricane attributes (e.g., storm duration, prevailing direction, accompanying rain) affects the concurrent and posthurricane selective landscape for anoles. A preliminary analysis found no relationship between time since last hurricane and toepad area in our *A. sagrei* samples (*SI Appendix*, section 2.2); however, repeated sampling following storms is needed to fully address this question. Moreover, toepads are only one of several traits in anoles linked to clinging capacity, and so future work comparing limb morphology (11) and claw shape (12, 13) may yet reveal new insights into the biomechanical predictors of survivorship during storms (14, 15) and the clade-wide impacts of hurricanes on the morphology in this genus.

Hurricanes are intensifying due to climate change (16–18) and can be powerful agents of natural selection (3). As such, they may represent overlooked drivers of biogeographic and phylogenetic patterns, necessitating a global, cooperative effort to determine their ecological and evolutionary effects (19). For anoles, hurricanes are severe selective events, leading to population-level changes in morphology that persist across generations. Moreover, as evidenced by the relationship between toepad surface area and hurricane activity within and among *Anolis* species, hurricanes can have long-lasting evolutionary effects. Our study therefore demonstrates that extreme climate events can have enduring evolutionary impacts that transcend phylogenetic and geographic scales.

Methods

No statistical methods were used to predetermine sample sizes for any aspect of this study. This research was approved by the Turks and Caicos DECR (Permit 19-03-04-10), Bahamas Environment, Science, and Technology Commission (2015, 2016, 2017), Cayman Department of Environment (2015-ACSS078), and the Harvard Institutional Animal Care and Use Committee (26-11).

***Anolis scriptus* in Turks and Caicos.** Pine Cay and Water Cay—two small islands in the TCI—are home to the endemic Turks and Caicos anole, *Anolis s. scriptus*. Both islands are relatively small (Pine Cay, 350 ha; Water Cay, 250 ha), flat, and covered by vegetation that averages between 1 and 3 m in height. Adult Turks and Caicos anoles range in size between 40 and 65 mm in snout-to-vent length (SVL) and are sexually dimorphic: Adult females are smaller than males. The species is conspicuous and abundant and can typically be found perched on small branches in the lower 1.5 m of the islands' vegetation (20).

Between August 28 and September 4, 2017, we surveyed the *A. scriptus* populations on Pine Cay and Water Cay to establish baselines for the populations in anticipation of a conservation project. Following a direct hit by Hurricane Irma (September 8, 2017) and glancing blow by Hurricane Maria (September 22, 2017), we revisited the islands between October 16 and 20, 2017, to determine whether the surviving lizard populations differed significantly in morphology from the prehurricane populations (detailed in ref. 3).

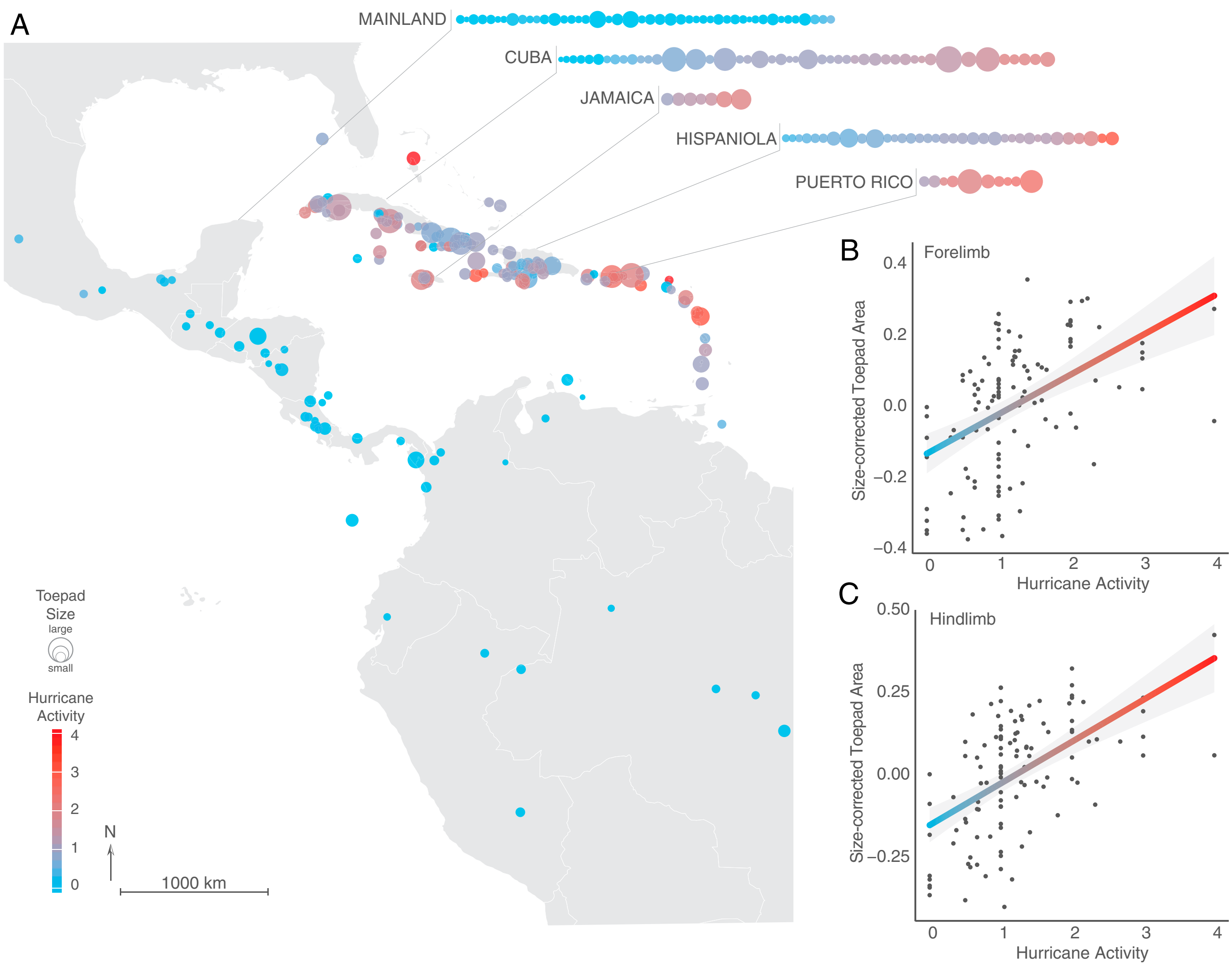

Fig. 3. Across the full geographic expanse of the *Anolis* clade, here with each point representing one of 188 species, toepad area—accounting for phylogeny and body size—is significantly positively correlated with the number of hurricanes experienced by that species over the last 70 y. (*A*) Each point represents the centroid of a species range, the color of that point indicates the mean number of hurricanes experienced across the species' range, and the size of the point corresponds to the average body size-corrected toepad area. For clarity, we highlighted the species on the mainland and on each of the Greater Antillean islands in callouts and ordered them by increasing hurricane activity. Size-corrected residuals of insular forelimb (*B*) and hindlimb (*C*) toepad areas are positively related to hurricane activity.

We repeated those surveys 18 mo (April 1 to 8, 2019) after our initial posthurricane survey. For those revisits, the same researchers (C.M.D., A.-C.F., and A.H.) walked the same, approximately 2-km-long transect on each island and caught lizards by hand or with a pole and fishing line slipknot (following ref. 3). In this way, we caught 117 lizards in 2019 (*SI Appendix*, Table S1.1).

We repeated the morphological measurements from the prehurricane and posthurricane sampling for those lizards caught in 2018 and 2019. In brief, the same researcher (A.H.) measured morphology using digital calipers (Mitutoyo 500-752), and C.M.D. took a high-resolution photograph of the right forefoot and hindfoot of each lizard using an iPhone 7 with a Moment Macro Lens attachment (see ref. 3 for additional details). Using ImageJ (version 1.51a; W. Rasband, National Institutes of Health, Bethesda, MD), C.M.D. measured the toepad area of the longest toe (digit III on forelimb, digit IV on hindlimb) on each lizard's right forelimb and hindlimb to the first scale after the toepad begins to widen (*SI Appendix*, Fig. S1).

Table 1. The explanatory power of ecomorph class and historical hurricane activity in the observed patterns of forelimb and hindlimb toepad surface area (*SI Appendix, Supplemental Material*)

Factor	Forelimb R^2	Hindlimb R^2
Hurricane Activity + Ecomorph	0.48	0.39
Hurricane Activity	0.20	0.13
Ecomorph	0.27	0.27

Identifying lizards hatched since the 2017 hurricanes. In order to determine whether the hurricanes had a sustained impact on the subsequent generation of *A. scriptus* on Pine Cay and Water Cay, we calculated an estimate for how large a lizard that hatched 1 y before the 2019 survey (and thus necessarily the offspring of hurricane survivors) might have grown. We used a logistic-by-length model (*SI Appendix*, section 1) that previous researchers have demonstrated adequately characterizes growth for small-bodied anoles that are ecologically similar to *A. scriptus* (21–24). This model predicted that the maximum size of an individual hatched on or after April 1, 2018, would be 46.13 mm for females and 51.55 mm for males during our 2019 survey. April 1, 2018, was chosen as the earliest included hatch date because lizards hatched earlier may have been derived from eggs that survived the hurricanes, even if their parents did not, or could be the result of sperm storage from a male who did not survive. We used these as cutoffs and analyzed all smaller lizards caught in 2019, assuming that these lizards had hatched within the previous year (*SI Appendix*, Table S1.3). See *SI Appendix*, section 1, for additional data and details.

Data analysis. Our primary aim was to determine whether the toepads of the *A. scriptus* surveyed in 2019 were statistically different from those measured in 2017, either before or after the hurricanes. To do so we used general linear models (GLMs) with the surface area of the forelimb toepads, or hindlimb toepads as the response variable. We included body size—SVL—as a factor in the GLM to account for differences in body size between the sampling times. In addition, we added a factor for island of origin—Pine Cay or Water Cay—and an additional fixed effect for each of the three sampling periods: prehurricane, posthurricane, and 2019. Both SVL and the toepad surface areas were $\log_{10}$ transformed to improve normality of the data. See *SI Appendix*, section 1, for complete model description. To evaluate differences between survey years, we used the "lsmeans" (25) and "effects" (26, 27) packages in R (R Core Team). We used the same analytical methods with the subset of lizards caught in 2019 and most likely having hatched within the previous year.

Comparative Analyses among Anole Populations and Species.

Identifying lizard localities. *Anolis sagrei* is a common and widespread anole and is ecologically similar to *A. scriptus* (9). It can be found on numerous islands in the West Indies, including the Bahamas, Cuba, Jamaica, and the Caymans. As part of an ongoing comparative study on *A. sagrei* across its range, C.M.D., A.J.G., and R.G.R. collected data on individuals from 12 islands. All of these lizards were captured in similar closed-canopy coppice forest in 2016 and 2017. We recorded the GPS locations of these sampling sites during the collection surveys.

Locality data for the entire genus were drawn from a dataset published by Velasco et al. (28). These locality data were collected from multiple sources including the Global Biodiversity Information Facility (GBIF) (https://www.gbif.org/), HerpNET (http://herpnet.org), and previously published distribution datasets (see ref. 28 for complete list of sources).

Calculating a hurricane activity measure. We used each of the lizard locality points—for field-caught *A. sagrei* and the Velasco et al. (28) records for the genus as a whole—to calculate the average number of hurricane hits for each species.

We first obtained the latitude–longitude position and maximum sustained wind speed for all tropical cyclones in the North Atlantic and eastern North Pacific basins between 1949 and 2017. Data from 1949 to 2016 were obtained from the International Best Track Archive for Climate Stewardship v03r10 (IBTrACS) (29). Because 2017 IBTrACS data were not yet available, we obtained the 2017 data from the Tropical Cyclone Extended Best Track dataset (EBT) (30). Both of these datasets provide position and maximum sustained wind speed data for each tropical cyclone every 6 h at 0000, 0600, 1200, and 1800 UTC. IBTrACS also provides data for some storms at intermediate times such as landfall events. Because 2017 EBT data did not include these intermediate times, we added them using National Hurricane Center storm reports (31) to ensure consistency across the dataset.

After all tropical cyclone data were compiled, we interpolated the storm position and wind speed to 24 evenly spaced time intervals between each available data point. These interpolated points provide an estimate of each tropical cyclone's position and intensity every 15 min, or occasionally somewhat more frequently when intermediate time points (e.g., landfall time) are also recorded. We interpolated both position and wind speed to ensure a hit was counted: Fast-moving storms may hit a population within the 6-h window and yet exceed the distance threshold at the 6-h increment, and had we not interpolated, they would not have been counted.

For each of the anole locality points, we counted the number of tropical cyclones that passed within a radius (30, 50, or 100 km), while meeting or exceeding a wind speed intensity threshold (65-, 80-, 100-kn sustained winds [$1 \text{ kn} = 0.514 \text{ m}\cdot\text{s}^{-1}$]) during the 1949 to 2017 period. We specified in our counting algorithm that each tropical cyclone could only produce a single hit at each GPS location, regardless of the number of time steps at which it satisfied the specified distance and intensity criteria, or whether the storm reversed direction and hit a locality a second time. We used MATLAB to calculate these hurricane counts (The MathWorks, 2019; *SI Appendix*, section 8). Using these data, we then calculated the mean hurricane hits for each species by averaging the hurricane counts for each locality recorded for each species. This resulted in a continuous hurricane activity measure. For our main analyses, we focused on strong hurricanes reaching or exceeding 80 kn of sustained wind speed (see *SI Appendix*, section 6, for additional thresholds), as we previously found in laboratory conditions that *A. scriptus* lizards were, on average, blown off perches at 74.3 ± 2.3 kn (3). We also focused on direct hits, within 30 km of a GPS point in the spatial database. We conducted a sensitivity analysis to investigate how different wind speeds and radii thresholds affected our models (*SI Appendix*, section 6). In general, we found that increasing the threshold radius decreased the explanatory power for our model, *ergo* very distant hurricanes did not substantially affect populations. We also found that more powerful hurricanes (wind speed reaching or exceeding 100 kn) had a stronger effect than weaker storms (*SI Appendix*, section 6). See *SI Appendix* for additional details and considerations about the hurricane activity measure.

Calculating mean tree heights. Using the same locality database employed in calculating the number of hurricanes for each species, we calculated the mean height of trees at that location using a tree heights dataset published by Simard et al. (32) in which they used 2005 satellite-based lidar to estimate global tree heights. We calculated mean tree heights within a 30-, 50-, and 100-km radius of each locality. The radii were chosen to match the radii of the hurricane activity algorithm. We then averaged these tree heights for each radius and each locality to calculate a mean tree height for every species in the database.

Measuring toepads. Toepad images of 10 *A. sagrei* individuals per island population were collected in the field by R.G.R., A.J.G., and C.M.D. and from museum specimens of all other species by D.L.M., H.K.F., and assistants using a flatbed scanner (Epson Perfection V500 Photo or Canon CanoScan LiDE 70). The preserved *Anolis* specimens used for this study are from the collections of the Harvard Museum of Comparative Zoology, Field Museum of Natural History, Institute of Ecology and Systematics (Havana, Cuba), and Steven Poe, University of New Mexico, Albuquerque, NM, and Richard Glor, University of Kansas, Lawrence, KS. For all species in the interspecific dataset, C.M.D. measured toepad surface area (ImageJ) of the third toe on the forelimb and the fourth (longest) toe on the hindlimb following the same methods as the *A. sagrei* and *A. scriptus* analyses (*SI Appendix*, Fig. S1). Three adult individuals were measured for each of 175 species, and those measurements were averaged to calculate a species mean. For five additional species, only two specimens were available, and eight species in the dataset had only one available specimen. While these species with fewer than three specimens were included in the published results, repeating the analysis with only those species with exactly three specimens yielded similar significant results. Because mismatches between a species' average toepad characteristics as estimated from our sample and the average hurricanes experienced by that species were potentially systematically exacerbated for widespread species, we repeated the whole-genus analysis without the seven most widespread species (*SI Appendix*, section 7). We found the same significant results.

Data Analysis.

Phylogenetic methods. The phylogeny of *Anolis sagrei* populations (*SI Appendix*, Fig. S2.1) was generated by pruning a larger tree previously inferred by van de Schoot (33). Briefly, the mitochondrial-encoded locus NADPH dehydrogenase subunit 2 (plus some postterminal tRNA-encoding sequence) was amplified and sequenced for specimens of *Anolis sagrei* from across the species' natural range. Contig assembly and manual alignment was performed using Geneious R9.1 (https://www.geneious.com). The optimal partitioning scheme and the model of molecular evolution best fitting each partition was determined using PartitionFinder v1.1.1 (34). van de Schoot used Bayesian inference to estimate the phylogeny of this group using MrBayes v3.2.6 (35) and found all of the islands included in our sample to be monophyletic; therefore, for the present study, we pruned the phylogeny down to a single individual per island. For most islands, the individual used for the pruned phylogeny was a lizard for which we had also collected morphological data. To represent the remaining islands (Eleuthera, South Bimini, Cay Sal, Cayman Brac) in the phylogeny, we selected an individual collected from the same site and at the same time as the lizards that were measured. For the phylogenetic comparative analyses spanning the entire genus, we used a recent tree by Poe et al. (36).

To account for phylogenetic nonindependence in our comparative datasets, either between the 12 *A. sagrei* populations or across the genus as a whole, we used phylogenetic comparative linear models evaluated using the phytools (37), caper (38), GEIGER (39), ape (40), and picante (41) packages in R (R Core Team).

Our phylogenetic generalized least-squares models took the form:

$$\log_{10}(\text{toepad area}) \sim \log_{10}(\text{SVL}) + \text{HurricaneActivity},$$

with delta and kappa transformations set to 1, and the lambda phylogenetic signal parameter freely estimated ("ML").

Spatial autocorrelation. For the *A. sagrei* and genus-wide analyses, we tested whether phylogenetic regression results were potentially influenced by residual spatial autocorrelation by constructing Moran's *I* correlograms. We calculated Moran's *I* using 25-km lag distances, e.g., all points separated by less than 25 km (in any direction), then points between 25 and 50 km apart, and so on to a maximum of 600 km. We tested for significance using randomization tests. Correlograms were generated using the correlog() function in the ncf package (42). We found no significant spatial autocorrelation in residuals of any regression model at any lag distance ($P > 0.10$ in all cases), suggesting that phylogenetic autocorrelation and hurricane activity can account for spatial patterns in toepads and regression results are not confounded by spatial autocorrelation. Thus, we did not consider spatial autocorrelation further (*SI Appendix*, Fig. S2.2, S3.1, and S3.6).

Data and Materials Availability. All data reported in this paper have been deposited in the Dryad digital repository (8).

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