Extreme climate events 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.

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.
the hurricane survivors [forelimb: $\beta \pm SE: -0.009 \pm 0.006$, $t_{(290)} = -1.37; P = 0.1709$; hindlimb: $\beta \pm SE: -0.007 \pm 0.006$, $t_{(291)} = -1.278; P = 0.2024$], and remained significantly larger than those of the prehurricane populations [forelimb: $\beta \pm SE: 0.050 \pm 0.007$, $t_{(290)} = 7.117; P < 0.0001$; hindlimb: $\beta \pm SE: 0.038 \pm 0.006$, $t_{(291)} = 6.074; P < 0.0001$; 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: $\beta \pm SE: -0.006 \pm 0.018$, $t_{(267)} = -0.332; P = 0.7401$; hindlimb: $\beta \pm SE: -0.011 \pm 0.015$, $t_{(290)} = -0.711; P = 0.4774$] and remained significantly larger than the prehurricane populations [forelimb: $\beta \pm SE: 0.124 \pm 0.020$, $t_{(267)} = 6.086; P < 0.0001$; hindlimb: $\beta \pm SE: 0.093 \pm 0.017$, $t_{(290)} = 5.246; P < 0.0001$; 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: $\beta \pm SE: 0.050 \pm 0.018$, $t_{(9)} = 2.878; P = 0.0182$; hindlimb: $\beta \pm SE: 0.055 \pm 0.014$, $t_{(9)} = 3.881; P = 0.0037$; Fig. 2; analyses accounted for body size and phylogenetic non-independence; 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 [$\beta \pm SE: 0.061 \pm 0.012$, $t_{(165)} = 5.031; P < 0.0001$] and hindlimbs [$\beta \pm SE: 0.050 \pm 0.013$, $t_{(165)} = 3.90; P = 0.0001$; 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: $\beta \pm SE: 0.056 \pm 0.013$, $t_{(121)} = 4.467; P < 0.0001$; hindlimb: $\beta \pm SE: 0.048 \pm 0.012$, $t_{(121)} = 3.882; P = 0.00017$; SI Appendix, section 3].

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

![Fig. 1](image-url) **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 TC (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-ACS5078), 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).
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).

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

| 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            |
had hatched within the previous year (SI Appendix, Table S1.3). See SI Appendix, section 1, for additional data and details.

Donihue et al. PNAS Latest Articles 2020

Our phylogenetic generalized least-squares models took the form:

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

with delta and kappa transformations set to 1, and the lambda phylogenetic effects as estimated from our sample and the average hurricanes experienced by that species were, on average, blown off perches at 74.3 km (3). We also focused on 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 analyses for all 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 LiDE70). The preserved A. sagrei 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 analyses for all 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 LiDE70). The preserved A. sagrei 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 analyses for all 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 LiDE70). The preserved A. sagrei 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 analyses for all 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 LiDE70). The preserved A. sagrei 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 analyses for all 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 LiDE70). The preserved A. sagrei 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 analyses for all species in the database.
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 toepad and regression results are not found by spatial autocorrelation. Thus, we did not consider spatial auto-correlation further (SI Appendix, Fig. 52.2, 53.1, and 53.6).

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

ACKNOWLEDGMENTS. This work was made possible thanks to the Pine Cay Homeowners Association with fieldwork and logistical support from C. Santoro and E. Bell. We also thank E. Salamanca at the TCI Department of Environment and Coastal Resources (DECR). This work was funded by the following: National Science Foundation (NSF), IOS-1354620 to J.B.L. and A.H.; NSF, RAPID ISO-1806420 to J.J.K. and J.B.L.; NSF, Postdoctoral Fellowship 1609284 to C.M.D.; NSF, Doctoral Dissertation Improvement Grant Division of Environmental Biology 1500761 to A.J.G.; Harvard Museum of Comparative Zoology Putnam Expedition Grant to R.G.R.; Research Foundation Fland- ers Postdoctoral Fellowship 12IB819N to S.B.; Dirección General Asuntos del Personal—Universidad Nacional Autónoma de México Postdoctoral Fel- lowship to J.A.V.; and Natural Sciences and Engineering Research Council of Canada Discovery Grant 499376 to D.L.M. In addition, this publication was made possible through the support of a grant from the John Tem- pleton Foundation. The opinions expressed in this publication are those of the author(s) and do not necessarily reflect the views of the John Templeton Foundation.