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1 Classification: Biological Sciences: Evolution

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4 **Hurricane Effects on Neotropical Lizards Span Geographic and Phylogenetic Scales**

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7 C.M. Donihue<sup>1\*</sup>, A. Kowaleski<sup>2</sup>, J.B. Losos<sup>1,3</sup>, A. Algar<sup>4</sup>, S. Baeckens<sup>5,6</sup>, R.W. Buchkowsky<sup>7</sup>,  
8 A.-C. Fabre<sup>8</sup>, H.K. Frank<sup>9,10</sup>, A.J. Geneva<sup>1,11</sup>, R.G. Reynolds<sup>12</sup>, J.T. Stroud<sup>1</sup>, J.A. Velasco<sup>13</sup>,  
9 J.J. Kolbe<sup>14</sup>, D.L. Mahler<sup>15</sup>, A. Herrel<sup>5,16,17</sup>

10 <sup>1</sup>Department of Biology, Washington University in St. Louis, St. Louis MO, USA

11 <sup>2</sup>Department of Meteorology and Atmospheric Science, The Pennsylvania State University,  
12 University Park PA, USA

13 <sup>3</sup> Living Earth Collaborative, Washington University in St. Louis, St. Louis MO, USA

14 <sup>4</sup> School of Geography, University of Nottingham, Nottingham NG7 2RD, UK

15 <sup>5</sup> Functional Morphology Lab, Department of Biology, University of Antwerp Wilrijk, BE

16 <sup>6</sup> Department of Biological Science, Macquarie University, Sydney, AU

17 <sup>7</sup> School of Forestry & Environmental Studies, Yale University, New Haven CT, USA

18 <sup>8</sup> Department of Life Sciences, The Natural History Museum, London, UK

19 <sup>9</sup> Department of Pathology, Stanford University, Stanford CA, USA

20 <sup>10</sup> Department of Ecology and Evolutionary Biology, Tulane University, New Orleans, LA, USA

21 <sup>11</sup> The Academy of Natural Sciences of Drexel University, Philadelphia PA, USA

22 <sup>12</sup> Department of Biology, University of North Carolina Asheville, Asheville NC, USA

23 <sup>13</sup> Centro de Ciencias de la Atmósfera, Universidad Nacional Autónoma de México, Mexico  
24 City, MX

25 <sup>14</sup> Department of Biological Sciences, University of Rhode Island, Kingston RI, USA

26 <sup>15</sup> Department of Ecology of Ecology and Evolutionary Biology, University of Toronto, Toronto  
27 ON, CA

28 <sup>16</sup> UMR7179, CNRS/MNHN, 55 rue Buffon, Paris, FR

29 <sup>17</sup> Evolutionary Morphology of Vertebrates, Ghent University, K. L. Ledeganckstraat 35, Ghent,  
30 BE

31

32 \*Correspondence author: Colin M. Donihue, Department of Biology, Washington University in  
33 St. Louis, St. Louis MO, USA; colindonihue@gmail.com

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

49

50 Keywords: Cyclones, Extreme Climate Events, Rapid Evolution, *Anolis*

51

52 **Significance statement:** Extreme climate events can act as agents of natural selection. We  
53 demonstrate that lizards hit by Hurricanes Irma and Maria in 2017 passed on their large, strong-  
54 gripping toepads to the next generation of lizards. Moreover, we found that across 12 insular  
55 populations of *A. sagrei*, and 188 *Anolis* species across the neotropics, those hit by more  
56 hurricanes in the last 70 years tended to have proportionately larger toepads. Our study suggests

57 that hurricanes can have long-term and large-scale evolutionary impacts that transcend  
58 biogeographic and phylogenetic scales. As hurricanes become more severe due to climate  
59 change, these extreme climate events may have a much larger impact on the evolutionary  
60 trajectory of the affected ecological communities than previously appreciated.

61

62

63

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

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

86           In 2019, we revisited the *A. scriptus* populations on Pine and Water Cays (TCI) to  
87   determine whether the hurricane effect had persisted in the 18 months following the initial  
88   selective event. We resurveyed the populations following the same methods used in 2017 (see  
89   Methods). The relative surface areas of the fore- and hind limb toepads of the populations  
90   measured 18 months after the hurricanes were statistically indistinguishable from those of the  
91   hurricane survivors (forelimb:  $\beta \pm \text{s.e.}: -0.009 \pm 0.006$ ,  $t_{290} = -1.37$ ;  $P = 0.1709$ ; hind limb:  $\beta \pm$   
92    $\text{s.e.}: -0.007 \pm 0.006$ ,  $t_{291} = -1.278$ ;  $P = 0.2024$ ), and remained significantly larger than those of  
93   the pre-hurricane populations (forelimb:  $\beta \pm \text{s.e.}: 0.050 \pm 0.007$ ,  $t_{290} = 7.117$ ;  $P < 0.0001$ ; hind  
94   limb:  $\beta \pm \text{s.e.}: 0.038 \pm 0.006$ ,  $t_{291} = 6.074$ ;  $P < 0.0001$ ; Fig. 1; all analyses corrected for body  
95   size). Moreover, these patterns of selection (3) and persistence (shown here) were parallel across  
96   both island populations (see Appendix 1 for full model output).

97           To test whether these trait shifts transcended generations, we further analyzed these data,  
98   restricting the analyses to those individuals measured in 2019 that, based upon estimated growth  
99   rates, most likely hatched after the hurricane and thus were offspring of hurricane survivors  
100   (Supplemental Information). Results were unchanged: the relative surface area of the toepads of  
101   these next-generation lizards was indistinguishable from that of the hurricane survivors  
102   (forelimb:  $\beta \pm \text{s.e.}: -0.006 \pm 0.018$ ,  $t_{267} = -0.332$ ;  $P = 0.7401$ ; hind limb:  $\beta \pm \text{s.e.}: -0.011 \pm 0.015$ ,

103  $t_{269} = -0.711$ ;  $P = 0.4774$ ), and remained significantly larger than the pre-hurricane populations  
104 (forelimb:  $\beta \pm \text{s.e.}: 0.124 \pm 0.020$ ,  $t_{267} = 6.086$ ;  $P < 0.0001$ ; hind limb:  $\beta \pm \text{s.e.}: 0.093 \pm 0.017$ ,  
105  $t_{269} = 5.246$ ;  $P < 0.0001$ ; Fig. 1). The shifts were parallel on the two islands and robust for  
106 different growth rate estimates (Appendix 1).

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

112         To do so, we surveyed populations of the brown anole (*A. sagrei*), a species that is  
113 similar in ecology and morphology to *A. scriptus* (8). Across 12 islands that span the natural  
114 range of *A. sagrei* from the Bahamas to the Cayman Islands, the number of hurricane events in  
115 the preceding 70 years significantly predicted the surface area of an island population's toepads  
116 (forelimb:  $\beta \pm \text{s.e.}: 0.050 \pm 0.018$ ,  $t_9 = 2.878$ ;  $P = 0.0182$ ; hind limb:  $\beta \pm \text{s.e.}: 0.055 \pm 0.014$ ,  $t_9 =$   
117  $3.881$ ;  $P = 0.0037$ ; Fig. 2; analyses accounted for body size and phylogenetic non-independence;  
118 see Methods for hurricane activity calculations and Appendix 2 for full model output). Island  
119 populations of *A. sagrei* that experienced more hurricanes have relatively larger toepads than  
120 those that experienced fewer hurricanes.

121         We next investigated whether the hurricane-driven pattern would hold true across the  
122 distribution of the *Anolis* genus as a whole. We measured toepad size for 188 species of *Anolis*  
123 lizards across the clade's distribution (Fig. 3). Species that experienced more hurricanes had  
124 relatively larger toepads on both forelimbs ( $\beta \pm \text{s.e.}: 0.061 \pm 0.012$ ,  $t_{165} = 5.031$ ;  $P < 0.0001$ ) and  
125 hind limbs ( $\beta \pm \text{s.e.}: 0.050 \pm 0.013$ ,  $t_{165} = 3.90$ ;  $P = 0.0001$ ; Fig 3; analyses accounted for body

126 size and phylogenetic non-independence; Appendix 3). We tested additional potential  
127 explanatory variables across the range of the anoles including local maximum tree height, air  
128 temperature, and precipitation and found no significant correlations with toepad area (Appendix  
129 4, Appendix 5). Eliminating mainland species – which typically experience fewer hurricanes  
130 than their insular counterparts – yielded a similar positive relationship (forelimb:  $\beta \pm \text{s.e.}: 0.056$   
131  $\pm 0.013$ ,  $t_{121} = 4.467$ ;  $P < 0.0001$ ; hind limb:  $\beta \pm \text{s.e.}: 0.048 \pm 0.012$ ,  $t_{121} = 3.882$ ;  $P = 0.00017$ ;  
132 Appendix 3).

133         The correlation between toepad surface area and hurricane activity seen among  
134 populations of *A. sagrei* and across Neotropical *Anolis* could arise in two ways. On one hand,  
135 selection for larger toepads, as seen in *A. scriptus* in the Turks and Caicos, may have long-lasting  
136 consequences that are not erased by different selection pressures in periods between hurricanes.  
137 Alternatively, hurricanes may change the environment in ways that change selection pressures in  
138 subsequent years when hurricanes don't occur. However, given that hurricane-prone areas tend  
139 to have shorter trees (Appendix 4) and that a general positive correlation between perch height  
140 and toepad area exists (8), one might expect hurricane-prone areas to have smaller toepads, the  
141 opposite of the trend we observed. More detailed analysis of how hurricanes affect vegetation  
142 structure vis-à-vis anole habitat use, as well as long-term selection studies, are needed to clarify  
143 this mechanism.

144         Our demonstration that rare but extreme events can impact evolution raises the further  
145 question of what role such events play in shaping phylogenetic patterns of trait diversity  
146 compared to other selective factors. Caribbean anoles are an excellent group in which to  
147 investigate this pattern because of the well-documented replicated patterns of adaptive radiation  
148 across Greater Antillean islands (8, 9). Anoles have repeatedly diverged into multiple habitat

149 specialist types, termed ecomorphs, that differ in morphological traits related to habitat use. In  
150 the context of this adaptive divergence, we can ask what effect hurricane activity has on this  
151 variation in relative toepad surface area. For all ecomorphs, species in areas more frequently hit  
152 by hurricanes have larger toepads (Appendix 3). One might predict that the effect of hurricanes  
153 would differ among habitats—more arboreal species, for example, might be more exposed to the  
154 storm’s force. Our analyses, however, find that the response to hurricanes was consistent and  
155 positive across habitat specialist types (Appendix 3). Moreover, hurricane activity explains a  
156 substantial portion of variation in relative toepad area (Table 1), revealing a hitherto unsuspected  
157 driver of anole diversity and demonstrating that extreme events can be a major contributor to  
158 phenotypic diversity patterns at large phylogenetic and biogeographic scales.

159         More remains to be discovered about how variation in hurricane attributes (e.g., storm  
160 duration, prevailing direction, accompanying rain) affects the concurrent and post-hurricane  
161 selective landscape for anoles. A preliminary analysis found no relationship between time since  
162 last hurricane and toepad area in our *A. sagrei* samples (Appendix 2.2); however, repeated  
163 sampling following storms is needed to fully address this question. Moreover, toepads are only  
164 one of several traits in anoles linked to clinging capacity, and so future work comparing limb  
165 morphology (10) and claw shape (11, 12) may yet reveal new insights into the biomechanical  
166 predictors of survivorship during storms (13, 14) and the clade-wide impacts of hurricanes on the  
167 morphology in this genus.

168         Hurricanes are intensifying due to climate change (15–17) and can be powerful agents of  
169 natural selection (3). As such, they may represent overlooked drivers of biogeographic and  
170 phylogenetic patterns, necessitating a global, cooperative effort to determine their ecological and  
171 evolutionary effects (18). For anoles, hurricanes are severe selective events, leading to



172 population-level changes in morphology that persist across generations. Moreover, as evidenced  
173 by the relationship between toepad surface area and hurricane activity within and among *Anolis*  
174 species, hurricanes can have long-lasting evolutionary effects. Our study therefore demonstrates  
175 that extreme climate events can have enduring evolutionary impacts that transcend phylogenetic  
176 and geographic scales.

177 **References and Notes:**

- 178 1. P. R. Grant, B. R. Grant, R. B. Huey, M. T. J. Johnson, A. H. Knoll, J. Schmitt, Evolution  
179 caused by extreme events. *Phil. Trans. R. Soc. B* 372, 20160146 (2017).
- 180 2. S. C. Campbell-Staton, Z. A. Cheviron, N. Rochette, J. Catchen, J.B. Losos, S. V. Edwards,  
181 Winter storms drive rapid phenotypic, regulatory, and genomic shifts in the green anole  
182 lizard. *Science* 357, 495-498 (2017).
- 183 3. C. M. Donihue, A. Herrel, A.-C. Fabre, A. Kamath, A. J. Geneva, T. W. Schoener, J. J.  
184 Kolbe, J. B. Losos, Hurricane-induced selection on the morphology of an island lizard.  
185 *Nature* 560, 88-91 (2018).
- 186 4. S. J. Gould, The paradox of the first tier: an agenda for Paleobiology. *Paleobiology* 11, 2-12  
187 (1985).
- 188 5. P. R. Grant, Evolution, climate change, and extreme events. *Science* 357, 451-452 (2017).
- 189 6. P. R. Grant, B. R. Grant, Unpredictable evolution in a 30-year study of Darwin's finches.  
190 *Science* 296, 707-711 (2002).
- 191 7. D. J. Irschick, A. Herrel, B. Vanhooydonck, Whole-organism studies of adhesion in pad-  
192 bearing lizards: creative evolutionary solutions to functional problems. *J. Comp. Physiol. A*.  
193 192, 1169-1177 (2006).
- 194 8. J. B. Losos, Lizards in an evolutionary tree: ecology and adaptive radiation of anoles (Univ.  
195 of California Press, Berkeley, 2009).
- 196 9. E. E. Williams, The origin of faunas. Evolution of lizard congeners in a complex island  
197 fauna: A trial analysis. *Evol. Biol.* 6, 47-89 (1972).
- 198 10. J. Kolbe, Effects of hind-limb length and perch diameter on clinging performance in *Anolis*  
199 lizards from the British Virgin Islands. *J. Herp.* 49, 284-290 (2015).
- 200 11. P. A. Zani, The comparative evolution of lizard claw and toe morphology and clinging  
201 performance. *J. Evol. Biol.* 13, 316-325 (2000).
- 202 12. K. E. Crandell, A. Herrel, M. Sasa, J. B. Losos, K. Autumn, Stick or grip? Co-evolution of  
203 adhesive toepads and claws in *Anolis* lizards. *Zoology* 117, 363-369 (2014).
- 204 13. M. Denny, Extreme drag forces and the survival of wind- and water-swept organisms. *J. Exp.*  
205 *Biol.* 194, 97-115 (1994).
- 206 14. M. Denny, Predicting physical disturbance: Mechanistic approaches to the study of  
207 survivorship on wave-swept shores. *Ecol. Monographs* 65, 371-418 (1995).
- 208 15. G. C. Hegerl, H. Hanlon, C. Beierkuhnlein, Climate science: elusive extremes. *Nat. Geosci.*  
209 4, 142-143 (2011).
- 210 16. A. H. Sobel, S. J. Camargo, T. M. Hall, C.-Y. Lee, M. K. Tippett, A. A. Wing, Human  
211 influence on tropical cyclone intensity. *Science* 353, 242-246 (2016).
- 212 17. K. J. E. Walsh, J. L. McBride, P. J. Klotzbach, S. Balachandran, S. J. Camargo, G. Holland,  
213 T. R. Knutson, J. P. Kossin, T. Lee, A. Sobel, M. Sugi, Tropical cyclones and climate  
214 change. *Wire's Climate Change* 7, 65-89 (2016).

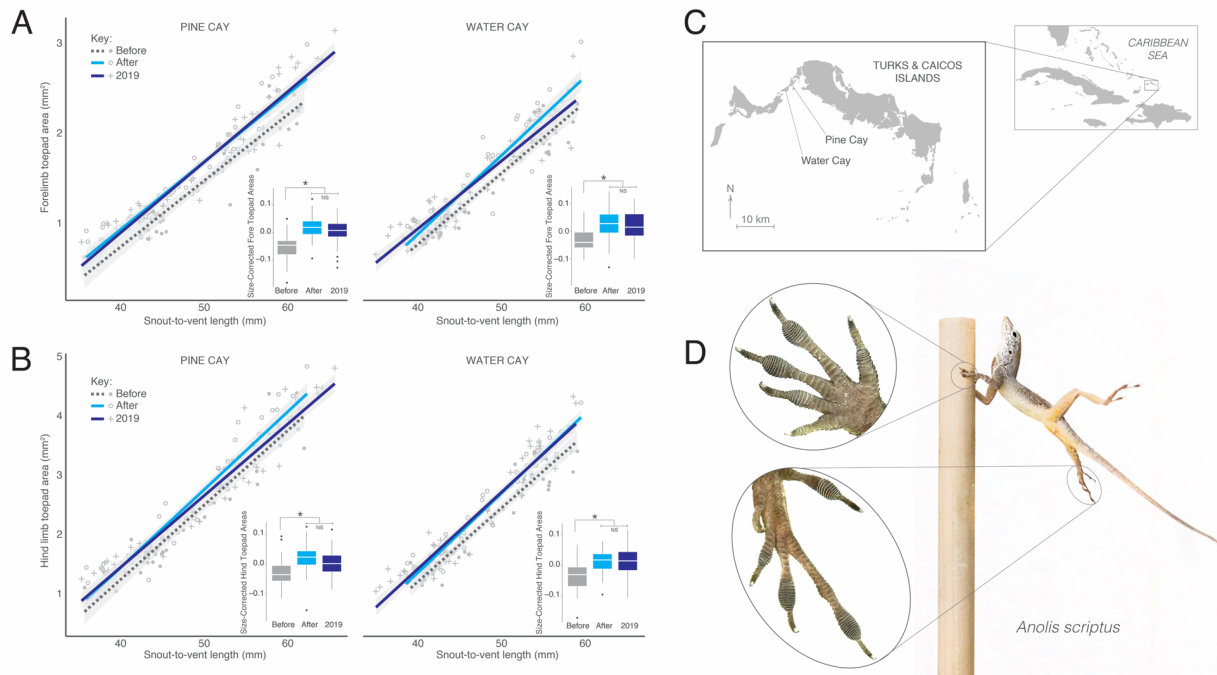
215 18. J. N. Pruitt, A. G. Little, S. J. Majumadar, T. W. Schoener, D. N. Fisher, Call-to-action: A  
216 global consortium for tropical cyclone ecology. *Trends Ecol. Evol.* 34, 588-590 (2019).

<b>Factor</b>	<b>Forelimb R<sup>2</sup></b>	<b>Hind Limb R<sup>2</sup></b>
Hurricane Activity + Ecomorph	0.50	0.40
Hurricane Activity	0.19	0.11
Ecomorph	0.29	0.26

217

218 **Table 1:** The explanatory power of ecomorph class and historical hurricane activity in the  
 219 observed patterns of forelimb and hind limb toepad surface area (see Supplemental Material).

220



221

222

**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 3). Populations of *A. scriptus* on Pine and Water Cays in the Turks and Caicos  
Islands (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.

223

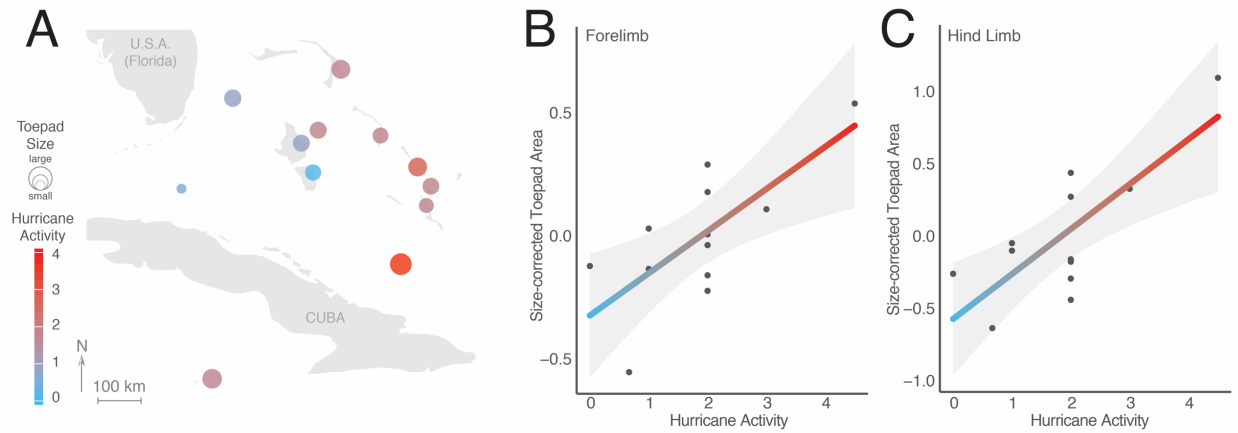
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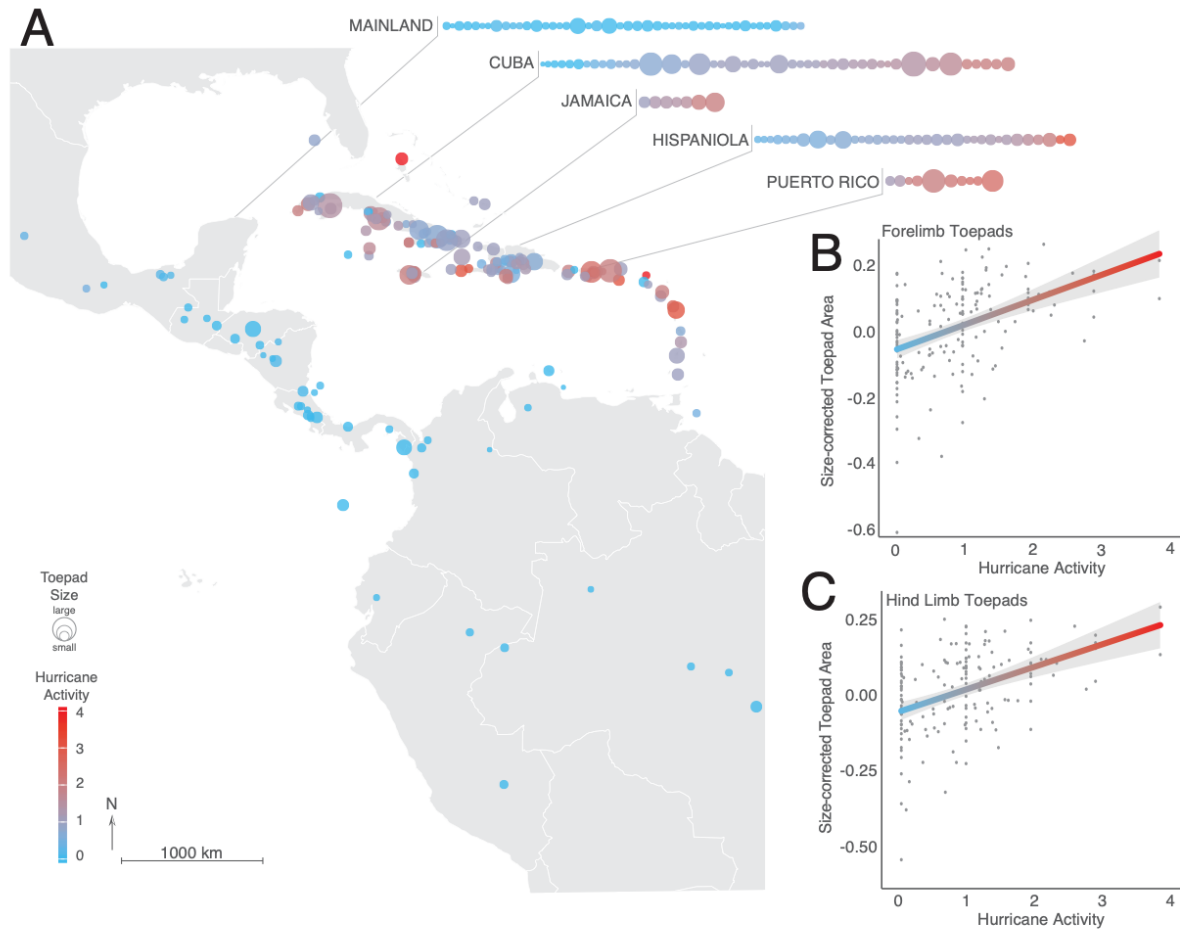
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228



229  
 230 **Fig 2.** By measuring toepad areas of individuals from 12 populations of *A. sagrei* (A), we found  
 231 that populations that experienced more hurricanes in the last 70 years (red) had larger toepads  
 232 than those that were hit less often (blue). In the map, each point corresponds to an island  
 233 population, the size of the point corresponds to the relative toepad surface area of that  
 234 population, and the color to the number of hurricanes experienced in the last 70 years.  
 235 Regressions are of phylogenetically and body-size-corrected toepad area residuals for forelimbs  
 236 (B) and hind limbs (C). See Supplemental Information for additional detail about the hurricane  
 237 activity calculation.



238

239 **Fig 3.** Across the full geographic expanse of the *Anolis* clade, here with each point representing

240 one of 188 species, toepad area – accounting for phylogeny and body size – is significantly

241 positively correlated with the number of hurricanes experienced by that species over the last 70

242 years. (A) Each point represents the centroid of a species range, the color of that point indicates

243 the mean number of hurricanes experienced across the species’ range, and the size of the point

244 corresponds to the average body-size-corrected toepad area. For clarity, we highlighted the

245 species on the mainland and on each of the Greater Antillean islands in callouts and ordered

246 them by increasing hurricane activity. Size-corrected residuals of forelimb (B) and hind limb (C)

247 toepad areas are positively related to hurricane activity.

248 **Methods:**

249 No statistical methods were used to pre-determine sample sizes for any aspect of this study.

250

251 ***Anolis scriptus* in Turks and Caicos**

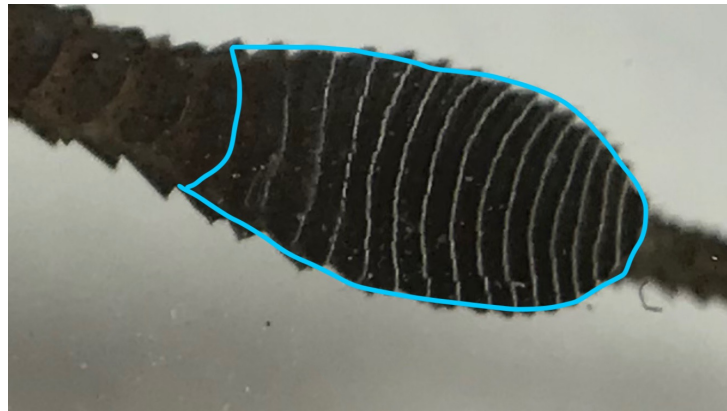
252 Pine Cay and Water Cay – two small islands in the Turks and Caicos Islands – are home  
253 to the endemic Turks and Caicos anole, *Anolis s. scriptus*. Both islands are relatively small (Pine  
254 Cay: 350 ha; Water Cay: 250 ha), flat, and covered by vegetation that averages between one and  
255 three meters in height. Adult Turks and Caicos anoles range in size between 40 – 65 mm in  
256 snout-to-vent length (SVL) and are sexually dimorphic: adult females are smaller than males.  
257 The species is conspicuous and abundant and can typically be found perched on small branches  
258 in the lower 1.5 m of the islands' vegetation (19).

259 Between 28 August and 4 September 2017, we surveyed the *A. scriptus* populations on  
260 Pine Cay and Water Cay to establish baselines for the populations in anticipation of a  
261 conservation project. Following a direct hit by Hurricane Irma (8 September 2017) and glancing  
262 blow by Hurricane Maria (22 September 2017), we revisited the islands between 16 October and  
263 20 October 2017 to determine whether the surviving lizard populations differed significantly in  
264 morphology from the pre-hurricane populations (detailed in 3).

265 We repeated those surveys 18 months (1 April to 8 April 2019) after our initial post-  
266 hurricane survey. For those revisits, the same researchers (CMD, A-CF, AH) walked the same,  
267 approximately two-km-long transect on each island and caught lizards by hand or with a pole  
268 and fishing line slipknot (following 3). In this way, we caught 117 lizards in 2019 (See Table  
269 S1.1).



270 We repeated the morphological measurements from the pre- and post-hurricane sampling  
271 for those lizards caught in 2018 and 2019. In brief, the same researcher (AH) measured  
272 morphology using digital calipers (Mitutoyo 500-752), and CMD took a high-resolution  
273 photograph of the right fore- and hind feet of each lizard using an iPhone 7 with a Moment  
274 Macro Lens attachment (See 3 for additional details). Using ImageJ (v.1.51a., W. Rasband,  
275 National Institute of Health, Bethesda), CMD measured the toepad area of the longest toe (digit  
276 III on forelimb, digit IV on hind limb) on each lizard’s right forelimb and hind limb to the first  
277 scale after the toepad begins to widen (Fig. M1).



278  
279 Fig. M1: An illustration of the toepad surface area measurement used for this study.

280  
281 *Identifying lizards hatched since the 2017 hurricanes*

282 In order to determine whether the hurricanes had a sustained impact on the subsequent  
283 generation of *A. scriptus* on Pine Cay and Water Cay, we calculated an estimate for how large a  
284 lizard that hatched one year before the 2019 survey (and thus, necessarily the offspring of  
285 hurricane survivors) might have grown. We used a logistic-by-length model that previous  
286 researchers have demonstrated adequately characterizes growth for small-bodied anoles that are  
287 ecologically similar to *A. scriptus* (20–22).

288

$$L_2 = \frac{\alpha L_1}{L_1 + (\alpha - L_1)e^{-rD}}$$

289  
290 This model estimates final estimated body size ( $L_2$ ) based upon initial size ( $L_1$ ), time elapsed  
291 ( $D$ ), characteristic growth rates for the population ( $r$ ) and the asymptotic maximum size ( $\alpha$ ). For  
292 initial size we used 19 mm, an average hatchling size for *A. sagrei* (23). We parameterized  $D$  as  
293 365 days, signifying an April 1, 2018 hatch date. We used separate values of  $\alpha$  for males and  
294 females using the largest *A. scriptus* individual of each sex we measured in any survey (male  
295 maximum SVL: 65.75 mm in 2019 sample; female maximum SVL: 49.74 mm in 2017, post-  
296 hurricane sample). As characteristic growth rate estimates have never been calculated for *A.*  
297 *scriptus*, we identified studies that have previously calculated growth rates in ecologically  
298 similar species (*A. sagrei*: 20, 22, *A. acutus*: 21). For our primary analysis, we used the lowest,  
299 most conservative growth rates (male = 0.006, 21, and female = 0.0083, 22). Andrews'  
300 calculated female growth rate was 0.009 resulting in a slightly larger, less conservative, female  
301 body size estimate (Table S1.2). We re-analyzed the data using other growth rates and found the  
302 same results (Appendix 1). Using these parameters, we calculated the maximum size of an  
303 individual hatched on or after April 1, 2018 would be 46.13 mm for females and 51.55 mm for  
304 males during our 2019 survey. April 1, 2018 was chosen as the earliest included hatch date  
305 because lizards hatched earlier may have been derived from eggs that survived the hurricanes,  
306 even if their parents did not, or could be the result of sperm storage from a male who did not  
307 survive. We used these as cutoffs and analyzed all smaller lizards caught in 2019, assuming that  
308 these lizards had hatched within the previous year (Table S1.3). See Appendix 1 for additional  
309 data and details.

### 310 *Data analysis*

311 Our primary aim was to determine whether the toepads of the *A. scriptus* surveyed in  
312 2019 were statistically different from those measured in 2017, either before or after the

313 hurricanes. To do so we used general linear models (GLM) with the surface area of the forelimb  
314 toepads, or hind limb toepads as the response variable. We included body size – SVL – as a  
315 factor in the GLM to account for differences in body size between the sampling times. In  
316 addition, we added a factor for island of origin – Pine Cay or Water Cay – and an additional  
317 fixed effect for each of the three sampling periods: pre-hurricane, post-hurricane, and 2019. Both  
318 SVL and the toepad surface areas were log<sub>10</sub> transformed to improve normality of the data. See  
319 Appendix 1 for complete model description. To evaluate differences between survey years, we  
320 used the ‘lsmeans’ (24) and ‘effects’ (25, 26), packages in R (R Core Team). We used the same  
321 analytical methods with the subset of lizards caught in 2019 and most likely having hatched  
322 within the previous year.

323

## 324 **Comparative analyses among anole populations and species**

325 *Identifying lizard localities:*

326 *Anolis sagrei* is a common and widespread anole and is ecologically similar to *A. scriptus*  
327 (8). It can be found on numerous islands in the West Indies, including the Bahamas, Cuba,  
328 Jamaica, and the Caymans. As part of an ongoing comparative study on *A. sagrei* across its  
329 range, CMD, AJG, and RGR collected data on individuals from 12 islands. All of these lizards  
330 were captured in similar closed-canopy coppice forest in 2016 and 2017. We recorded the GPS  
331 locations of these sampling sites during the collection surveys.

332 Locality data for the entire genus were drawn from a dataset published by Velasco et al.  
333 (27). These locality data were collected from multiple sources including the Global Biodiversity  
334 Information Facility (GBIF, <http://gbif.org>), HerpNet (<http://herpnet.org>) and previously  
335 published distribution datasets (see 27 for complete list of sources).

336

337 *Calculating a hurricane activity measure*

338           We used each of the lizard locality points – for field-caught *A. sagrei* and the Velasco et  
339 al. (27) records for the genus as a whole – to calculate the average number of hurricane hits for  
340 each species.

341           We first obtained the latitude-longitude position and maximum sustained wind speed for  
342 all tropical cyclones in the North Atlantic and eastern North Pacific basins between 1949 and  
343 2017. Data from 1949 to 2016 were obtained from the International Best Track Archive for  
344 Climate Stewardship v03r10 (IBTrACS; 28). Because 2017 IBTrACS data were not yet  
345 available, we obtained the 2017 data from the Tropical Cyclone Extended Best Track dataset  
346 (EBT; 29). Both of these datasets provide position and maximum sustained wind speed data for  
347 each tropical cyclone every six hours at 0000, 0600, 1200, and 1800 UTC. IBTrACS also  
348 provides data for some storms at intermediate times such as landfall events. Because 2017 EBT  
349 data did not include these intermediate times, we added them using National Hurricane Center  
350 storm reports (30) to ensure consistency across the dataset.

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

359 For each of the anole locality points, we counted the number of tropical cyclones that  
360 passed within a radius (30, 50, or 100 km), while meeting or exceeding a windspeed intensity  
361 threshold (65, 80, 100 kt sustained winds; [1 kt = 0.514 ms<sup>-1</sup>]) during the 1949-2017 period. We  
362 specified in our counting algorithm that each tropical cyclone could only produce a single hit at  
363 each GPS location, regardless of the number of time steps at which it satisfied the specified  
364 distance and intensity criteria, or whether the storm reversed direction and hit a locality a second  
365 time. We used MATLAB to calculate these hurricane counts (The MathWorks Inc., 2019;  
366 Appendix 8). Using these data, we then calculated the mean hurricane hits for each species by  
367 averaging the hurricane counts for each locality recorded for each species. This resulted in a  
368 continuous hurricane activity measure. For our main analyses, we focused on strong hurricanes  
369 reaching or exceeding 80 knots of sustained wind speed (see Appendix 6 for additional  
370 thresholds), as we previously found in laboratory conditions that *A. scriptus* lizards were, on  
371 average, blown off perches at  $74.3 \pm 2.3$  knots (3). We also focused on direct hits, within 30 km  
372 of a GPS point in the spatial database. We conducted a sensitivity analysis to investigate how  
373 different windspeeds and radii thresholds affected our models (Appendix 6). In general, we  
374 found that increasing the threshold radius decreased the explanatory power for our model, *ergo*  
375 very distant hurricanes did not substantially affect populations. We also found that more  
376 powerful hurricanes (windspeed reaching or exceeding 100 kts) had a stronger effect than  
377 weaker storms (Appendix 6).

378 A consideration inherent to this dataset is that longer-term hurricane frequency at each  
379 location almost certainly differs from the frequency during the seven-decade dataset available for  
380 study (1949-2017). Direct strikes from hurricanes, especially strong hurricanes, are infrequent  
381 events; thus, it is likely that some vulnerable locations did not experience any direct strikes

382 during this seven-decade window, even though they have experienced hurricanes on longer  
383 timescales.

384 Beyond the infrequent, stochastic nature of hurricane strikes, hurricane activity  
385 throughout the North Atlantic basin varies on time scales that are not well-reflected in this seven-  
386 decade dataset. Atlantic hurricane activity is modulated on multidecadal scales by the Atlantic  
387 Multidecadal Oscillation (AMO; 31), which affects North Atlantic sea-surface temperatures and  
388 sea-level pressures. Positive (warm) AMO phases are associated with more numerous and  
389 intense North Atlantic hurricanes (32). The interval covered in this study spans 44 years of  
390 positive AMO (1949-1969; 1995-2017) and 25 years of negative AMO (1970-1994).

391 Research on prehistoric hurricanes has also revealed that North Atlantic hurricane  
392 activity has also varied across much longer timescales. Using both sedimentary records and a  
393 statistical model based on past climate reconstructions, Mann et al. (33) found a period of  
394 enhanced North Atlantic hurricane activity approximately 1000 years Before Present (BP), with  
395 a relatively quiescent period following it. Paleotempestological records also indicate low-  
396 frequency variations in the locations impacted by hurricanes. Liu and Fearn (34) showed that  
397 catastrophic hurricane strikes in northwest Florida were three to five times more frequent  
398 between 3400-1000 years BP, compared to 5000-3400 years and 1000-0 years BP. Elsner et al.  
399 (35) concluded that variations in the position and strength of the Bermuda High, associated with  
400 the North Atlantic Oscillation, affected hurricane tracks and thus the regions impacted by  
401 hurricanes. They found that periods of enhanced Gulf of Mexico hurricane activity coincided  
402 with suppressed activity on the United States northeast coast on several time scales. Similarly,  
403 McCloskey and Liu (36) found that periods of higher hurricane frequency in Nicaragua showed  
404 lower hurricane frequency in the northern Caribbean and North American Atlantic coast,

405 whereas Baldini et al. (37) concluded that North Atlantic hurricane tracks have gradually shifted  
406 northward during the last five centuries from natural, and more recently, anthropogenic  
407 processes. Therefore, we do not assume that hurricane frequency at a point in the North Atlantic  
408 basin during the 1949-2017 period is necessarily representative of hurricane frequency at that  
409 location on longer time scales.

410

#### 411 *Calculating mean tree heights*

412         Using the same locality database employed in calculating the number of hurricanes for  
413 each species, we calculated the mean height of trees at that location using a tree heights dataset  
414 published by Simard et al. in which they used 2005 satellite-based lidar to estimate global tree  
415 heights (38). We calculated mean tree heights within a 30, 50, and 100 km radius of each  
416 locality. The radii were chosen to match the radii of the hurricane activity algorithm. We then  
417 averaged these tree heights for each radius and each locality to calculate a mean tree height for  
418 every species in the database.

419

#### 420 *Measuring toepads*

421         Toepad images of 10 *A. sagrei* individuals per island population were collected in the  
422 field by RGR, AJG, and CMD and from museum specimens of all other species by DLM, HKF  
423 and assistants using a flatbed scanner (Epson Perfection V500 Photo or Canon CanoScan LiDE  
424 70). The preserved *Anolis* specimens used for this study are from the collections of the Harvard  
425 Museum of Comparative Zoology, Field Museum of Natural History, Institute of Ecology and  
426 Systematics (Havana, Cuba), and Drs. Steven Poe and Richard Glor. For all species in the  
427 interspecific dataset, CMD measured toepad surface area (ImageJ) of the third toe on the

428 forelimb and the fourth (longest) toe on the hind limb following the same methods as the *A.*  
429 *sagrei* and *A. scriptus* analyses (Fig. M1). Three adult individuals were measured for each of 175  
430 species, and those measurements were averaged to calculate a species mean. For five additional  
431 species, only two specimens were available, and eight species in the dataset had only one  
432 available specimen. While these species with fewer than three specimens were included in the  
433 published results, repeating the analysis with only those subsets of species with exactly three  
434 specimens yielded similar significant results. Because mismatches between a species' average  
435 toepad characteristics as estimated from our sample, and the average hurricanes experienced by  
436 that species were potentially systematically exacerbated for wide-spread species, we repeated the  
437 whole-genus analysis without the seven most widespread species (Appendix 7). We found the  
438 same significant results.

439

#### 440 ***Data analysis***

##### 441 *Phylogenetic methods*

442 The phylogeny of *Anolis sagrei* populations (Fig. S2.1) was generated by pruning a larger  
443 tree previously inferred by van de Schoot (39). Briefly, the mitochondrial-encoded locus  
444 NADPH Dehydrogenase Subunit 2 (plus some post-terminal tRNA-encoding sequence) was  
445 amplified and sequenced for specimens of *Anolis sagrei* from across the species' natural range.  
446 Contig assembly and manual alignment was performed using Geneious R9.1  
447 (<https://www.geneious.com>). The optimal partitioning scheme, and the model of molecular  
448 evolution best fitting each partition was determined using PartitionFinder v1.1.1 (40). van de  
449 Schoot used Bayesian Inference to estimate the phylogeny of this group using MrBayes v3.2.6  
450 (41) and found all of the islands included in our sample to be monophyletic; therefore, for the



451 present study we pruned the phylogeny down to a single individual per island. For most islands  
452 the individual used for the pruned phylogeny was a lizard for which we had also collected  
453 morphological data. To represent the remaining islands (Eleuthera, South Bimini, Cay Sal,  
454 Cayman Brac) in the phylogeny, we selected an individual collected from the same site and at  
455 the same time as the lizards that were measured. For the phylogenetic comparative analyses  
456 spanning the entire genus, we used a recent tree by Poe et al (42).

457 To account for phylogenetic non-independence in our comparative datasets, either  
458 between the 12 *A. sagrei* populations or across the genus as a whole, we used phylogenetic  
459 comparative linear models evaluated using the phytools (43), caper (44), GEIGER (45), ape (46),  
460 and picante (47) packages in R (R core team).

461 Our phylogenetic generalized least squares models took the form:

$$462 \log_{10}(\text{toepad area}) \sim \log_{10}(\text{SVL}) + \text{Hurricane Activity}$$

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

465

#### 466 *Spatial Autocorrelation*

467 For the *A. sagrei* and genus-wide analyses, we tested whether phylogenetic regression  
468 results were potentially influenced by residual spatial autocorrelation by constructing Moran’s I  
469 correlograms. We calculated Moran’s I using 25km lag distances, e.g. all points separated by less  
470 than 25km (in any direction), then points between 25km and 50km apart, and so on to a  
471 maximum of 600km. We tested for significance using randomization tests. Correlograms were  
472 generated using the correlog() function in the ncf package (48). We found no significant spatial  
473 autocorrelation in residuals of any regression model at any lag distance ( $P > 0.10$  in all cases),

474 suggesting that phylogenetic autocorrelation and hurricane activity can account for spatial  
475 patterns in toepads and regression results are not confounded by spatial autocorrelation. Thus, we  
476 did not consider spatial autocorrelation further (Fig. S2.2; S3.1, S3.6).

477

#### 478 **Methods References:**

- 479 19. A. L. Laska, The structural niche of *Anolis scriptus* on Inagua. *Breviora* 349, 1-6 (1970).
- 480 20. T. W. Schoener, A. Schoener, Estimating and interpreting body-size growth in some *Anolis*  
481 lizards. *Copeia* 3, 390–405 (1978).
- 482 21. R. B. Andrews, “Patterns of growth in reptiles” in: *Biology of the Reptilia*, C. Gans, F. H.  
483 Pough, Eds. (Academic Press 1982), vol. 13, pp. 273–320.
- 484 22. A. N. Wright, J. Piovia-Scott, D. A. Spiller, G. Takimoto, L. H. Yang, T. W. Schoener,  
485 Pulses of marine subsidies amplify reproductive potential of lizards by increasing individual  
486 growth rate. *Oikos* 122: 1496-1504 (2013).
- 487 23. P. R. Pearson, D. A. Warner, Early hatching enhances survival despite beneficial phenotypic  
488 effects of late-season developmental environments. *Proc. R. Soc. B.* 285, 20180256 (2018).
- 489 24. R. V. Lenth, Least-squares means: The R package lsmeans. *J of Stat. Softw.* 69, 1-33 (2016).
- 490 25. J. Fox, Effect displays in R for generalised linear models. *J. Stat. Softw.* 8, 1-27 (2003).
- 491 26. J. Fox, S. Weisberg, *An R companion to applied regression, 3<sup>rd</sup> edition* (Sage Publications,  
492 Thousand Oaks, CA, 2019).
- 493 27. J. A. Velasco, F. Villalobos, J. A. F. Diniz-Filho, S. Poe, O. Flores-Villela, Macroecology  
494 and macroevolution of body size in *Anolis* lizards. *Ecography* (2020).
- 495 28. National Centers for Environmental Information (NCEI), last accessed – 25 April 2019.  
496 International Best Track Archive for Climate Stewardship (IBTrACS). Available online at  
497 <https://www.ncdc.noaa.gov/ibtracs/index.php?name=ibtracs-data>.
- 498 29. Regional and Mesoscale Meteorology Branch (RAMMB), last accessed – 25 April 2019. The  
499 Tropical Cyclone Extended Best Track Dataset. Available online at  
500 [http://rammb.cira.colostate.edu/research/tropical\\_cyclones/tc\\_extended\\_best\\_track\\_dataset/](http://rammb.cira.colostate.edu/research/tropical_cyclones/tc_extended_best_track_dataset/).
- 501 30. National Hurricane Center (NHC), last accessed – 25 April 2019. 2017 Atlantic Hurricane  
502 Season. Available online at <https://www.nhc.noaa.gov/data/tcr/index.php?season=2017>
- 503 31. R. A. Kerr, A North Atlantic climate pacemaker for the centuries. *Science* 288, 1984-1985  
504 (2000).
- 505 32. P. J. Klotzbach, W. M. Gray, Multidecadal variability in North Atlantic tropical cyclone  
506 activity. *J. Climate* 21, 3929-3935 (2008).
- 507 33. M. E. Mann, J. D. Woodruff, J. P. Donnelly, Z. Zhang, Atlantic hurricanes and climate over  
508 the past 1,500 years. *Nature* 460, 880-883 (2009).

- 509 34. K. Liu, M. L. Fearn, Reconstruction of prehistoric landfall frequencies of catastrophic  
510 hurricanes in Northwestern Florida from lake sediment records. *Quaternary Res.* 54, 238-245  
511 (2000).
- 512 35. J. B. Elsner, K. Liu, B. Kocher, Spatial variations in major U.S. hurricane activity: statistics  
513 and a physical mechanism. *J. Climate* 13, 2293-2305 (2000).
- 514 36. T. A. McCloskey, K. Liu, A sedimentary-based history of hurricane strikes on the southern  
515 Caribbean coast of Nicaragua. *Quaternary Res.* 78, 454-464 (2012).
- 516 37. L. M. Baldini, J. U. L. Baldini, J. N. McElwaine, A. Benoit Frappier, Y. Asmerom, K. Liu,  
517 K. M. Prufer, H. E. Ridley, V. Polyak, D. J. Kennett, C. G. Macpherson, V. V. Aquino, J.  
518 Awe, S. F. M. Breitenbach, Persistent northward North Atlantic tropical cyclone track  
519 migration over the past five centuries. *Sci. Rep.* 6, 37522 (2016).
- 520 38. M. Simard, N. Pinto, J.B. Fisher, A. Baccini. Mapping Forest Canopy Height Globally with  
521 Spaceborne Lidar. *Journal of Geophysical Research* 116 (2011).
- 522 39. M. van de Schoot, Within and between island radiation and genetic variation in *Anolis sagrei*  
523 MSc Thesis, Wageningen University, Netherlands (2016).
- 524 40. R. Lanfear, B. Calcott, S. Y. Ho, S. Guindon, PartitionFinder: combined selection of  
525 partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology*  
526 *and Evolution*, 29, 1695-1701 (2012).
- 527 41. F. Ronquist, M. Teslenko, P. Van Der Mark, D. L. Ayres, A. Darling, S. Höhna, B. Larget, L.  
528 Liu, M. A. Suchard, J. P. Huelsenbeck, MrBayes 3.2: efficient Bayesian phylogenetic  
529 inference and model choice across a large model space. *Systematic Biology*, 61, 539-542  
530 (2012).
- 531 42. S. Poe, A. Nieto-Montes de Oca, O. Torres-Carvajal, K. de Queiroz, J. A. Velasco, B. Truett,  
532 L. N. Grey, M. J. Ryan, G. Köhler, F. Ayala-Varela, I. Latella, A phylogenetic,  
533 biogeographic, and taxonomic study of all extant species of *Anolis* (Squamata; Iguanidae).  
534 *Syst. Biol.* 66, 663-697 (2017).
- 535 43. L. J. Revell, phytools: An R package for phylogenetic comparative biology (and other  
536 things). *Methods Ecol. Evol.* 3, 217-223 (2012).
- 537 44. D. Orme, R. Freckleton, G. Thomas, T. Petzoldt, S. Fritz, N. Isaac, W. Pearse, CAPER:  
538 comparative analyses of phylogenetics and evolution in R. R package version 1.0.1.  
539 <https://CRAN.R-project.org/package=caper> (2018).
- 540 45. L. J. Harmon, J. T. Weir, C. D. Brock, R. E. Glor, W. Challenger, GEIGER: investigating  
541 evolutionary radiations. *Bioinformatics* 24, 129-131 (2008).
- 542 46. E. Paradis, K. Schliep, ape 5.0: an environment for modern phylogenetics and evolutionary  
543 analyses in R. *Bioinformatics* 35, 526-528 (2018).
- 544 47. S. W. Kembel, P. D. Cowan, M. R. Helmus, W. K. Cornwell, H. Morlon, D. D. Ackerly, S.  
545 P. Blomberg, C. O. Webb, Picante: R tools for integrating phylogenies and ecology.  
546 *Bioinformatics* 26, 1463-1464 (2010).
- 547 48. O. N. Bjornstad, NCF: spatial covariance functions. R package version 1.2-8, (2019).

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565 CMD initiated the study; CMD, AH, and A-CF collected *A. scriptus* field data, CMD, AJG, and  
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569 analyzed the data; CMD prepared figures; CMD, JTS, and JBL wrote the manuscript; all authors  
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571

572 **Competing Interests:** The authors declare no competing interests.

573

574 **Data and Materials Availability:** Upon publication, all data will be made available on the  
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