

## **Why Montane *Anolis* Lizards are Moving Downhill**

### **While Puerto Rico Warms**

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ABSTRACT: Puerto Rico has warmed in recent decades, leading to a prediction that ectotherms should have shifted their elevational ranges uphill. However, by comparing historical versus recent distributional records of *Anolis* lizards, we found that three “montane-forest” species have actually moved *downhill* in recent decades, almost to sea level. This downward shift may be related to the massive regeneration of Puerto Rican forests – especially in lowland areas – starting in the mid-20th century, when the economy shifted from agriculture to manufacturing. Regenerated forests drastically cool an environment, counteract climate warming, and probably enable “montane” lizards to follow forests dispersing downhill from isolated mountain refugia. We suspect that contemporary distributional patterns approximate those occurring before the arrival of European settlers, who cleared most lowland forests for agriculture, thereby restricting forests and associated species to high-elevation areas. By contrast, three lowland species did expand their ranges to higher elevations in recent decades; but whether this movement reflects warming, collecting bias, or hurricane-induced destruction of upland forests is unclear.

*Keywords:* *Anolis*, climate warming, forest regeneration, land-use changes, range shifts, thermal biology, hurricane impacts on distributions, human influences



24 body temperatures, is intolerant of high body temperatures, has high rates of evaporative water  
25 loss (Gorman and Hillman, 1977; Gunderson and Leal, 2012; Heatwole, 1970; Hertz et al., 1979;  
26 Hertz, 1981; Huey and Webster, 1976; Rand, 1964), and avoids sunny habitats and perches  
27 (Hertz, 1992; Rodríguez-Robles et al., 2005; Schoener, 1971). Therefore, its lower range limit  
28 should be a sensitive sentinel of climate warming. Moreover, warming temperatures should  
29 enable *A. cristatellus* (a more warm-adapted, lowland congener) to invade mid-elevation forests  
30 from adjacent open habitats, adding competitive pressure on *A. gundlachi* (Buckley, 2013; Huey  
31 et al., 2009).

32         Extensive field research up through the 1980s placed the lower limit of *A. gundlachi*'s  
33 elevational range as ~ 200 to 250 m (Huey and Webster, 1976; Rivero, 1998; Schwartz and  
34 Henderson, 1991; Williams, 1972). In 2011, we decided to determine whether that limit had  
35 shifted upwards. We drove down P.R. Highway 191 through Luquillo National Forest, stopped  
36 every ~ 50-m drop in elevation, and checked adjacent forest for *A. gundlachi*. We kept finding  
37 this species at elevations below 250 m, and even found it as low as ~20 m, adjacent to the  
38 floodplain of the Río Grande Luquillo! Thus, *A. gundlachi* appeared to have moved *downhill*  
39 since the 1970s, completely contrary to our expectations. We weren't the only ones surprised:  
40 Richard Thomas, a very experienced herpetologist (Thomas and Joglar, 1996) at the University  
41 of Puerto Rico, Río Piedras, was also surprised (personal communication).

42         Our 2011 observations provided an opportunity to focus on several questions concerning  
43 historical shifts in the distributional patterns of Puerto Rican anoles. First, were our anecdotal  
44 impressions on Highway 191 correct and general for *A. gundlachi*? If so, the presence of *A.*  
45 *gundlachi* at other lowland localities would be recent; and this assumption could be evaluated by  
46 comparing historical versus contemporary museum and locality records. Second, did the pattern

47 for *A. gundlachi* match elevational shifts in other montane anoles: if so, lower limits of these  
48 species should also show similar descending trends. Finally, if both patterns hold, we needed to  
49 ask, “Why would lower range limits shift downward when temperatures are rising?”

50 Our attempt to answer that last question soon led us to the literature on historical changes  
51 in forest cover in Puerto Rico. Although forest cover has been long declining in many parts of  
52 the tropics and elsewhere (Achard et al., 2014; Hansen et al., 2010), forest cover in Puerto Rico  
53 has increased dramatically since the middle of the 20<sup>th</sup> century (Álvarez-Berrios et al., 2013;  
54 Helmer et al., 2008; Lugo and Helmer, 2004), reflecting an economic and cultural shift from an  
55 agrarian rural economy to a manufacturing urban one (Grau et al., 2003; Rivera-Collazo, 2015;  
56 Yackulic et al., 2011). Reforestation occurred during this period despite massive forest  
57 blowdowns caused by Hurricanes Hugo (1989) and Georges (1998).

58 Here we analyze historical versus recent patterns of locality records (largely museum  
59 collections) for the six most common species of Puerto Rican anoles. We find that montane  
60 species have in fact been moving downhill, consistent with our anecdotal observations in 2011,  
61 and are likely driven by expansion of forests into lowland areas from upland refugia. A  
62 regenerated forest apparently cools and humidifies the local environment sufficiently to enable  
63 montane animal species – despite their sensitivity to high temperature and dry conditions – to re-  
64 invade the lowlands, which they likely occupied before Europeans began settling in the 16<sup>th</sup>  
65 century and subsequently cleared nearly all natural lowland forests (Lugo et al., 1981).

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## Methods

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### *Study Species*

70           The six common *Anolis* species studied here (*A. cristatellus*, *A. evermanni*, *A. gundlachi*,  
71 *A. krugi*, *A. pulchellus*, and *A. stratulus*) are members of a clade that evolved in situ on the greater  
72 Puerto Rican bank (Helmus et al., 2014). They are often partitioned into three pairs of  
73 “ecomorphs,” each of which has characteristic microhabitat associations and morphologies  
74 (Williams, 1972). Within each pair, one typically has a more lowland distribution. Even so,  
75 members of each pair are broadly sympatric; but where sympatric, the lowland species is found  
76 in warmer, more open habitats and has higher body temperatures (Hertz et al., 2013; Huey and  
77 Webster, 1976; Rand, 1964), higher heat tolerance (Gorman and Licht, 1974; Gunderson et al.,  
78 2016; Huey and Webster, 1976), lower cold tolerance (Heatwole et al., 1969), and greater  
79 desiccation resistance (Gorman and Hillman, 1977; Hertz et al., 1979).

80           The two “trunk-ground” ecomorphs (*A. cristatellus* and *A. gundlachi*) typically perch and  
81 low on shrubs and trees and forage there or on adjacent ground. The former has higher body  
82 temperatures, higher heat tolerances, and lower rates of evaporative water loss: it is found from  
83 sea level to high elevation, in both forest and open habitats in the lowlands, but only in open  
84 habitats at mid- to high-elevation (Huey, 1974; Huey and Webster, 1976; Otero et al., 2015).  
85 Traditionally, *Anolis gundlachi* was considered a “montane forest specialist” and was thought to  
86 be restricted to deeply shaded, upland forests because of its sensitivity to high temperatures and  
87 its high rates of evaporative water loss (Gorman and Licht, 1974; Heatwole, 1970; Hertz et al.,  
88 1979; Huey and Webster, 1976; Lister, 1981; Rand, 1964; Rivero, 1998; Schmidt, 1918;  
89 Schoener, 1971; Williams, 1972).

90           Two “grass-bush” anoles (*A. pulchellus* and *A. krugi*) occur over broad elevational  
91 ranges. *Anolis pulchellus* is abundant at low to moderate elevation in relatively exposed habitats.  
92 *Anolis krugi* is more of a montane species but was sometimes found at low elevation, but only

93 “under conditions of extreme shade” (Gorman and Licht, 1974). The two “trunk-crown” anoles  
94 (*A. stratulus* and *A. evermanni*) perch somewhat higher in trees than do the other species  
95 (Schoener, 1971). *Anolis stratulus* is broadly distributed, whereas *A. evermanni* is more of an  
96 upland form and is found at sea level only in very shaded habitats (Gorman and Licht, 1974).

97

#### 98 *Specimen Records and Georeferencing*

99 We downloaded all specimen records of Puerto Rican *Anolis* from the Global Biodiversity  
100 Information Facility (GBIF) and developed scripts to remove duplicate records and to apply  
101 consistent formatting across museums. Some records were geo-referenced, but many were not.  
102 Consequently, we manually georeferenced all non-GPS collection localities that had at least 10  
103 specimens. We used Google Maps to measure road kilometers (many sites were listed as 10 km  
104 SE of a given town) and Google Earth to locate point localities. We followed MANIS best-  
105 practices for georeferencing (Wieczorek, 2001) and estimated uncertainty for all points to the  
106 nearest 100 m. To group adjacent collecting sites or those visited by multiple collectors  
107 (hereafter “locality clusters”), we calculated pairwise geographic distances among all unique  
108 specimen localities, applied a complete-linkage hierarchical clustering algorithm, and extracted  
109 clusters of localities within approximately 1 km of each other. We also added a few sight records  
110 made by us or by colleagues experienced with Puerto Rican *Anolis*.

111 After removing localities with greater than 2-km georeferencing uncertainty and splitting  
112 out sites with verbatim elevations provided by the collector, we estimated the elevation of each  
113 collecting locality as the mean elevation across the full uncertainty radius in the USGS National  
114 Elevation Database (U.S. Geological Survey, 2016) at 1-arc-second resolution, using the “rgeos”  
115 and “Raster” packages in R (Bivand and Rundel, 2013; Hijmans and van Etten, 2014; R Core

116 Team, 2015). Specimen records were binned into four period classes (see below) bracketing  
117 1935-2015, based on the forest age ranges used in Helmer et al.'s 2008 analysis of land-cover  
118 change on Puerto Rico. We subset records to include only the six most common species of  
119 *Anolis* (above), all of which occur in the mountains. The final dataset includes 8,839 specimens  
120 and 121 sight records across 505 localities and 293 locality clusters (Appendix S1: Fig. S1).  
121 Most collecting occurred during the periods 1952–1977 or 1991–2016 (Appendix S1: Fig. S2).

122

### 123 *Shifts in Elevation Distribution*

124 We determined the absolute elevation range of each species during each time period, then used a  
125 Wilcoxon rank sum test to evaluate whether the elevation distribution of specimen collections  
126 had shifted from 1952–1977 to 1991–2015. Because such shifts might merely reflect elevational  
127 shifts in collecting or survey effort between time periods, we set the null hypothesis for each  
128 species as the median difference in collecting elevation for all species other than the focal  
129 species. Thus, our test addresses the question “did the elevation distribution of species *i* shift  
130 more than expected, given overall shifts in *Anolis* collections?” Analyses were conducted on  
131 both a per-occurrence and a per-locality-cluster basis. In the per-locality-cluster analysis, we  
132 coded locality clusters as present/absent for each species and weighted all locality clusters  
133 equally in the analysis. In the per-occurrence analysis, we treated each specimen or sight record  
134 as an independent data point, which potentially allows greater resolution of shifts in abundance  
135 within a preexisting range but may be biased by uneven sampling effort across species when  
136 surveyors sought to collect a specific taxon for a targeted study.

137 To assess potential changes in species composition at low elevations, we extracted  
138 specimen reports at elevations lower than 250 m, split them by species, and used a McNemar test

139 to compare the relative abundance of each species across time periods (i.e., the number of  
140 specimens of species  $i$  relative to the number of all *Anolis* specimens in each period). This  
141 procedure is conceptually similar to the specimen-derived abundance index used in Linck et al.  
142 (2016) and Rohwer et al., (2012), in which the observed abundance of a target species is  
143 corrected for survey effort by dividing by the number of specimens collected with similar  
144 techniques in a given area. For all analyses conducted separately on each species, we include  $p$ -  
145 values corrected for multiple testing ( $n=6$ ) using a Holm-Bonferroni correction (Holm, 1979).

146 Finally, to investigate changes in diversity across elevations and time periods (see  
147 Colwell et al., 2008), we calculated Shannon diversity (Shannon, 1948) for each locality cluster,  
148 dropped sites with only one reported (probably targeted) species, and tested for significant  
149 change over time and across elevations in two ways. In the first analysis, we binned locality  
150 clusters by 250-m elevation increments and used a Wilcoxon rank-sum test to ask if diversity  
151 was significantly different between time periods for each elevation band. In the second analysis,  
152 we treated elevation as a continuous variable and fit a simple linear model to the data using  
153 ordinary least-squares regression in R.

154

#### 155 *Changes in Land Cover and in Temperature*

156 To assess changes in forest cover on Puerto Rico over the 20<sup>th</sup> century, we modified an existing  
157 raster layer of forest age and soil types across the island developed from analysis of aerial and  
158 satellite imagery (Helmer et al., 2008). We merged forest ages across soil types and subset the  
159 original raster layer to produce maps of forested areas at 30-m resolution in four time bins:  
160 1935–1951, 1952–1977, 1977–1990, and 1991–2000 (matching the age classes in Helmer et al.  
161 2008). We then extracted the elevations of forested grid cells in each time period and plotted

162 these as a histogram showing total forested area in approximately 12-m elevation bands (Figure  
163 2).

164 Several studies have documented small increases in Puerto Rican temperatures during the  
165 late 20<sup>th</sup> Century (Burrowes et al., 2004; Comarazamy and González, 2011; Jennings et al., 2014;  
166 Méndez-Lázaro et al., 2015; Waide et al., 2013), and average air temperatures on the island are  
167 predicted to continue to increase (Harmsen et al., 2009; Patz et al., 1998). To determine whether  
168 local warming is consistent with global observations and global climate model predictions (Karl  
169 et al., 2015), we examined temperature data (1950-2015) from the NOAA National Climate Data  
170 Center (<https://www.ncdc.noaa.gov/cdo-web/search>). Eight weather stations on Puerto Rico  
171 reported at least 40 years of complete monthly data starting in 1950: Roosevelt Roads, Rio  
172 Piedras Experimental Station, Borinquén Airport, Lajas Substation, Manatí, Corozal, Ponce 4E,  
173 and Dos Bocas. Six of these stations are distributed around the periphery of the island near sea  
174 level, whereas two are in interior valleys at elevations between 100 and 200 meters (Appendix  
175 S1: Fig S4). No station above 200 meters reported sufficient data for analysis of trends over time  
176 since the 1950's. For each of the eight stations we removed any years without 12 months of data,  
177 calculated average annual temperatures, and used a Welch's two-sample *t*-test to compare the  
178 average temperatures between 1952–1977 and 1991–2015. To avoid biases in temperature  
179 records caused by the urban heat island effect (Oke, 1982), we also identified stations in urban  
180 areas as of 1991 by extracting the land cover class from Helmer et al.'s 2008 forest map.

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## Results

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184

### *Shifts in Elevation Ranges*

185 Analyzed on a per-occurrence basis, of all six common *Anolis* species significantly  
186 shifted their elevation distributions between 1952–1977 and 1991–2015 (Figure 1, Appendix S1:  
187 Table S1). In general, highland species expanded downhill, while lowland species expanded  
188 uphill, though the magnitude of the shift was highly variable across species. *Anolis gundlachi*  
189 showed the largest decreases both in median elevation (480 to 385 m) and lower elevation limit  
190 (223 to 24 m). *Anolis cristatellus* had the largest increase in maximum elevation; rising from 880  
191 m in the mid-20th century to 942 m after 1991. Repeating these analyses on a per-locality-cluster  
192 basis (thus reducing power) resulted in similar patterns in absolute maximum and minimum  
193 values, but after correction for multiple comparisons the median shift was significant only for  
194 *cristatellus* (Figure 1, Appendix S1: Table S1).

195 At sites below 250 m, frequencies of all six species also shifted significantly (Table 1).  
196 *Anolis gundlachi* showed the largest change; increasing from only 0.2% of collections in 1952–  
197 1977 to 8.2% in 1991–2015. In contrast, the most common low-elevation species (*A. pulchellus*  
198 and *A. cristatellus*) decreased in frequency by 6.3% and 5.7% at sites below 250 m, respectively;  
199 mirroring the general trends observed across the full elevation range.

200 Comparing Shannon diversity of locality clusters in elevation bins across time periods,  
201 we found no evidence of the loss of lowland diversity predicted in (Colwell et al., 2008).  
202 Observed diversity increased at elevations below 500 m, but these changes were not statistically  
203 significant after dropping sites with only one observed species (Table 2, Appendix S1: Fig. S3).  
204 Diversity is weakly but positively correlated with elevation in both time periods, with recent  
205 records showing a shallower slope and higher y-intercept (1952–1977:  $p=0.047$ ,  $df=46$ ,  
206  $R^2=0.063$ , equation  $y=0.0004x+0.728$ ; 1991–2015:  $p=0.016$ ,  $df=132$ ,  $R^2=0.036$ , equation  
207  $y=0.0003x+0.867$ ).

208

209

*Lowland and Resurveyed Localities*

210 As noted above, *A. gundlachi* was historically the dominant trunk-ground anole in forests  
211 elevations above ~250 m, but not in forests below that level. During our recent-surveys (2011  
212 on), we found *A. gundlachi* at several localities below 100 m. For example, at the Carabali  
213 Rainforest Park (~ 24 m), *A. gundlachi* was restricted to the forest, whereas *A. cristatellus* was  
214 restricted to open habitats. According to Alejandro Díaz (land owner, 32 years old), the forest did  
215 not exist there when he was a boy; and thus *A. gundlachi* there now must be the descendants of  
216 recent invaders into the lowlands.

217 Campamento Eliza Colberg (80 to 100 m) has both open and forest habitats, but forest  
218 coverage in the vicinity (1-km radius) increased by roughly 55% from 1951 to 2000. Huey and  
219 Webster (1976) collected there in July 1973, and found only *A. cristatellus* in both habitats (15 in  
220 open, 11 in forest). Similarly, Gorman and Licht (Gorman and Licht, 1974) recorded only *A.*  
221 *cristatellus* in the early 1970s at the adjacent Ranger House. Otero and Huey revisited this site  
222 frequently between 2012-2014 (sight records only). In the open, they found only *A. cristatellus*  
223 (N = 74); but in forest, they found mainly *A. gundlachi* (*A. gundlachi* = 82, *A. cristatellus* = 9).  
224 Thus, *A. gundlachi* appears to have invaded the forest at the Campamento – presumably from  
225 nearby upland forests – sometime between 1973 and 2009 and has largely replaced *A.*  
226 *cristatellus* in the forest.

227

228

*Land Cover & Temperature*

229 Forests in Puerto Rico expanded dramatically from approximately 8.9% of total land area  
230 in 1935–1951 to 43.1% in 1991–2000 (Helmer et al., 2008; Fig. 2). All elevation bands showed

231 significant increases in forested area, but the largest absolute (as well as relative) increases  
232 occurred in elevations of 100–300 m (Fig. 2).

233 Average annual temperatures differed significantly between 1952–1977 and 1991–2015  
234 at four of eight weather stations (Table 3; Appendix S1: Fig S4), with an average shift across all  
235 sites of 0.31°C. One site at moderate elevations (Dos Bocas) was cooler after 1991, but all other  
236 sites increased in temperature. If sites in urban areas are removed, the change in temperatures  
237 drops to 0.22°C. Though no long-term data was available for high-elevation sites, one study  
238 (Burrowes et al., 2004) recorded an average temperature increase of 0.72°C at an altitude of  
239 approximately 1000 meters over the period 1970–2000; suggesting that temperature increases  
240 might have been higher in montane areas than in lowland areas.

241

#### 242 *Operative Temperatures in Forest versus Open Habitats*

243 The observed increases in air temperatures in Puerto Rico over the past 60+ years are relatively  
244 low, certainly less than 1°C (see above). Although this warming might still have significant  
245 biological impacts, the magnitude of warming is tiny compared with the decreases in local  
246 operative temperatures that occur when a forest regenerates in an open habitat: a forest canopy  
247 reduces incident radiation, maximum air temperature, and maximum wind speed, and also  
248 increases relative humidity (Bastable et al., 1993; Geiger et al., 2009).

249 Otero et al. (2015) monitored and reported operative temperatures in open versus forest  
250 (secondary) habitats at two lowland localities in Puerto Rico. At Monagas in summer, for  
251 example, operative temperatures in the open often exceeded 40°C (maximum = 46.4°C), well  
252 above the critical thermal maximum of *A. gundlachi* (37.5°C, Huey and Webster, 1976), whereas  
253 operative temperatures in the forest rarely exceeded 30°C (maximum = 33.3°C). Thus, a

254 regenerated lowland forest lowers operative temperatures much more than the cumulative rise in  
255 temperatures associated with recent climate warming – at least so far (Nowakowski et al., 2017).

256

257

### Discussion

258 We expected that elevational ranges of “montane” species of *Anolis* lizards (especially *A.*  
259 *gundlachi*) in Puerto Rico would have shifted upward as a correlated response to observed recent  
260 warming (Burrowes et al., 2004; Jennings et al., 2014; Méndez-Lázaro et al., 2015; Waide et al.,  
261 2013). To our surprise, we found the opposite: all three of the montane species now occur at  
262 lower elevations than in the past (Fig. 1), and *A. gundlachi* – the least heat tolerant of these  
263 species – is now found even near sea level.

264 One potential explanation for the descent of montane species could be that Puerto Rico  
265 has become cooler rather than warmer in recent decades. However, the studies (cited above),  
266 including our present one, suggest that temperatures have either been stable or have warmed  
267 modestly, at least at low elevations. Thus, this potential explanation is unlikely.

268 A more plausible explanation relates to historical changes in land use in Puerto Rico. In  
269 many tropical regions, logging and agriculture have reduced forest cover (Álvarez-Berríos et al.,  
270 2013). In Puerto Rico, however, forests have expanded dramatically since the middle of the 20<sup>th</sup>  
271 century (Helmer et al., 2008; Lugo and Helmer, 2004) (Fig. 2), reflecting a shift from an  
272 agricultural and rural economy to a manufacturing and urban one (Yackulic et al., 2011). [Note:  
273 Such rapid re-forestation may seem implausible to biologists without tropical experience.  
274 However, Puerto Rican forests recover basic structure within a decade or two after hurricane  
275 blowdowns (Lugo et al., 1981; Walker, 1991), and are indistinguishable from primary forest in  
276 terms of density and tree size after only 40 years of recovery (Aide et al., 1996).]

277 A regenerated forest will generate operative temperatures (below the canopy) that are  
278 much cooler than those in adjacent open habitats (Kaspari et al., 2015; Otero et al., 2015). In  
279 fact, the magnitude of cooling from re-forestation more than compensates for the minor  
280 temperature increases from long-term warming (Table 5). Thus, by cooling and humidifying  
281 lowland areas, regenerating forests have apparently enabled the ‘montane’ anoles to follow the  
282 forests as they move downslope from relic to lowland habitats (Fig. 1). Downslope range  
283 movement of some species elsewhere also appear related to habitat modifications (Lenoir et al.,  
284 2010).

285 But are downward movements of *Anolis* invasions or re-invasions? Lowland Puerto Rico  
286 was heavily forested prior to 4,800 years BP, when humans first settled in Puerto Rico and began  
287 clearing forests and collecting hardwoods for tools, furniture, and ceremonial objects (Rivera-  
288 Collazo, 2015). Europeans invaded in the late 15<sup>th</sup> century, introducing large-scale agriculture,  
289 which accelerated forest clearing, even in remote upland areas (Rivera-Collazo, 2015). Thus,  
290 when biologists first began studying *Anolis* in Puerto Rico in early to mid- 20<sup>th</sup> Century, the only  
291 surviving forests were in montane (or karst) refugia (Fig. 3) (Helmer et al., 2008; Lugo and  
292 Helmer, 2004). It is therefore not surprising that early biologists incorrectly interpreted forest-  
293 restricted species such as *A. gundlachi* to be “montane.” Biogeographic interpretation is  
294 sometimes confounded by the ghosts of past human activities (Williams, 1972).

295 We propose that *A. gundlachi* was – prior to European invasions – widespread in both  
296 lowland and upland forests, at least on the northern side of Puerto Rico, but was later extirpated  
297 from lowland areas when forests there were cleared for agriculture. This anole currently occupies  
298 lowland forests, even near sea level, despite its a low-temperature physiology (Huey and  
299 Webster, 1976). In fact, *A. gundlachi* in the forest at Carabali (~ 24 m) does not show elevated

300 corticosterone titers (Otero-López, unpublished) nor has reduced reproduction in summer, as  
301 might be expected if these anoles were heat stressed in lowland areas. Moreover, 61.45 % of  
302 female *A. gundlachi* in the forest at Carabali were gravid in winter (Jan – Feb, N = 68), whereas  
303 essentially 0% of *A. cristatellus* in the forest at Pta. Salinas (sea level) were gravid during that  
304 season (Otero et al., 2015). Thus, *A. gundlachi* appears better suited to lowland forests than does  
305 *A. cristatellus*, at least in cool seasons.

306 *Anolis gundlachi* not only survives in lowland forests, but can even displace *A.*  
307 *cristatellus* there. In the early 1970s, only *A. cristatellus* was known to occur inside lowland  
308 forests (Huey, 1974; Huey and Webster, 1976). Since then, however, *A. gundlachi* has replaced  
309 *A. cristatellus* in the forests at Campamento Eliza Colberg (~ 100 m) and likely can do so in  
310 other regenerated lowland forests, at least those that are inter-connected. This ecological  
311 replacement hypothesis is experimentally testable by introducing (or “re-introducing”) *A.*  
312 *gundlachi* to lowland forest sites (e.g., at Pta. Salinas) that are isolated from other forest patches  
313 and where *A. cristatellus* is currently the only trunk-ground anole. Of course, whether such  
314 lowland forest patches have survived Hurricane Maria remains to be seen.

315 Although our primary focus has been on the lowland shifts by montane species, we did  
316 find that lowland species (*A. cristatellus*, *A. pulchellus*, *A. stratulus*) – though still common in  
317 the lowlands – are now found at higher elevations than recorded in early collections. Although  
318 this shift might reflect a warming-promoted invasion of highland sites, it might simply reflect  
319 access to newly opened habitats in upland areas following massive forest blow-downs caused by  
320 two major hurricanes (Hugo in 1989, George in 1998). Such blowdowns lead to warmer and  
321 drier operative conditions, transiently favoring lowland species, at least until the forests

322 regenerate. Increased collecting at high elevation might also be a factor, but our analyses (above)  
323 do not support this alternative.

324

325 **Concluding remarks**

326 Our study underscores two obvious – but often overlooked – lessons for studies of responses to  
327 climate change:

328 (1) Contemporary biogeographic patterns can reflect real but often well-hidden influences  
329 of past human intervention (Nogués-Bravo et al., 2008; Rivera-Collazo, 2015; Williams, 1983).  
330 For example, the classic assignment of *A. gundlachi* as a ‘montane forest’ species is likely an  
331 historical artifact. When biologists began studying these forest lizards, the only remnant forests  
332 were largely in the mountains (Fig. 2), as lowland forests had long before been cleared for  
333 agriculture (Helmer et al., 2008; Lugo and Helmer, 2004). The low-temperature (and high water  
334 loss) physiology of *A. gundlachi* in particular reinforced the assumption that this species should  
335 be restricted to cool upland forests (Gorman and Hillman, 1977; Huey and Webster, 1976).  
336 However, our discovery of *A. gundlachi* in newly regenerated lowland forests suggests that this  
337 species was likely once native to lowland – as well as upland – forests, and thus is more properly  
338 considered a ‘forest’ species. The hypothesis that this species was native to lowland forests is  
339 potentially testable by fossil evidence; and the hypothesis that lowland populations are recent  
340 invaders is potentially testable by genetic analysis.

341 (2) Scientists analyzing impacts of climate change must recognize that climate might not  
342 be the only environmental factor that has changed or that will change in the future (Lenoir et al.,  
343 2010; Lenoir and Svenning, 2015; Nogués-Bravo et al., 2008; Seabra et al., 2015), and they must  
344 recognize as well that climate is not necessarily even the most influential factor that is changing.

345 In the present case, the magnitude of local cooling (and of humidity increase) caused when a  
346 lowland forest regenerates completely swamps minor temperature increases caused by  
347 anthropogenic warming to date. Moreover, regenerating forests at low elevations dramatically  
348 expands the area suitable for montane lizards (though this pattern is likely to reverse given  
349 sufficient warming; Nowakowski et al., 2017). Perhaps more importantly, temperature and  
350 humidity are just two axes of variation in the complex ecosystem in which montane *Anolis* are  
351 embedded. Shifts in food availability, disease, and predation (among many other factors) occur  
352 along with the thermal and hydric impacts of lowland forest regeneration, and these factors all  
353 affect the expansion of *Anolis* populations at low elevation.

354 The regeneration of Puerto Rican forests should not be interpreted as a general model for  
355 the future of tropical forests, as human-driven deforestation is clearly the norm in most tropical  
356 regions. Moreover, forest coverage and age in Puerto Rico is also strongly and dynamically  
357 affected by frequent hurricanes, which dynamically alter the ecology and distributions of plants  
358 and animals (Lugo et al., 1981; Uriarte et al., 2009). In any case, when tropical climate warming  
359 (Battisti and Naylor, 2009) combines with deforestation – caused either by natural (e.g., from  
360 hurricanes) or anthropogenic forces – local operative temperatures will increase substantially and  
361 may harm all but the most heat tolerant species (Colwell et al., 2008; Frishkoff et al., 2015;  
362 Sunday et al., 2011).

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557 **Table 1. Shifts in relative abundance below 250 meters**

558

	species & distribution					
	lowland			<i>montane</i>		
	<i>crisatellus</i>	<i>pulchellus</i>	<i>stratulus</i>	<i>evermanni</i>	<i>gundlachi</i>	<i>krugi</i>
1952-1977	<b>0.417</b>	<b>0.318</b>	<b>0.162</b>	0.015	0.002	0.087
1991-2015	0.356	0.260	0.123	<b>0.068</b>	<b>0.082</b>	<b>0.110</b>
<i>p</i>	0.011	0.006	0.007	< 0.001	< 0.001	0.015

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561 **Table 1.** Frequency of each species (as a proportion of all *Anolis* occurrences) below 250 meters  
 562 and holm-corrected *p* values from a chi-squared test for change between periods. The higher  
 563 frequency is bolded for each species, and shows that lowland species decreased while montane  
 564 species increased in frequency at low elevations.

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**Table 2. Difference in Shannon diversity by elevation and time period.**

<b>Elevation range (m)</b>	<b>Years</b>	<b><i>n</i> locality clusters</b>	<b>Median Shannon diversity</b>	<b>Shift</b>	<b><i>p</i></b>
0-250	1952-1977	23	0.683	0.115	0.066
	1991-2015	83	0.783		
251-500	1952-1977	13	1.040	0.126	0.423
	1991-2015	25	1.100		
501-750	1952-1977	6	0.818	0.025	0.743
	1991-2015	12	1.015		
751-1150	1952-1977	5	1.004	0.065	0.853
	1991-2015	14	1.017		

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**Table 2.** Difference in Shannon diversity of locality clusters by elevation and time period, with *p* values from a Wilcoxon rank-sum test.

575 **Table 3. Difference in mean annual temperature, 1952-1977 vs. 1991-2015**

Station	Elevation (m)	Mean annual temperature (°C)		Difference	<i>p</i>	df
		1952- 1977	1991- 2015			
Borinquen <sup>†</sup>	63	25.42	26.12	0.70	0.035	12.2
Corozal	187	24.31	24.90	0.59	0.003	27.9
Dos Bocas	119	25.69	25.22	-0.47	0.001	36.8
Lajas	30	24.93	25.46	0.53	0.005	44.0
Manati	78	25.33	25.45	0.12	0.24	33.4
Ponce	22	26.09	26.44	0.34	0.056	32.3
Rio Piedras <sup>†</sup>	17	25.47	25.83	0.35	0.068	21.6
Roosevelt <sup>†</sup>	6	26.68	26.99	0.31	0.11	22.9

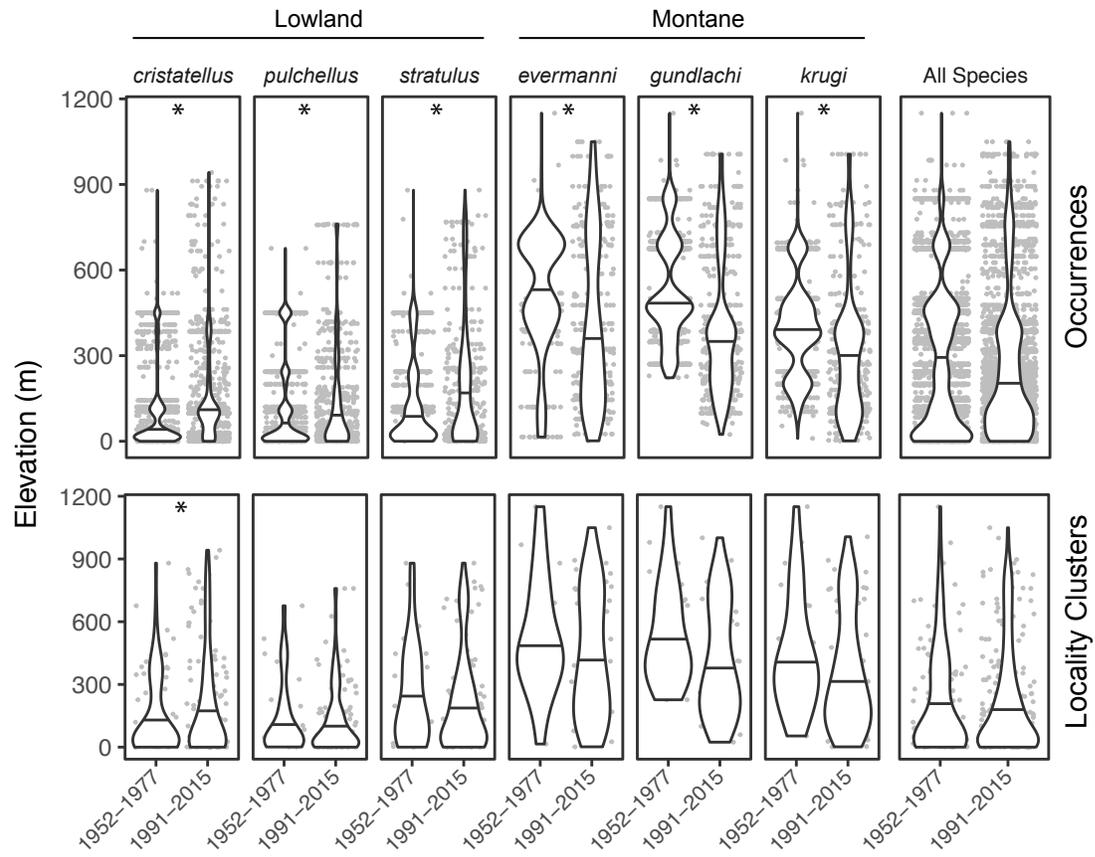
**Table 3.** Difference in mean annual temperature at NOAA weather stations on Puerto Rico, 1952-1977 vs 1991-2015, with *p* values and degrees of freedom for a Welch's two-sample *t*-test. †: stations in urban areas.

576 **Figure 1.** Elevation distributions for six common species of Puerto Rican *Anolis* in the periods  
577 1952-1977 and 1991-2015. “Violins” are density estimates, with width proportional to the  
578 number of occurrences at a given elevation. Asterisks indicate significant differences between  
579 time periods. Horizontal lines give the median elevation.

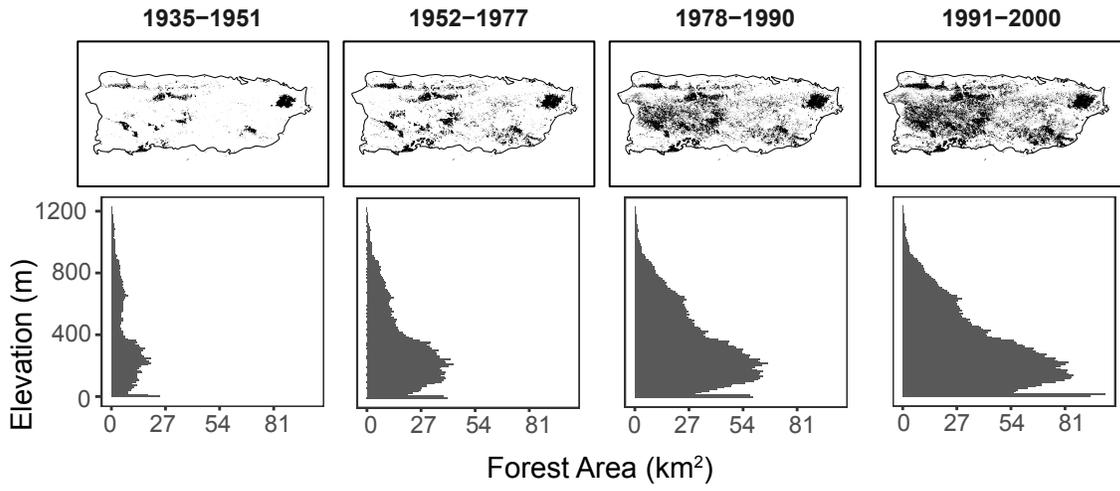
580  
581 **Figure 2.** Top: Maximum age of forested lands in Puerto Rico, 1931-2008. Bottom: area of  
582 forested land at different elevations (12-m bands).

583

Figure 1



**Figure 2**



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