

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

### **While Puerto Rico Warms**

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**ABSTRACT:** Puerto Rico has warmed slightly in recent decades, and consequently elevational ranges of *Anolis* lizards there should be shifting uphill. However, by comparing historical versus recent collecting records and by resurveying specific sites, we find that three “montane” species have moved downhill in recent decades, even reaching the coastal plain. This paradoxical downward shift appears to be related to the massive regeneration of Puerto Rican forests – especially down into the lowlands – which started in mid-20th century, when the island’s economy began shifting from agriculture to manufacturing. The cooler microhabitats in regenerated forests counteract recent climate warming and probably enabled lizards to migrate downhill, following the dispersal of forests from montane refugia into lowland areas. Very likely both forests and lizards were native in the lowlands until European settlers arrived centuries ago and cleared most lowland forests for agriculture. Three lowland species have seemingly expanded their ranges to higher elevations in recent decades, but whether this movement reflects warming, collecting bias, or hurricane-induced destruction of forests is unclear. The impact of Hurricane Maria (2017) on distributional patterns described herein is unknown. We expect that forest-dwelling lizard species will be largely extirpated in lowland areas, at least until those forests again regenerate and until lizards can recolonize these sites.

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

## Introduction

A biogeographic shift to higher elevations is a common (Colwell et al., 2008; Freeman and Freeman, 2014; Moritz et al., 2008; Parmesan, 2006) though not universal (Lenoir and Svenning, 2015) response of species to warming climates, at least where mountains are accessible. Ultimately, such shifts can lead to “biotic attrition” in lowland regions (Colwell et al., 2008). Tropical ectotherms might show conspicuous elevational responses to warming because their ecology is tightly coupled to environmental temperature, because their physiology is relatively specialized for temperature, and because mountains are “higher” in the tropics (Ghalambor et al., 2006; Janzen, 1967; Sunday et al., 2011; van Berkum, 1988). *Anolis* lizards on the tropical island of Puerto Rico provide an opportunity to explore such shifts, because their distribution, behavior, ecology, and thermal biology are well known (Gorman and Licht, 1974; Gunderson and Leal, 2012; Hertz et al., 1979; Huey and Webster, 1976; Leal and Fleishman, 2002; Lister, 1981; Losos, 2011; Rand, 1964; Rodríguez-Robles et al., 2005; Schoener, 1971; Williams, 1972). Moreover, Puerto Rico has warmed slightly in recent decades (Burrowes et al., 2004; Comarazamy and González, 2011; Jennings et al., 2014; Méndez-Lázaro et al., 2015; Waide et al., 2013), thus setting both an expectation for uphill range shifts.

We have been studying responses of Puerto Rican anoles to recent climate warming, and one of our initial planned projects was to evaluate whether the lower elevational range limit of *Anolis gundlachi* had shifted uphill in recent decades. This lizard has historically been described as a montane, forest, thermoconformer (Gorman and Licht, 1974; Heatwole, 1970; Hertz et al., 1979; Hertz, 1981; Huey and Webster, 1976; Lister, 1981; Rand, 1964; Rivero, 1998; Schmidt, 1918; Schoener, 1971; Williams, 1972). Relative to other Puerto Rican anoles, it is active at low

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

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

Our 2011 observations forced us to cancel our original research goal and to focus instead on several questions concerning historical shifts in the distributional patterns of Puerto Rican anoles. First, were our anecdotal impressions on Highway 191 correct and general for *A. gundlachi*? If so, the presence of *A. gundlachi* at other lowland localities would be recent; and this could be evaluated by comparing historical versus contemporary museum and locality

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

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

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

## Methods

*Study Species*

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

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

Two “grass-bush” anoles (*A. pulchellus* and *A. krugi*) occur over broad elevational ranges. *Anolis pulchellus* is abundant at low to moderate elevation in relatively exposed habitats.

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

### *Specimen Records and Georeferencing*

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

After removing localities with greater than 2-km georeferencing uncertainty and splitting out sites with verbatim elevations provided by the collector, we estimated the elevation of each collecting locality as the mean elevation across the full uncertainty radius in the USGS National Elevation Database (U.S. Geological Survey, 2016) at 1-arc-second resolution, using the “rgeos”

and “Raster” packages in R (Bivand and Rundel, 2013; Hijmans and van Etten, 2014; R Core Team, 2015). Specimen records were binned into four period classes (see below) bracketing 1935-2015, based on the forest age ranges used in Helmer et al.’s 2008 analysis of land-cover change on Puerto Rico. We subset records to include only the six most common species of *Anolis* (above), all of which occur in the mountains. The final dataset includes 8,839 specimens and 121 sight records across 505 localities and 293 locality clusters (Appendix S1: Fig. S1). Most collecting occurred during the periods 1952-1977 or 1991-2016 (Appendix S1: Fig. S2).

### *Shifts in Elevation Distribution*

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



To assess potential changes in species composition at low elevations, we extracted specimen reports at elevations lower than 250 m, split them by species, and used a McNemar test to compare the relative abundance of each species across time periods (i.e., the number of specimens of species *i* relative to the number of all *Anolis* specimens in each period). This procedure is conceptually similar to the specimen-derived abundance index used in Linck et al. (2016) and Rohwer et al., (2012), in which the observed abundance of a target species is corrected for survey effort by dividing by the number of specimens collected with similar techniques in a given area. For all analyses conducted separately on each species, we include *p*-values corrected for multiple testing ( $n=6$ ) using a Holm-Bonferroni correction (Holm, 1979).

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

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

To assess changes in forest cover on Puerto Rico over the 20<sup>th</sup> century, we modified an existing raster layer of forest age and soil types across the island developed from analysis of aerial and satellite imagery (Helmer et al., 2008). We merged forest ages across soil types and subset the original raster layer to produce maps of forested areas at 30-m resolution in four time bins: 1935-

1951, 1952-1977, 1977-1990, and 1991-2000 (matching the age classes in Helmer et al. 2008).

We then extracted the elevations of forested grid cells in each time period and plotted these as a histogram showing total forested area in approximately 12-m elevation bands (Figure 2).

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

## Results

*Shifts in Elevation Ranges*

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

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

Comparing Shannon diversity of locality clusters in elevation bins across time periods, we found no evidence of the loss of lowland diversity predicted in (Colwell et al., 2008). Observed diversity increased at elevations below 500M, but these changes were not statistically significant after dropping sites with only one observed species (Table 2, Appendix S1: Fig. S3). Diversity is weakly but positively correlated with elevation in both time periods, with recent records showing a shallower slope and higher y-intercept (1952-1977:  $p=0.047$ ,  $df=46$ ,

$R^2=0.063$ , equation  $y=0.0004x+0.728$ ; 1991-2015:  $p=0.016$ ,  $df=132$ ,  $R^2=0.036$ , equation  $y=0.0003x+0.867$ ).

### *Lowland and Resurveyed Localities*

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

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

### *Land Cover & Temperature*

Forests in Puerto Rico expanded dramatically from approximately 8.9% of total land area in 1935-1951 to 43.1% in 1991-2000 (Helmer et al., 2008; Fig. 2). All elevation bands saw significant increases in forested area, but the largest absolute (as well as relative) increases occurred in elevations of 100-300 m (Fig. 2).

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

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

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

Otero et al. (2015) monitored and reported operative temperatures in open versus forest (secondary) habitats at two lowland localities in Puerto Rico. At Monagas in summer, for example, operative temperatures in the open often exceeded 40°C (maximum = 46.4°C), well

above the critical thermal maximum of *A. gundlachi* (37.5°C, Huey and Webster, 1976); whereas operative temperatures in the forest rarely exceeded 30°C (maximum = 33.3°C). Thus, a regenerated lowland forest lowers operative temperatures much more than the cumulative rise in temperatures associated with recent climate warming – at least so far (Nowakowski et al., 2017).

## Discussion

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

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

A more plausible explanation relates to historical changes in land use in Puerto Rico. In many tropical regions, logging and agriculture have reduced forest cover (Álvarez-Berríos et al., 2013). In Puerto Rico, however, forests have expanded dramatically since the middle of the 20<sup>th</sup> century (Helmer et al., 2008; Lugo and Helmer, 2004) (Fig. 2), reflecting a shift from an agricultural and rural economy to a manufacturing and urban one (Yackulic et al., 2011). [Note: Such rapid re-forestation may seem implausible to biologists without tropical experience. However, Puerto Rican forests recover basic structure within a decade or two after hurricane

blowdowns (Lugo et al., 1981; Walker, 1991), and are indistinguishable from primary forest in terms of density and tree size after only 40 years of recovery (Aide et al., 1996).]

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

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

We propose that *A. gundlachi* was – prior to European invasions – widespread in both lowland and upland forests, at least on the northern side of Puerto Rico, but was later extirpated from lowland areas when forests there were cleared for agriculture. This anole currently survives lowland forests, and even near sea level, despite its a low-temperature physiology (Huey and

Webster, 1976). In fact, *A. gundlachi* in the forest at Carabali (~ 24 m) does not show elevated corticosterone titers (Otero-López, unpublished) nor has reduced reproduction in summer, as might be expected if these anoles were heat stressed in lowland areas. Moreover, 61.45 % of female *A. gundlachi* in the forest at Carabali were gravid in winter (Jan – Feb, N = 68), whereas essentially 0% of *A. cristatellus* in the forest at Pta. Salinas (sea level) were gravid during that same season (Otero et al., 2015). Thus, *A. gundlachi* appears better suited to lowland forests than does *A. cristatellus*, at least in cool seasons.

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

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



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

### Concluding remarks

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

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

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

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

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

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### Literature Cited

- Achard, F., Beuchle, R., Mayaux, P., Stibig, H.-J., Bodart, C., Brink, A., Carboni, S., Desclée, B., Donnay, F., Eva, H.D., 2014. Determination of tropical deforestation rates and related carbon losses from 1990 to 2010. *Glob. Change Biol.* 20, 2540–2554.
- Aide, T.M., Zimmerman, J.K., Rosario, M., Marciano, H., 1996. Forest Recovery in Abandoned Cattle Pastures Along an Elevational Gradient in Northeastern Puerto Rico. *Biotropica* 28, 537–548. <https://doi.org/10.2307/2389095>
- Álvarez-Berrios, N.L., Redo, D.J., Aide, T.M., Clark, M.L., Grau, R., 2013. Land Change in the Greater Antilles between 2001 and 2010. *Land* 2, 81–107.
- Bastable, H.G., Shuttleworth, W.J., Dallarosa, R.L.G., Fisch, G., Nobre, C.A., 1993. Observations of climate, albedo, and surface radiation over cleared and undisturbed Amazonian forest. *Int. J. Climatol.* 13, 783–796.
- Battisti, D.S., Naylor, R.L., 2009. Historical warnings of future food insecurity with unprecedented seasonal heat. *Science* 323, 240–244.
- Bivand, R., Rundel, C., 2013. rgeos: interface to geometry engine-open source (GEOS). R Package Version 03-2.
- Buckley, L.B., 2013. Get real: putting models of climate change and species interactions in practice. *Ann. N. Y. Acad. Sci.* 1297, 126–138.
- Burrowes, P.A., Joglar, R.L., Green, D.E., 2004. Potential causes for amphibian declines in Puerto Rico. *Herpetologica* 60, 141–154.
- Colwell, R.K., Brehm, G., Cardelús, C.L., Gilman, A.C., Longino, J.T., 2008. Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *science* 322, 258–261.
- Comarazamy, D.E., González, J.E., 2011. Regional long-term climate change (1950–2000) in the midtropical Atlantic and its impacts on the hydrological cycle of Puerto Rico. *J. Geophys. Res. Atmospheres* 116.
- Freeman, B.G., Freeman, A.M.C., 2014. Rapid upslope shifts in New Guinean birds illustrate strong distributional responses of tropical montane species to global warming. *Proc. Natl. Acad. Sci.* 111, 4490–4494.

- Frishkoff, L.O., Hadly, E.A., Daily, G.C., 2015. Thermal niche predicts tolerance to habitat conversion in tropical amphibians and reptiles. *Glob. Change Biol.* 21, 3901–3916.
- Geiger, R., Aron, R.H., Todhunter, P., 2009. The climate near the ground, 7th ed. Rowman & Littlefield, Lanham, MD.
- Ghalambor, C.K., Huey, R.B., Martin, P.R., Tewksbury, J.J., Wang, G., 2006. Are mountain passes higher in the tropics? Janzen’s hypothesis revisited. *Integr. Comp. Biol.* 46, 5–17.
- Gorman, G.C., Hillman, S., 1977. Physiological basis for climatic niche partitioning in two species of Puerto Rican *Anolis* (Reptilia, Lacertilia, Iguanidae). *J. Herpetol.* 337–340.
- Gorman, G.C., Licht, P., 1974. Seasonality in ovarian cycles among tropical *Anolis* lizards. *Ecology* 55, 360–369.
- Grau, H.R., Aide, T.M., Zimmerman, J.K., Thomlinson, J.R., Helmer, E., Zou, X., 2003. The ecological consequences of socioeconomic and land-use changes in postagriculture Puerto Rico. *AIBS Bull.* 53, 1159–1168.
- Gunderson, A.R., Leal, M., 2012. Geographic variation in vulnerability to climate warming in a tropical Caribbean lizard. *Funct. Ecol.* 26, 783–793.
- Gunderson, A.R., Mahler, D.L., Leal, M., 2016. A functional analysis of the contribution of climatic niche divergence to adaptive radiation. *bioRxiv* 69294.
- Hansen, M.C., Stehman, S.V., Potapov, P.V., 2010. Quantification of global gross forest cover loss. *Proc. Natl. Acad. Sci.* 107, 8650–8655.
- Harmsen, E.W., Miller, N.L., Schlegel, N.J., Gonzalez, J.E., 2009. Seasonal climate change impacts on evapotranspiration, precipitation deficit and crop yield in Puerto Rico. *Agric. Water Manag.* 96, 1085–1095.
- Heatwole, H., 1970. Thermal ecology of the desert dragon *Amphibolurus inermis*. *Ecol. Monogr.* 40, 425–457.
- Heatwole, H., Lin, T.-H., Villalón, E., Muñoz, A., Matta, A., 1969. Some aspects of the thermal ecology of Puerto Rican anoline lizards. *J. Herpetol.* 65–77.
- Helmer, E.H., Brandeis, T.J., Lugo, A.E., Kennaway, T., 2008. Factors influencing spatial pattern in tropical forest clearance and stand age: implications for carbon storage and species diversity. *J. Geophys. Res. Biogeosciences* 113.
- Helmus, M.R., Mahler, D.L., Losos, J.B., 2014. Island biogeography of the Anthropocene. *Nature* 513, 543.
- Hertz, P.E., 1992. Temperature regulation in Puerto Rican *Anolis* lizards: a field test using null hypotheses. *Ecology* 73, 1405–1417.
- Hertz, P.E., 1981. Adaptation to altitude in two West Indian anoles (Reptilia: Iguanidae): thermal biology and physiological ecology. *J. Zool.* 195, 25–37. <https://doi.org/10.1111/j.1469-7798.1981.tb01891.x>
- Hertz, P.E., Arce-Hernandez, A., Ramirez-Vazquez, J., Tirado-Rivera, W., Vazquez-Vives, L., 1979. Geographical variation of heat sensitivity and water loss rates in the tropical lizard, *Anolis gundlachi*. *Comp. Biochem. Physiol. A Physiol.* 62, 947–953.

- 442 Hertz, P.E., Arima, Y., Harrison, A., Huey, R.B., Losos, J.B., Glor, R.E., 2013. Asynchronous  
443 evolution of physiology and morphology in *Anolis* lizards. *Evolution* 67, 2101–2113.
- 444 Hijmans, R.J., van Etten, J., 2014. raster: Geographic data analysis and modeling. R Package  
445 Version 2, 15.
- 446 Holm, S., 1979. A Simple Sequentially Rejective Multiple Test Procedure. *Scand. J. Stat.* 6, 65–  
447 70.
- 448 Huey, R.B., 1974. Behavioral thermoregulation in lizards: importance of associated costs.  
449 American Association for the Advancement of Science.
- 450 Huey, R.B., Deutsch, C.A., Tewksbury, J.J., Vitt, L.J., Hertz, P.E., Pérez, H.J.Á., Garland, T.,  
451 2009. Why tropical forest lizards are vulnerable to climate warming. *Proc. R. Soc. Lond.*  
452 *B Biol. Sci.* 276, 1939–1948.
- 453 Huey, R.B., Webster, T.P., 1976. Thermal biology of *Anolis* lizards in a complex fauna: the  
454 *Christatellus* group on Puerto Rico. *Ecology* 57, 985–994.
- 455 Janzen, D.H., 1967. Why mountain passes are higher in the tropics. *Am. Nat.* 101, 233–249.
- 456 Jennings, L.N., Douglas, J., Treasure, E., González, G., 2014. Climate change effects in El  
457 Yunque National Forest, Puerto Rico, and the Caribbean region (Gen Tech Rep No. SRS-  
458 GTR-193). USDA-Forest Service, Southern Research Station, Asheville, NC.
- 459 Karl, T.R., Arguez, A., Huang, B., Lawrimore, J.H., McMahon, J.R., Menne, M.J., Peterson,  
460 T.C., Vose, R.S., Zhang, H.-M., 2015. Possible artifacts of data biases in the recent global  
461 surface warming hiatus. *Science* 348, 1469–1472.
- 462 Kaspari, M., Clay, N.A., Lucas, J., Yanoviak, S.P., Kay, A., 2015. Thermal adaptation generates  
463 a diversity of thermal limits in a rainforest ant community. *Glob. Change Biol.* 21, 1092–  
464 1102.
- 465 Leal, M., Fleishman, L.J., 2002. Evidence for habitat partitioning based on adaptation to  
466 environmental light in a pair of sympatric lizard species. *Proc. R. Soc. Lond. B Biol. Sci.*  
467 269, 351–359.
- 468 Lenoir, J., Gégout, J.-C., Guisan, A., Vittoz, P., Wohlgemuth, T., Zimmermann, N.E., Dullinger,  
469 S., Pauli, H., Willner, W., Svenning, J.-C., 2010. Going against the flow: potential  
470 mechanisms for unexpected downslope range shifts in a warming climate. *Ecography* 33,  
471 295–303.
- 472 Lenoir, J., Svenning, J.-C., 2015. Climate-related range shifts—a global multidimensional  
473 synthesis and new research directions. *Ecography* 38, 15–28.
- 474 Linck, E., Bridge, E.S., Duckles, J.M., Navarro-Sigüenza, A.G., Rohwer, S., 2016. Assessing  
475 migration patterns in *Passerina ciris* using the world’s bird collections as an aggregated  
476 resource. *PeerJ* 4, e1871.
- 477 Lister, B.C., 1981. Seasonal niche relationships of rain forest anoles. *Ecology* 62, 1548–1560.
- 478 Losos, J.B., 2011. Lizards in an evolutionary tree: ecology and adaptive radiation of anoles. Univ  
479 of California Press.

- 480 Lugo, A.E., Helmer, E., 2004. Emerging forests on abandoned land: Puerto Rico's new forests.  
481 For. Ecol. Manag. 190, 145–161.
- 482 Lugo, A.E., Schmidt, R., Brown, S., 1981. Tropical Forests in the Caribbean. Ambio 10, 318–  
483 324.
- 484 Méndez-Lázaro, P., Martínez-Sánchez, O., Méndez-Tejeda, R., Rodríguez, E., Morales, E.,  
485 Schmitt-Cortijo, N., 2015. Extreme heat events in San Juan Puerto Rico: trends and  
486 variability of unusual hot weather and its possible effects on ecology and society. J.  
487 Climatol. Weather Forecast. 3, 135.
- 488 Moritz, C., Patton, J.L., Conroy, C.J., Parra, J.L., White, G.C., Beissinger, S.R., 2008. Impact of  
489 a century of climate change on small-mammal communities in Yosemite National Park,  
490 USA. Science 322, 261–264.
- 491 Nogués-Bravo, D., Araújo, M.B., Romdal, T., Rahbek, C., 2008. Scale effects and human impact  
492 on the elevational species richness gradients. Nature 453, 216.
- 493 Nowakowski, A.J., Watling, J.I., Whitfield, S.M., Todd, B.D., Kurz, D.J., Donnelly, M.A., 2017.  
494 Tropical amphibians in shifting thermal landscapes under land-use and climate change.  
495 Conserv. Biol. 31, 96–105.
- 496 Oke, T.R., 1982. The energetic basis of the urban heat island. Q. J. R. Meteorol. Soc. 108, 1–24.  
497 <https://doi.org/10.1002/qj.49710845502>
- 498 Otero, L.M., Huey, R.B., Gorman, G.C., 2015. A few meters matter: local habitats drive  
499 reproductive cycles in a tropical lizard. Am. Nat. 186, E72–E80.
- 500 Otero-López, L.M., 2015. Reproductive phenology, fecundity, survival and growth of Puerto  
501 Rican Anolis lizards in the context of climate warming. (p 119). University of Puerto  
502 Rico, Departamento de Biología, Río Piedras, Puerto Rico.
- 503 Parmesan, C., 2006. Ecological and evolutionary responses to recent climate change. Annu Rev  
504 Ecol Evol Syst 37, 637–669.
- 505 Patz, J.A., Martens, W.J., Focks, D.A., Jetten, T.H., 1998. Dengue fever epidemic potential as  
506 projected by general circulation models of global climate change. Environ. Health  
507 Perspect. 106, 147.
- 508 R Core Team, 2015. R: A language and environment for statistical computing [Internet]. Vienna,  
509 Austria: R Foundation for Statistical Computing; 2014.
- 510 Rand, A.S., 1964. Ecological distribution in anoline lizards of Puerto Rico. Ecology 45, 745–  
511 752.
- 512 Rivera-Collazo, I.C., 2015. Por el camino verde: Long-term tropical socioecosystem dynamics  
513 and the Anthropocene as seen from Puerto Rico. The Holocene 25, 1604–1611.
- 514 Rivero, J.A., 1998. Amphibians and reptiles of Puerto Rico. La Editorial, UPR.
- 515 Rodríguez-Robles, J.A., Leal, M., Losos, J.B., 2005. Habitat selection by the Puerto Rican  
516 yellow-chinned anole, *Anolis gundlachi*. Can. J. Zool. 83, 983–988.

- 517 Rohwer, S., Rohwer, V.G., Peterson, A.T., Navarro-Sigüenza, A.G., English, P., 2012. Assessing  
518 migratory double breeding through complementary specimen densities and breeding  
519 records. *The Condor* 114, 1–14.
- 520 Schmidt, K.P., 1918. Contributions to the herpetology of Porto Rico. *Ann. N. Y. Acad. Sci.* 28,  
521 167–200.
- 522 Schoener, T.W., 1971. Structural habitats of West Indian *Anolis* lizards. Harvard University,  
523 Museum of Comparative Zoology.
- 524 Schwartz, A., Henderson, R.W., 1991. Amphibians and reptiles of the West Indies: descriptions,  
525 distributions, and natural history. University Press of Florida.
- 526 Seabra, R., Wethey, D.S., Santos, A.M., Lima, F.P., 2015. Understanding complex  
527 biogeographic responses to climate change. *Sci. Rep.* 5.
- 528 Shannon, C.E., 1948. A Mathematical Theory of Communication. *Bell Syst. Tech. J.* 27, 379–  
529 423. <https://doi.org/10.1002/j.1538-7305.1948.tb01338.x>
- 530 Sunday, J.M., Bates, A.E., Dulvy, N.K., 2011. Global analysis of thermal tolerance and latitude  
531 in ectotherms. *Proc. R. Soc. Lond. B Biol. Sci.* 278, 1823–1830.
- 532 Thomas, R., Joglar, R., 1996. The herpetology of Puerto Rico. *Ann. N. Y. Acad. Sci.* 776, 181–  
533 196.
- 534 Uriarte, M., Canham, C.D., Thompson, J., Zimmerman, J.K., Murphy, L., Sabat, A.M., Fetcher,  
535 N., Haines, B.L., 2009. Natural disturbance and human land use as determinants of  
536 tropical forest dynamics: results from a forest simulator. *Ecol. Monogr.* 79, 423–443.
- 537 U.S. Geological Survey, 2016. The National Map, 3D Elevation program Web Page [WWW  
538 Document]. URL [http://nationalmap.gov/3DEP/3dep\\_prodserv.html](http://nationalmap.gov/3DEP/3dep_prodserv.html) (accessed 5.10.16).
- 539 van Berkum, F.H., 1988. Latitudinal patterns of the thermal sensitivity of sprint speed in lizards.  
540 *Am. Nat.* 132, 327–343.
- 541 Waide, R.B., Comarazamy, D.E., González, J.E., Hall, C.A., Lugo, A.E., Luvall, J.C., Murphy,  
542 D.J., Ortiz-Zayas, J.R., Ramírez-Beltran, N.D., Scatena, F.N., 2013. Climate variability at  
543 multiple spatial and temporal scales in the Luquillo Mountains, Puerto Rico.
- 544 Walker, L.R., 1991. Tree Damage and Recovery From Hurricane Hugo in Luquillo Experimental  
545 Forest, Puerto Rico. *Biotropica* 23, 379–385. <https://doi.org/10.2307/2388255>
- 546 Wiecezorek, J., 2001. MaNIS: Georeferencing Guidelines. Univ. Calif. Berkeley–MaNIScited 26  
547 January 2004 37.
- 548 Williams, E.E., 1983. Ecomorphs, faunas, island size, and diverse end points in island radiations  
549 of *Anolis*, in: Huey, R.B., Pianka, E.R., Schoener, T.W. (Eds.), *Lizard Ecology: Studies*  
550 *of a Model Organism*. Harvard Univ Pr, Cambridge, Massachusetts.
- 551 Williams, E.E., 1972. The origin of faunas. Evolution of lizard congeners in a complex island  
552 fauna: a trial analysis, in: *Evolutionary Biology*. Springer, pp. 47–89.
- 553 Yackulic, C., Fagan, M., Jain, M., Jina, A., Lim, Y., Marlier, M., Muscarella, R., Adame, P.,  
554 DeFries, R., Uriarte, M., 2011. Biophysical and socioeconomic factors associated with  
555 forest transitions at multiple spatial and temporal scales. *Ecol. Soc.* 16.
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**Table 1. Shifts in relative abundance below 250 meters**

	species & distribution					
	lowland			montane		
	<i>cristatellus</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

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



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

Elevation range (m)	Years	<i>n</i> locality clusters	Median Shannon diversity	Shift	<i>p</i>
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		

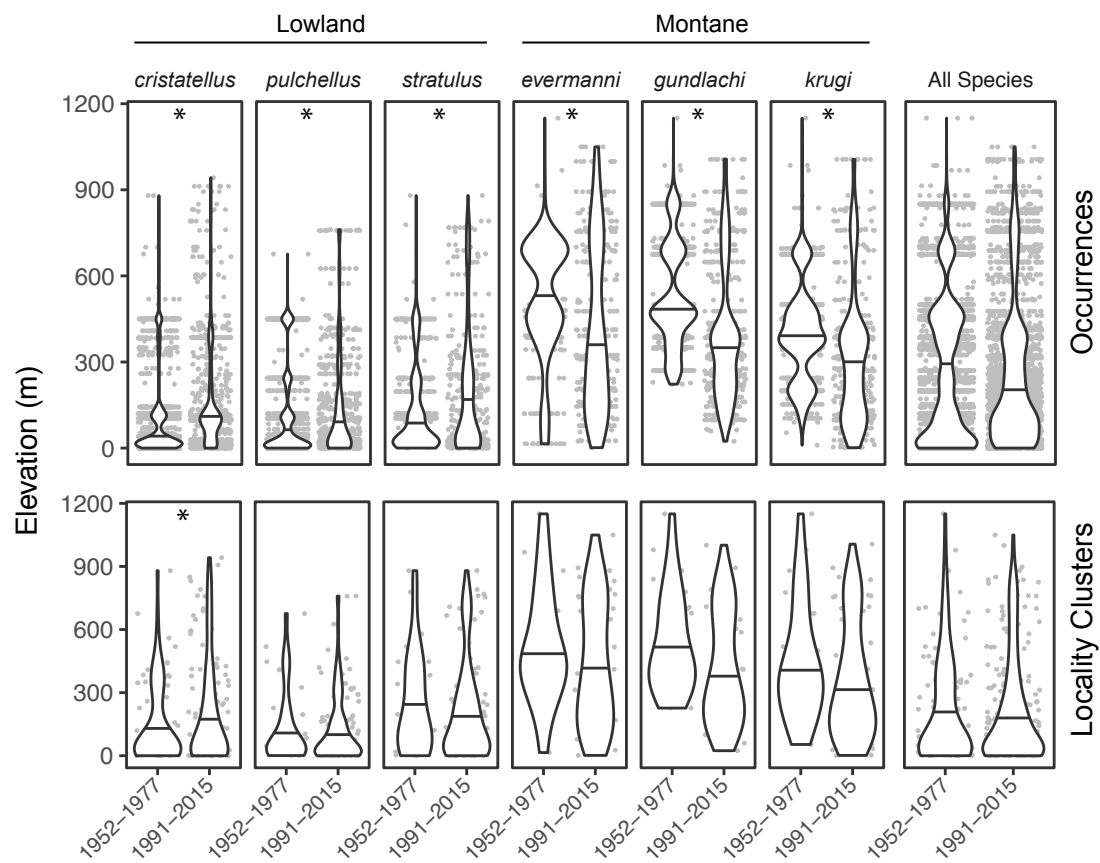
**Table 2.** Difference in Shannon diversity of locality clusters by elevation and time period, with *p* values from a Wilcoxon rank-sum test.

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

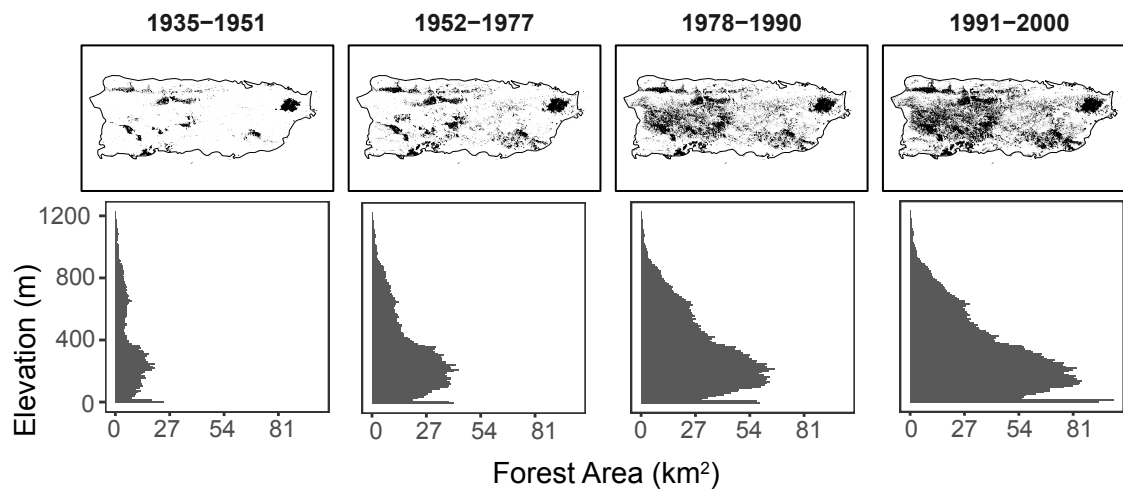
Station	Elevation (m)	Mean annual temperature (°C)		Difference	<i>p</i>	df
		1952- 1977	1991- 2015			
Borinquen <sup>†</sup>	63	25.42	26.12	0.70	0.035	12.2
Corozal	187	24.31	24.90	0.59	0.003	27.9
Dos Bocas	119	25.69	25.22	-0.47	0.001	36.8
Lajas	30	24.93	25.46	0.53	0.005	44.0
Manati	78	25.33	25.45	0.12	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. <sup>†</sup>: stations in urban areas.

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



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