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*
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 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 through Luquillo National Forest, 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 provided an opportunity to focus 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 assumption 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 the 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 20th century (Álvarez-Berríos 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 expansion of forests into lowland areas from upland refugia. A regenerated forest apparently cools and humidifies the local environment sufficiently to enable montane animal 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 16th 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
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 20th 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 20th 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 500 m, 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 Carabalí 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 be the descendants of 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 showed
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 higher in montane areas than in lowland 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 \textit{Anolis} lizards (especially \textit{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 \textit{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\textsuperscript{th} 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 cooling from re-forestation 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, furniture, and ceremonial objects (Rivera-Collazo, 2015). Europeans invaded in the late 15th 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-20th Century, the only surviving forests were in montane (or karst) refugia (Fig. 3) (Helmer et al., 2008; Lugo and Helmer, 2004). It is therefore 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 occupies lowland forests, even near sea level, despite its a low-temperature physiology (Huey and Webster, 1976). In fact, *A. gundlachi* in the forest at Carabalí (~24 m) does not show elevated
corticosterone titer (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 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 *A. cristatellus* is currently the only trunk-ground anole. 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 simply 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 is 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**


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Table 1. Shifts in relative abundance below 250 meters

<table>
<thead>
<tr>
<th>Species &amp; Distribution</th>
<th>Lowland</th>
<th>Montane</th>
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<td></td>
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<td>pulchellus</td>
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<td>p</td>
<td>0.011</td>
<td>0.006</td>
</tr>
</tbody>
</table>

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.

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

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

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

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.
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).
**Figure 1**

The figure shows the elevation range for different species of lizards in lowland and montane regions over two time periods: 1952-1977 and 1991-2015. The species included are *cristatellus*, *pulchellus*, *stratulus*, *evermanni*, *gundlachi*, and *krugi*. The occurrences and locality clusters are depicted for each species and time period.
Figure 2

[Diagram showing changes in forest area and elevation from 1935-1951 to 1991-2000. The diagrams illustrate the trend of lizards moving downhill over the years.]

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