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ORIGINAL PAPER

Population density of the tropical lizard *Anolis cristatellus* in urban and forested habitats after a major hurricane

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Abstract
Urbanization, the process whereby natural environments are modified for human habitation, is increasing worldwide. Many species are extirpated from urban settings, but others can survive and thrive in this environment. Few studies have compared population densities between urban and natural sites and none have investigated how hurricanes might interact with urbanization to affect animal species population dynamics in cities, which is crucial in evaluating population persistence in urban habitats. We quantified post-hurricane population dynamics between urban and forest populations of the tropical lizard *Anolis cristatellus* in paired urban and forest sites across the island of Puerto Rico at 4, 11, and 16 months following Hurricane Maria. Though we lacked pre-hurricane population density data, we expected lower than normal densities after the hurricane and a gradual increase through time. We found that urban population density was lower compared to natural areas across all pairs of sites. In forested areas, we found increases in perch density, likely associated with post-disturbance succession, but urban structural habitats remained relatively constant through time, with most hurricane-damaged vegetation being rapidly removed by humans. The two sites in our study that were most heavily impacted by the hurricane initially doubled in population density, and density continued to increase through our sampling period. Our findings suggest that hurricanes and urbanization can interact to shape population dynamics in lizards. Moreover, urban sites experience constant human modifications. As such, understanding population dynamics of urban species will require careful consideration of the effect of human intervention in these habitats.

Keywords *Anolis cristatellus* · Hurricane Maria · Puerto Rico · Population density · Tropical storms · Urbanization

Introduction

Urbanization is an important dimension of global environmental change (Rivkin et al. 2019; Alberti et al. 2020). One consequence of urbanization is the impact that it can have on species composition, diversity, and abundance. For instance, species occurrences are influenced by the availability of suitable habitat in urban spaces, as well as by ecological interactions with other taxa in the urbanized landscape (Aronson et al. 2016; Fournier et al. 2020). As a result, some species can be fully extirpated from urban habitats, while others maintain robust populations (Delgado de la Flor et al. 2017; Pignataro et al. 2020). Others still can *increase* dramatically in relative abundance within urban areas compared to more natural sites nearby (Jokimäki et al. 2017; Pieniażek et al. 2017). For example, a species of field mouse in Poland maintains larger populations in urban habitats than in nearby forested areas (Pieniażek et al. 2017). On the other hand, Fournier et al. (2020) documented a reduction in species richness due to habitat filtering associated with drier condition and a less specialized diet in urban environments. Similar decreases in species richness have been reported with increasing degrees of urbanization, although this may depend on landscape heterogeneity which can vary as a function of the scale used to quantify the landscape (McKinney 2008). In other cases, urban areas could host population densities as high as non-urban sites, such as is the case for some species of Galapagos finches (De León et al. 2019). Thus, the overall effect of urbanization can be positive for some

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species and negative for others. Nonetheless, as a general rule the population density and dynamics of urban species tend to *differ* from natural habitats nearby (McKinney 2008).

Just as the intensity and extent of urbanization is predicted to continue to rise, most global environmental change models predict an increased frequency of catastrophic weather events such as hurricanes (Cochrane and Barber 2009; Knutson et al. 2010; Turner 2010; Holland and Bruyère 2014; Newman 2019). The effect of extreme weather events on urban populations will vary as a function of the interaction between disturbance, urbanization, and the pre- and post-disturbance fitness of urban populations. For example, if urban taxa lack specific habitat-disturbance adaptations they may suffer greater mortality compared to populations that have co-adapted with their disturbance regime (Seidl et al. 2016). An important yet relatively understudied element of urban evolutionary ecology is whether synanthropes (i.e., species that thrive in proximity to humans) in urban environments respond differently to disturbance events, compared to conspecifics in non-urban habitats of the same region.

Hurricanes are known to affect animal populations through the combined effects of the immediate kinetic energy of the storm and the consequent transformation of the structural habitat (Lugo 2000, 2008). For instance, snail density decreased significantly after Hurricane Hugo in 1989 as a result of both *direct* mortality from the storm, and *indirect* mortality due to drier conditions on the forest floor resulting from forest canopy damage (Secrest et al. 1996). Post-hurricane mortality can also result from scarcity of food resources, such as in the case of frugivorous bats following both Hurricane Hugo (1989) and Hurricane Georges (1998; Gannon and Willig 1994, 2009). Moreover, populations of some species have experienced rapid growth following a hurricane. For example, certain lepidopterans can increase in abundance in hurricane affected sites, and this is thought to be due to the increased availability of food resources such as young leaves after canopy sheering (Torres 1992). Despite this variety of studies that have investigated the effect of hurricanes on population density in natural environments, virtually nothing is known about patterns of mortality and/or recruitment in urban populations after a hurricane event.

Here, we examine this issue by quantifying changes in population dynamics in urban and forest populations of the tropical lizard *Anolis cristatellus* following the 2017 category 5 Hurricane Maria in Puerto Rico. We evaluated paired forest and urban populations of *Anolis* lizards at 4, 11 and 16 months following the hurricane. No previous study had compared the population density of *Anolis cristatellus* between urban and forested environments. As such, we lacked baseline data to aid our predictions of the population dynamics following this catastrophic storm. We focus our hypothesis on contrasting forest and urban population densities immediately after the hurricane and at 11 and 16 months afterwards. Prior research has established that urban habitats are less structurally complex than nearby forested environments, and large parts of the urban habitat are inhospitable to arboreal lizards (Winchell et al. 2016, 2018a; Avilés-Rodríguez and Kolbe 2019). We hypothesized that reduced vegetation in urban habitats could lead to lower urban population densities, and that populations densities would be lowest 4 months after the hurricane and gradually increase with each sampling date, presumably as lizard populations recovered to their pre-hurricane densities.

Methods

Focal species

We studied the species *Anolis cristatellus*, a relatively small (50–70 mm adult snout-to-vent length) arboreal lizard, that is found at high densities in a variety of different types of habitats throughout Puerto Rico (Williams 1972), including urban environments (Winchell et al. 2016, 2018a). Caribbean *Anolis* species, including *A. cristatellus*, can have very high population densities in natural environments. For example, *A. sagrei*, a Cuban and Bahamian species, has measured densities ranging from 200 up to 9870 individuals per hectare (Schoener and Schoener 1980). Likewise, *A. cristatellus*, the focal taxon of this study, has estimated densities from around 1000 up to 7200 lizards per hectare (Lazell 1991; Rodda et al. 2001). Other *Anolis* congeners can occur in densities up to 32,867 lizards per hectare (Hite et al. 2008). Previous research on *A. cristatellus* has compared urban and forest populations with respect to behavior (Avilés-Rodríguez and Kolbe 2019), morphology (Winchell et al. 2016; Falvey et al. 2020), habitat use (Winchell et al. 2018a), and locomotor performance (Winchell et al. 2018b), but not population density.

Several congeners of *A. cristatellus* have been studied in the context of hurricanes (Reagan 1991; Spiller et al. 1998; Schoener et al. 2001, 2004). This body of work shows, among other things, that hurricanes can result in demographic changes due to varying levels of mortality, including total extirpation on very small islands (Schoener et al. 2004). Additionally, recent work suggests adaptive phenotypic shifts in response to hurricanes in anoles (Donihue et al. 2018, 2020), but the direction of these shifts vary as a function of habitat, including urbanization (Avilés-Rodríguez et al. 2021). Prior work on the population biology of *Anolis* following hurricanes has focused on species on small islands and in forested or otherwise ‘natural’ settings, rather than in urban areas.

Sampling

In September of 2017 the island of Puerto was affected by the strong winds and rainfall associated with two category 5 hurricanes. First, Hurricane Irma passed just north of Puerto Rico but nonetheless caused significant damage on the island. Subsequently, on September 20, 2017, Hurricane Maria made landfall in the southeast, near the municipality of Yabucoa, and then traversed the island eventually exiting via the northwest coast of the island near the municipality of Arecibo, about 8 h later (Fig. 1). Hurricane Maria was the strongest storm to make landfall in Puerto Rico since 1928 (Hurricane San Felipe II; Pasch et al. 2017).

We sampled three pairs of urban and forest habitats across the island of Puerto Rico. We chose sites to match areas where we had conducted prior research on *Anolis cristatellus* in urban areas. As such, our sites were not chosen based on their geographical relationship to the hurricane path. Nonetheless, because our sites covered a large range of the island, by happenstance these localities experienced varying degrees of winds due to their position with respect to the hurricane's trajectory across the island (Fig. 1). In particular, the municipality of San Juan was closest to the entry point of the hurricane and experienced the strongest winds. Aguadilla and Mayagüez experienced the weakest wind intensity due to their location in the west region of the island and thus farthest from the hurricane's path.

Another important consideration of site selection is that we were unable to select a random plot within urban environment to sample. This is due to a high level of landscape heterogeneity in urban environments (Cadenasso et al. 2007) which includes areas that are inhospitable to lizards and inaccessible to researchers. We address this limitation in the Discussion.

Field data collection

We sampled each of our six sites (three urban and three forested) during three time periods following Hurricane Maria's passage over Puerto Rico: 4, 11, and 16 months after the event. We used a three-sample capture-mark-recapture protocol in plots measuring 100 m^2 (0.01 ha) in area. One observer (KAR) sampled each plot for 3 h over three consecutive days, for a total of 9 h of sampling effort per site during each sampling period. On the first day of each sampling period, we randomized whether the urban or forest site would be visited in the morning. Subsequently, we alternated visiting the urban or the forest sites in the morning vs. the afternoon of each sampling day.

We captured lizards by hand or by lassoing, using a dental floss slip noose on a collapsible pole. We numbered each captured lizard using a non-toxic marker, measured the body size (snout-to-vent length: SVL) with a ruler, and marked it using a single injectable plastic elastomer bead. We employed redundant marking (non-toxic marker and injectable bead) to avoid counting the same individual multiple times due to skin shedding, which could cause the non-toxic mark to be lost. We re-marked any recaptured lizard with evidence of loss of its non-toxic skin marking, and matched it to our previously captured animals using SVL measurements and sex. Since each plot was sampled over three consecutive days, mark loss via shedding was relatively rare.

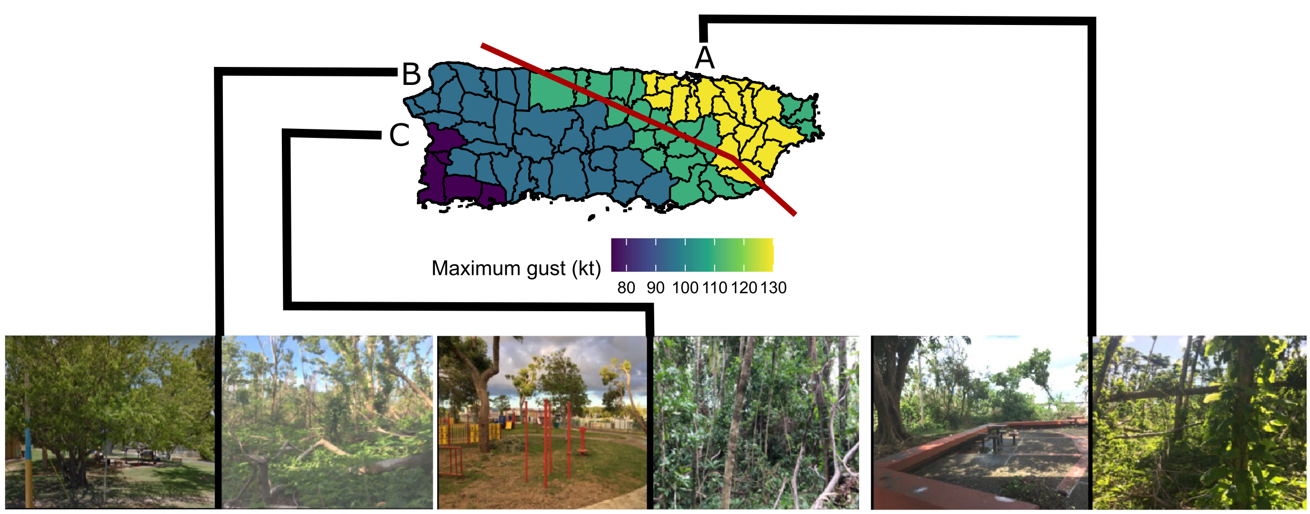

Fig. 1 Location of survey sites in Puerto Rico. Municipalities have been colored based on the average maximum gust sustained during the passage of Hurricane Maria based on data collected by the Pacific Disaster Center. The red line shows the passage over land of the hurricane and the photos show the sites at 4 months after Hurricane Maria. Note that at this time tree canopies were still damaged by the hurricane and downed tree branches and trunks commonly occurred at all sites. Letters correspond to paired urban and forest sites in the municipalities of to San Juan (A), Aguadilla (B) and Mayagüez (C) (Color figure online)

Although we collected data on all species of *Anolis* lizards encountered in our plots, we primarily estimated population density for *A. cristatellus* since it was the most abundant species across all sites. In addition, the other species that we encountered in our plots tend to be more specialized in the habitat they typically used and thus were not uniformly present in the full extent of our sampling area. Nonetheless, we document the total number of other anole species captured during our study (Fig. S1). Given that the density of *A. cristatellus* could be affected by niche overlap with other *Anolis* ecomorphs following the hurricane (Reagan 1991), we repeated our analyses by estimating the density of all *Anolis* lizards (regardless of species) captured at each site.

Finally, we quantified perch density for each site by tallying the substrates available as perches for lizards within each plot.

Statistical analyses

We performed all statistical analyses using R 3.6.1 (R Core team 2019). We first estimated population size of *Anolis cristatellus* using the R package *Rcapture* (Baillargeon and Rivest 2007), and selected the abundance estimator that best fit our data based on the Akaike Information Criterion (AIC). Subsequently, we compared paired differences within sites by contrasting the estimated abundances and standard errors using paired *t*-tests. We adjusted our P-values for multiple testing using the False Discovery Rate method (Benjamini and Hochberg 1995). To verify the effect of other anole congeners we repeated these analyzes using all anole species observed within our sites and verified whether including these observations led to a different result compared to a model including only *A. cristatellus*.

We evaluated changes in lizard body size (SVL) by first log-transforming all of our size data. Then we modeled the change in size as a function of sampling period after the hurricane, habitat (i.e, forest or urban), and sex. Because we did not sex juvenile lizards, we grouped them with females in our analyses. We also analyzed perch counts with a general linear mixed effect model using Poisson-distributed error, with sampling period and habitat as fixed effects, and municipality as a random effect.

Results

Population density estimates

Population density of *Anolis cristatellus* lizards was high for all sites and time periods (Fig. 2). Among all population density estimates, the lowest estimate obtained was 2150/ha (± 220) for our San Juan urban site, 4 months after Hurricane Maria. By contrast, the highest estimated population density (10,210/ha ± 860) was obtained for the San Juan forest site, 16 months after the hurricane. In general, for all municipalities and time periods, forested environments had *higher* overall lizard density compared to urban sites nearby (Kruskal–Walis H test: $\chi^2 = 8.75$, df =1, P = 0.003; Fig. 1).

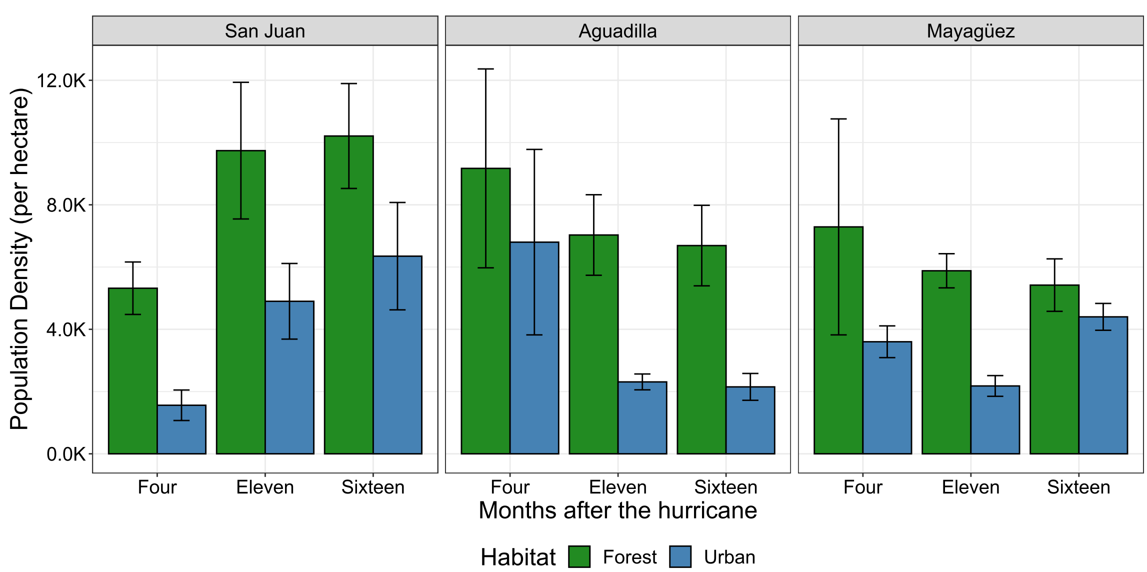

Fig. 2 Population size estimates per hectare for *Anolis cristatellus* across paired urban and forest sites at 4, 11 and 16 months after Hurricane Maria made landfall in September 2017. Error bars show the standard error around population estimates

Changes in population density

We observed the lowest population density for any site or context 4 months after the hurricane for the urban population in San Juan (all pairwise *t*-tests; P < 0.001). By 11 months post Hurricane Maria, this site had nearly doubled in population density ($\Delta_{[11mo.-4mo.]} = 3340$/ha ± 123.3; P < 0.001). Finally, by 16 months after the hurricane the urban San Juan population increased by approximately 30% ($\Delta_{[16mo.-11mo.]} = 1450$/ha ± 167.3; P < 0.01). We found a similar trend of population size increase with time after the hurricane in the San Juan forest population. Specifically, this population nearly doubled at 11 months after the hurricane ($\Delta_{[11mo.-4mo.]} = 4420$/ha ± 151.100; P < 0.01). Subsequently, San Juan forest population density increased by a further small amount by 16 months after the hurricane ($\Delta_{[16mo.-11mo.]} = 470$/ha ± 167.942; P = 0.008).

By contrast, we did not observe a significant increase in population density in successive periods after the hurricane in the other municipalities of our sampling. In Aguadilla, we found that forest populations *decreased* with time following the hurricane ($\Delta_{[11mo.-4mo.]} = -2140$/ha ± 242.928; P < 0.01; $\Delta_{[16mo.-11mo.]} = -340$/ha ± 266.333; P = 0.012). Urban populations in Aguadilla similarly *decreased* following the hurricane ($\Delta_{[11mo.-4mo.]} = -4490$/ha ± 251.419; P < 0.01; $\Delta_{[16mo.-11mo.]} = -160$/ha ± 57.581; P = 0.013).

Forest populations in Mayagüez first experienced a large decrease and then a smaller decrease in population density ($\Delta_{[11mo.-4mo.]} = -1,410$/ha ± 293.470; P < 0.01; $\Delta_{[16mo.-11mo.]} = -460$/ha ± 73.969; P < 0.01). By contrast, urban Mayagüez populations first decreased ($\Delta_{[11mo.-4mo.]} = -1,420$/ha ± 59.106; P < 0.001) and subsequently increased ($\Delta_{[11mo.-4mo.]} = 2,220$/ha ± 51.240; P < 0.01), resulting in a final population density that was larger than that sampled at 4 months after the hurricane ($\Delta_{[16mo.-4mo.]} = 800$/ha ± 56.824, P < 0.01).

Changes in population body size distribution

Mean body size did not differ significantly as a function of sampling period after the hurricane (Fig. 3; $F_{1/709} = 0.001$; P = 0.972), but was significantly different by sex, habitat, and municipality. Males were significantly larger than females and juveniles (ANOVA, $F_{1/709} = 801.238$; P < 0.001). Urban lizards were significantly larger than forest lizards ($F_{1/709} = 5.622$; P = 0.018), but populations in San Juan were more similarly sized to forest populations, with San Juan forest lizards having the largest mean body size overall ($\beta = 6.200 \pm 0.162$; Table 1). Comparing across municipalities, lizard mean body size was largest in San Juan and smallest in Mayagüez ($F_{2/709} = 64.423$; $P < 0.001$).

Structural habitat changes and anole community shifts

We found that perch density within our plots varied both as a function of time since the hurricane, and of habitat type (general mixed effect model, hurricane: $\chi = 161.11$, d.f. = 2, P < 0.001; habitat: $\chi = 396.58$, d.f. = 1, P < 0.001, Table 2). Specifically, we found that forest sites had a greater abundance of perches and that the number of perches increased over our sampling period. Secondary succession led to

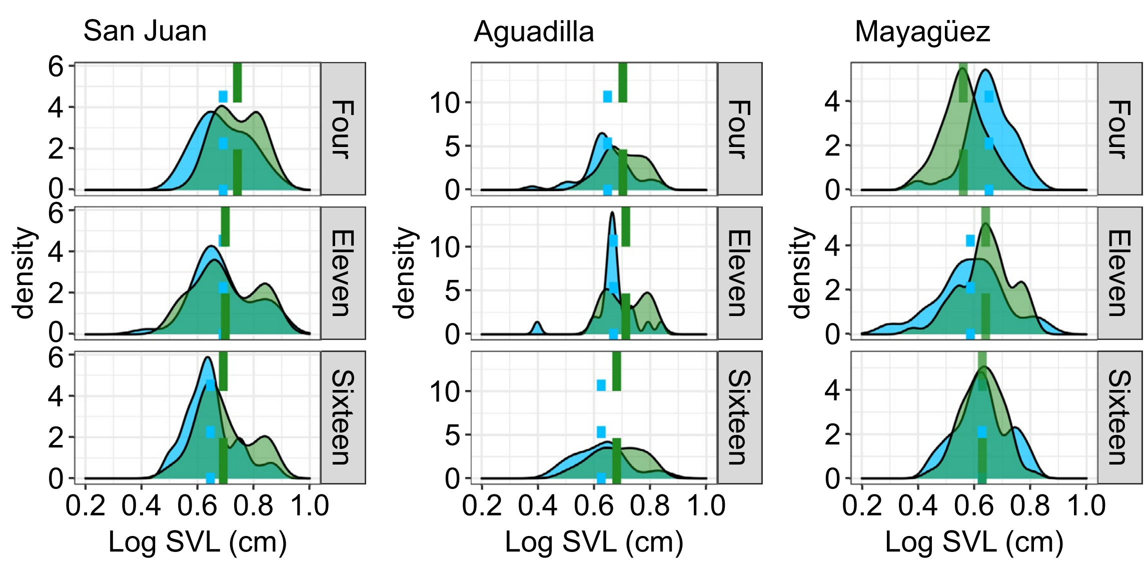

Fig. 3 Snout vent lengths of *Anolis cristatellus* across sites. Colors denote habitat with green for forest and blue for urban population. Means for each given are shown for each site and sampling period with lines colored according to habitat. Facet labels correspond to months after Hurricane Maria (Color figure online)

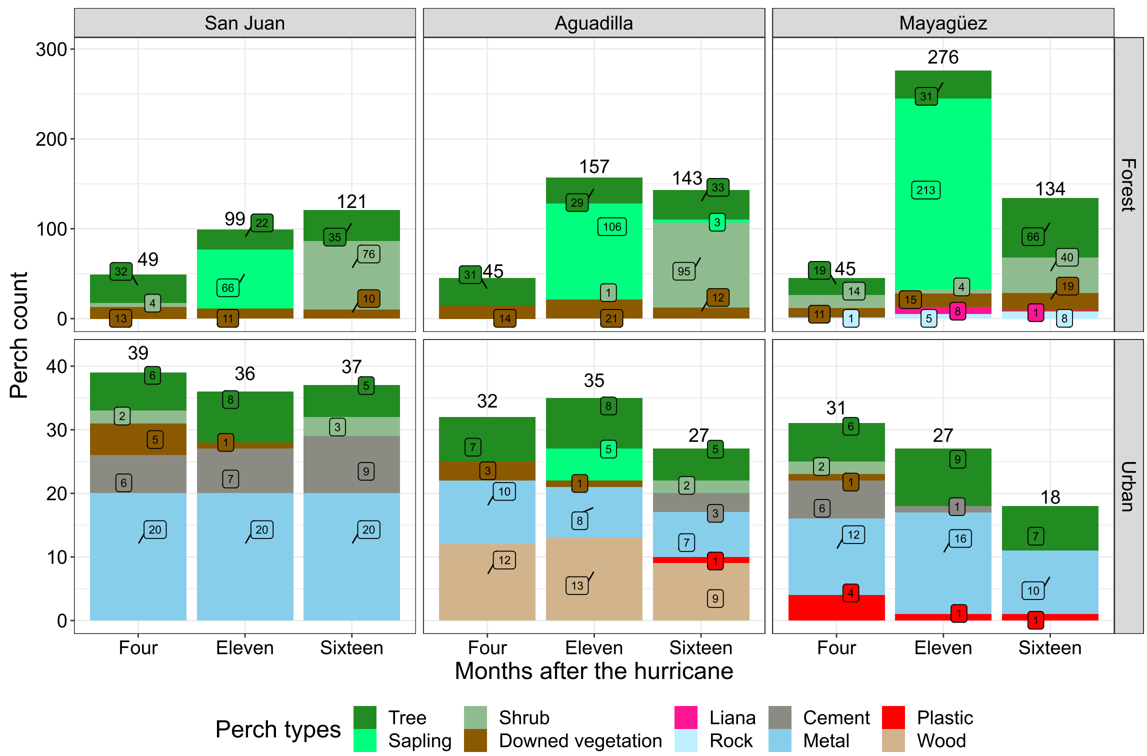

Fig. 4 Count of perches within plots sampled at 4, 11 and 16 months after the hurricane. Note the difference in scale between the upper (forest) and lower (urban) panels of the plot

Table 1 Mean and standard error of snout vent lengths of lizards

Site	Habitat	Sex	4 mo. After ($\beta \pm SE$)	11 mo. After ($\beta \pm SE$)	16 mo. After ($\beta \pm SE$)
Aguadilla	Forest	Female	4.337 ± 0.090	4.341 ± 0.055	4.114 ± 0.095
Aguadilla	Forest	Male	5.569 ± 0.117	5.634 ± 0.115	5.804 ± 0.103
Aguadilla	Urban	Female	4.095 ± 0.125	4.230 ± 0.208	4.006 ± 0.158
Aguadilla	Urban	Male	5.236 ± 0.244	5.175 ± 0.211	6.067 ± 0.689
Mayagüez	Forest	Female	3.453 ± 0.114	3.709 ± 0.131	3.889 ± 0.086
Mayagüez	Forest	Male	4.520 ± 0.246	5.003 ± 0.133	5.012 ± 0.119
Mayagüez	Urban	Female	3.900 ± 0.181	3.255 ± 0.191	3.792 ± 0.105
Mayagüez	Urban	Male	4.980 ± 0.158	4.944 ± 0.323	5.293 ± 0.179
San Juan	Forest	Female	4.625 ± 0.103	4.086 ± 0.107	4.224 ± 0.078
San Juan	Forest	Male	6.200 ± 0.162	6.071 ± 0.187	5.991 ± 0.184
San Juan	Urban	Female	4.214 ± 0.165	4.220 ± 0.120	4.007 ± 0.082
San Juan	Urban	Male	5.950 ± 0.347	6.106 ± 0.308	5.662 ± 0.273

Snout vent lengths were not significantly different throughout our sampling periods after the hurricane

Table 2 Coefficients for general linear mixed effect models of perch counts across our sampling periods respective to Hurricane Maria and by sites

Model	k	β_0	$\beta_{11\ mo.}$	$\beta_{16\ mo.}$	β_{urban}	$\beta_{11\ mo.\times urb.}$	$\beta_{16\ mo.\times urb.}$	log(L)	AIC
Null	3	4.31	—	—	—	—	—	− 467.679	939.357
Hurricane	5	3.685	0.961	0.690	—	—	—	− 376.215	760.431
Habitat	4	4.769	—	—	− 1.333	—	—	− 223.3199	452.640
Habitat + Hurricane	6	4.144	0.961	0.689	− 1.332	—	—	− 131.85	273.714
Habitat × Hurricane	**6**	**3.828**	**1.342**	**1.052**	**− 0.310**	**− 1.382**	**− 1.270**	**− 95.731**	**205.463**

The best-supported model (shown in bold) included the fixed effects of hurricane, habitat and their interaction nearly one hundred new plants within most of the forest localities (Fig. 4); however, not all the new saplings that colonized the plot at 11 months were still present 16 months after the storm. By contrast, urban sites did not experience a dramatic change in the quantity of available lizard perches through time (Fig. 4).

Including our focal taxon, *A. cristatellus*, we observed a total of six *Anolis* lizard species during our sampling efforts. *Anolis cristatellus* was the most abundant *Anolis* lizard species at all sampling periods and sites (Figure S1). The next most abundant species that we found in our plots was *A. stratulus*, a tree trunk and crown specialist. After the first sampling period (i.e., 11 and 16 months after the storm) we identified an established population of the grass-bush specialist *A. krugi* within the Mayagüez forest site (population estimate = 9.6 ± 1.9 and 13.3 ± 5.7, respectively), that was not present during our 4 month post-hurricane sampling period. (We did not extrapolate this population to individuals per hectare, as this species was only present in a small fraction of the plot.) The other three species that we encountered were extremely rare (less than five captures in total). *Anolis gundlachi* (a trunk-ground specialist that occurs in closed forest habitats) and *A. cuvieri* (a crown giant) were only observed at the Mayagüez forest site. The final species, *A. pulchellus* (a grass bush specialist), was only observed at the urban site in San Juan. Unsurprisingly, given the much higher relative abundance of *A. cristatellus* compared to co-occurring congeners, population density estimates across *all Anolis* species in the community closely recapitulated our findings with *A. cristatellus*. Specifically, we found an increase in population densities in San Juan after the hurricane and lower population densities in urban sites (Figure S3).

Discussion

Projected increases in the frequency and severity of environmental disturbance under most scenarios of global environmental change (Knutson et al. 2010; Mendelsohn et al. 2012) represent a major challenge for species persistence (Johnstone et al. 2016; Seidl et al. 2016). How other types of anthropogenic pressures, such as urbanization, interact with more frequent or more intense disturbances to affect population dynamics remains understudied.

Following Hurricane Maria, a major category 5 storm that cut a path of destruction across the island of Puerto Rico in 2017, we contrasted the population density of *A. cristatellus* in paired urban and forest sites. We hypothesized that reduced vegetation in urban habitats could lead to lower urban population densities, and that densities would be lowest 4 months after the hurricane and gradually increase, presumably as lizard populations recovered to their pre-hurricane densities. Indeed, all urban sites had lower population densities compared to forested sites nearby. Additionally, the two sites which were most severely impacted by the hurricane also exhibited the most consistent increases in estimated population density through time. Specifically, estimated population density in our forest and urban localities of San Juan nearly doubled at 11 months, and then increased again at 16 months, after the hurricane (Fig. 2). For the remaining four sites in our study, between 4 and 11 months after the hurricane estimated population density *decreased* irrespective of the habitat type. Subsequently, between 11 and 16 months after the hurricane, estimated population density decreased slightly, except for at our urban site in the municipality of Mayagüez where estimated population density nearly doubled.

Post-hurricane population dynamics between natural and urban habitats

An important motivation of this study was to evaluate whether urban populations differed in density compared to conspecific forest populations nearby. This has been an important, but unanswered part of our understanding of the success of *Anolis cristatellus* in urban environments (Winchell et al. 2016, 2018a). We found that, irrespective of our sampling period (i.e., 4, 11, and 16 months after the hurricane), estimated urban population densities were invariably almost 50% *smaller* than forest population densities nearby (Fig. 2). Furthermore, urban habitats tended to have fewer perches suitable for arboreal lizards, and the number of perches remained fairly stable through time (Fig. 4). By contrast, forest habitats experienced a dramatic increase in the number of perches due to secondary succession after the hurricane.

Three significant considerations substantially limit our ability to draw any conclusive generalities about the differences in population density between urban and forested sites in *A. cristatellus*.

First, for logistical reasons, neither our urban nor our forest sites were selected randomly with respect to available habitat for *A. cristatellus* in urban and forested areas. Unfortunately, this was unavoidable principally because of limited access to private property in urban environments. For instance, a randomly chosen study plot within nearly any urban area of Puerto Rico would include spaces (e.g., private dwellings and patios) off-limits to an investigator. Likewise, natural sites within or adjacent to urbanization in Puerto Rico are highly fragmented. Nonetheless, we do not think that our non-random site selection is likely to have downwardly biased our estimated population density of urban areas in *A. cristatellus*. To the contrary, a truly random urban plot would have included, with high probability, areas (such major roads and highways) largely inhospitable to both anoles and investigators; whereas our non-random sites (mostly within or adjacent to small urban parks) did not contain any habitat strictly unsuitable or off-limits to lizards.

Second, we did not estimate population density in any of our sites prior to Hurricane Maria. Unfortunately, no previous study (to our knowledge) had ever estimated population density of *A. cristatellus* in any urbanized site, let alone in the localities of our research. Instead, we surmised that population density, if affected by the storm (either positively or negatively), would gradually re-equilibrate to a pre-storm level. However, because we lacked pre-hurricane data, we cannot rule out other factors such as seasonal changes in reproduction and rainfall. Other research on *Anolis* lizards has found that higher densities during the dry season were in part associated with recruitment from wet season reproduction (Sexton et al. 1963; Fleming and Hooker 1975). In contrast, during the wet season population densities were lower, presumably as a consequence of increased territorial behavior coinciding with courtship and reproduction (Sexton et al. 1963; Fleming and Hooker 1975). Moreover, prior research has shown that over the course of 5 years green anole (*Anolis carolinensis*) populations fluctuated substantially both within and between seasons (Lailvaux 2020). In our data, urban and forest populations sampled in San Juan, which experienced the strongest hurricane winds, increased in estimated density irrespective of sampling season (Fig. 2), whereas at other sites population densities both increased and decreased from period to period after the storm. This might be because San Juan was also the site that experienced the highest kinetic wind energy during Hurricane Maria; however, we cannot rule out stochasticity or alternative deterministic factors.

Third, our methodological approach was designed to target lizards perching only up to 2.5 m from the ground level. Thus, our capture rates for the tree canopy specialists observed within our sites (crown and trunk-crown ecomorphs in Figure S1), may not reflect the density of these species that are typically found at each site. This limits our ability to address how the densities of *Anolis* congeners could influence the density of *A. cristatellus* at our localities. Nonetheless, we suspect that this effect is likely to be quite small, due to the fact that other *Anolis* species represent only a relatively small portion of our capture data (137 congeners compared to 753 *A. cristatellus*). Indeed, when including these density data in our analyses, we found a broadly similar pattern of increases in population density in San Juan after the hurricane, and lower population density in urban sites (Figure S3). In addition, even if this pattern is affected by both hurricane induced mortality and niche overlap with other species, our subsequent sampling periods showed both increases in the abundance of *A. cristatellus* and decreases in the presences of *A. stratulus*. We interpret these changes as the gradual recovery of tree canopy (decreasing niche overlap) and increases of the population densities of *A. cristatellus* (either due to reproduction and/or recolonization) following the hurricane. To further test the dynamics of niche overlap and mortality following a hurricane would require exhaustive sampling at each site of the habitat (e.g., searching tree canopies) and of individual anole lizards (e.g., not bound by a standardized sampling effort).

Temporal changes in population mean body size

In addition to merely affecting population density overall, hurricane-induced mortality could vary by sex and life stage. For instance, after Hurricane Iris in 2001, howler monkey social groups had relatively fewer males and juveniles when compared to their pre-hurricane proportions (Pavelka et al. 2007).

In *Anolis*, male lizards often perch at higher elevations compared to females (Stamps et al. 1997; Butler et al. 2000). This could influence sex and size-specific mortality associated to the hurricane. Because our study lacks pre-hurricane data, we evaluated changes in the overall distribution of size throughout the recovery period to see if the composition of size varied across our different sampling periods.

In general, we did not detect a significant change in body size in the months after the hurricane. We did observed a pattern of smaller body sizes in San Juan forest corresponding to an increased sampling of juveniles at this site (Figure S2). This increase in the proportion of smaller bodied lizards is temporally concurrent with the peak of the reproductive season for this species (Otero et al. 2015). We also noted remarkably few adult male lizards within our plots in the Mayagüez forest (Figure S2) immediately after the hurricane. However, it is important to note that this site was affected by landslides caused by heavy rainfall during the Hurricane (Bessette-Kirton et al. 2020), which may have contributed to increase adult mortality at the plot.

Post-hurricane structural habitat and Anolis community changes

Among the most dramatic effects of hurricanes on forest ecosystems are structural changes immediately following the hurricane and throughout the post-storm recovery (Brokaw and Grear 1991; Fernandez and Fetcher 1991; Lugo et al. 2000). Secondary succession of new plant species and refoliation of the canopy often occur rapidly in the Caribbean (Lugo et al. 2000). Thus, demographic responses to hurricanes are largely a function of both immediate and long-term habitat changes, they and can be either positive or negative (Lugo 2008; Sergio et al. 2018).

Our results are consistent with both of these assertions. First, we showed species composition changing according to both canopy defoliation and also due to secondary succession. We found that after the disturbance there were higher abundances of the trunk-crown specialist (*A. stratulus*, Figure S1). This might indicate that the habitat use of this species shifted downward as a result of canopy loss. A similar pattern has been observed between ground and crown specialists following a hurricane, with niche space diverging again after canopy refoliation (Reagan 1991). Second, we found that nearly 1 year after the hurricane all forest sites dramatically increased in perch densities (Fig. 4). Most of the newly established vegetation was either young saplings or shrubby vegetation (Fig. 4). Subsequently, we found a population of the grass bush anole specialist, *A. krugi*, at one of our forest sites (Figure S1), where none had been present in prior surveys.

An important contrast between forest and urban habitats is the lack of structural habitat change in urban habitats and overall lower perch density at all sampling periods (Fig. 4). Previous research has documented high male-male aggression in non-urban populations of *A. cristatellus* with relatively few males occupying the same tree (Philibosian 1975) and higher aggression toward lizard models in urban populations of *A. carolinensis* (McMillan and Irschick 2010). Perhaps lower urban perch density can partly account for the smaller population densities in urban sites observed here (Fig. 2). Additionally, constant human modification of urban sites may have limited recruitment of new plant species following the hurricane. Consequently, urban spaces could sustain nearly constant structural habitats in contrast to the more dynamic habitat features of post-hurricane forests [summarized in Zimmerman et al. (2021)].

Conclusions

Our present contribution is, to our knowledge, the first study to measure population densities of a synanthropic tropical lizard between urban and forest sites. It is also the first research contrasting population dynamics of a lizard following a major hurricane between forest and urban environments. We hypothesized that population density might have decreased due to mortality during the storm event and would increase and re-equilibrate around pre-hurricane levels. We found patterns of population density fluctuations that only partly fit our a priori expectation. Interestingly, in some sites we measured small but significant *decreases* in population density with increasing time after the hurricane. This likely reflect seasonal fluctuations in population densities of anoles (Lailvaux 2020), rather than an outcome resulting as a consequence of the storm.

Our measured population densities are comparable with what other studies have reported for *Anolis* lizards: ranging from around 0.2 to 1 lizard per m^2 (Schoener and Schoener 1980). Moreover, urban populations occupied habitats with fewer perches, and showed lower and more narrowly distributed population densities between sites and over time (0.16–0.64 lizards per m^2). By contrast, forest populations densities were larger overall (ranging from 0.43 to 1.02 lizards per m^2) and showed higher variation between sites and across the sampling periods. As such, we hypothesize that less dense urban populations could be at greater risk of extirpation following large scale mortality events. Furthermore, if the fragmented nature of the urban landscape limits migration and gene flow among sites, urban populations may be at even greater risk of extinction due to inbreeding depression (Benson et al. 2016). Although our ability to fully characterize the effect of the hurricane is limited by a lack of pre-hurricane population data, our findings indicate that both natural and anthropogenic disturbances can shape population dynamics in urban environments. Thus, given current rates of urbanization, further research in needed to understand how climatic disturbances and constant human modification of these habitats affect the persistence of populations in urban environments.

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