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Phylogenetic signal and evolutionary correlates of urban tolerance in a widespread neotropical lizard clade*

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Urbanization is intensifying worldwide, and while some species tolerate and even exploit urban environments, many others are excluded entirely from this new habitat. Understanding the factors that underlie tolerance of urbanization is thus of rapidly growing importance. Here, we examine urban tolerance across a diverse group of lizards: Caribbean members of the neotropical genus *Anolis*. Our analyses reveal that urban tolerance has strong phylogenetic signal, suggesting that closely related species tend to respond similarly to urban environments. We propose that this characteristic of urban tolerance in anoles may be used to forecast the possible responses of species to increasing urbanization. In addition, we identified several key ecological and morphological traits that tend to be associated with tolerance in *Anolis*. Specifically, species experiencing hot and dry conditions in their natural environment and those that maintain higher body temperatures tend to have greater tolerance of urban habitats. We also found that tolerance of urbanization is positively associated with toepad lamella number and negatively associated with ventral scale density and relative hindlimb length. The identification of factors that predispose a species to be more or less urban tolerant can provide a starting point for conservation and sustainable development in our increasingly urbanized world.

KEY WORDS: ***Anolis*, Anthropocene, Caribbean, phylogenetics, threshold model, urbanization.**

The impact of humans on wild areas has increased dramatically in recent decades. Presently, just over half of the world's population lives in urban areas and this figure is expected to grow to 66% by 2050 (an increase of 2.5 billion urban dwellers), leading to an expansion and intensification of human-dominated landscapes (United Nations 2015). The Caribbean has experienced anthropogenic pressures since the arrival of Amerindians to the region over 5000 years ago, with the effects of urbanization intensifying in the 500 or so years following European colonization (Fosberg 1983; Henderson and Powell 2001). The Caribbean is now one of the most urbanized areas of the globe and development is expected to continue in coming years (United Nations 2015). This growth is especially notable, and of conservation concern, because of the high levels of endemic biodiversity found throughout the region (Myers et al. 2000). Moreover, it is important to consider that many species have not yet encountered substantial habitat loss due to urbanization. Species currently not threatened may become so as urbanization intensifies and expands. Understanding which species can tolerate urbanization, and why, is thus a critical dimension of global change biology as the world becomes increasingly urbanized, particularly in the Caribbean. Such knowledge is an important first step to informing sustainable development and conservation, for example, by concentrating efforts on species that are likely to face the strongest negative impacts of urbanization.

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Species responses to the intense habitat modifications that accompany dense human settlements vary widely. Loss and alteration of habitat, including reduction in canopy cover, increases in impervious surface, and altered thermal and hydrological regimes, excludes many native species from urban environments (Forman 2014). Consequently, native species diversity is often reduced in urban centers compared to natural sites nearby (Aronson et al. 2014; Forman 2014). Urban communities are frequently dominated by a relatively small number of species capable of exploiting unique resources and novel ecological space associated with urbanization, whereas some other species occasionally utilize urbanized habitats and may form sink populations in urban areas (Shochat et al. 2006; McKinney 2008; Grant et al. 2011; Forman 2014). Urban ecologists have thus categorized species based on their tolerance of anthropogenic disturbance: those species that avoid urban habitats completely (avoiders); those that tolerate urbanization but rely on natural habitat elements (tolerators); and those that exploit urban habitats (exploiters; McKinney 2002). The last of these three groups, the urban exploiters (also referred to as "synanthropes" and "urbanophiles"; McKinney 2006; Grant et al. 2011; Forman 2014), is of growing interest in our increasingly urbanized world.

Recent work has shown that many species, including anoles, have adapted to urban life over relatively short timescales (Winchell et al. 2016; Johnson and Munshi-South 2017); however, the initial persistence of species in urban environments is likely at least in part a function of preexisting traits. Preexisting traits may prove to be beneficial in the novel urban environment due to trait-based species filtering (i.e., preadaptation) or because they are coopted for new functions (i.e., exaptation). Prior research in other taxa has shown that urban-tolerant species tend to have attributes commonly associated with a generalist ecological niche such as broad habitat preferences and a catholic diet (Croci et al. 2008; Evans et al. 2011; Grant et al. 2011; Ducatez et al. 2018; Santini et al. 2019). Additionally, traits such as high reproductive output, body size (often larger although this varies across taxonomic groups), large relative brain size, and sedentary habits have been found to be associated with urban tolerance across diverse animal taxa (Croci et al. 2008; Grant et al. 2011; Callaghan et al. 2019; Santini et al. 2019). Urban reptiles in particular often have broad diets, are heliothermic, and are scansorial (climbers capable of using vertical substrates; Powell and Henderson 2008). We suspect that a species' ability to persist in urban environments is most likely determined by some combination of the aforementioned and other characteristics, rather than by a single, specific phenotypic attribute: in other words, an accumulation of "tolerance" traits.

Neotropical lizards of the genus *Anolis* (commonly known as anoles) are well known for rapidly adapting to novel ecological circumstances (reviewed in Losos 2009). *Anolis* is composed of approximately 400 species, around 150 of which occur in the Caribbean, and many of which tolerate urbanization to varying degrees. Across the Caribbean, related species have diversified to occupy distinct structural and climatic niches, with frequent convergence in habitat use between distantly related lineages (Williams 1983). These ecologically convergent species have evolved similar morphological attributes in association with their shared structural and thermal niches, with similar species organized by anole biologists into one of six ecomorphological classes (termed "ecomorphs"; Williams 1983; Losos 2009), a phenomenon that has been dubbed "replicated adaptive radiation" (Schluter and McPhail 1993; Losos et al. 1998; Schluter 2000). Thus, within Caribbean anoles, traits associated with urban tolerance may be conserved within clades (i.e., similar because of common ancestry) or convergent among clades (i.e., similar because of shared adaptive responses). Caribbean anoles are a well-studied group (Losos 2009), but to date no prior work has examined the evolution of tolerance to urban areas in a phylogenetic context. If the ability to tolerate or thrive in urban habitats is an evolved feature (whatever its underlying mechanistic basis), then the evolutionary history and phylogenetic pattern of urban tolerance is relevant to a proper understanding of this complex ecological trait.

Herein, we undertake the task of analyzing tolerance to urbanization in Caribbean anoles. First, we use phylogenetic models of discrete character evolution to compare alternate hypotheses for the evolution of urban tolerance. We then use these models to test for evidence of correlated evolution between ecological, environmental, and morphological traits and urban tolerance. Note that although our methods, in a sense, involve the reconstruction of urban tolerance on a phylogeny whose total depth vastly exceeds the age of our own species (and thus the origin of urbanization), we do not suppose that we are reconstructing the use of urban areas. Rather, our intent is to understand the evolution of traits responsible for the predisposition to use urban areas, now that they have become so common in the regions in which anoles live. We hope that an advantage of our approach will be an enriched understanding of the evolutionary history of the latent trait of urban tolerance, and that it may also provide a predictive framework for the urban predilections of species for which limited data are presently available, all while taking into account the nonindependence of species due to phylogeny.

Specifically, we focus on three main questions: (1) Is there an underlying phylogenetic pattern to urban tolerance as a discrete trait in Caribbean anoles and, if so, which model of evolution best describes this pattern? (2) Can we predict urban tolerance in species for which we presently lack data (and as a hypothesis of future urban tolerance)? Finally, (3) what traits are associated with urban tolerance when controlling for phylogenetic relatedness? Taken together, these analyses will help us to better comprehend the factors that predispose species to be tolerant of urbanization and will provide a predictive framework for both future study and present-day conservation efforts, as natural areas are increasingly urbanized.

Methods

DATA COLLECTION

We focused on 131 species of *Anolis* from the Caribbean, including species from the Greater Antilles, the Lesser Antilles, and smaller Caribbean-region archipelagos. We initially classified species into two discrete character states: "urban" (commonly observed in urban areas) and "avoider" (never observed in urban sites). Although urban ecology theory supports the existence of a third, intermediate, "tolerant" category, this state can be difficult to accurately assess without on-the-ground ecological data (e.g., Winchell et al. 2018a). As such, we have elected to focus on the extremes of the urban tolerance spectrum of urbanophily and avoidance. This is not to say, that we have excluded intermediate, "tolerant" species from our analyses. Rather, we acknowledge that our data do not permit us to distinguish this third state. To accurately classify species as "tolerant," we would need field data for population demography and habitat use, which is simply not possible at the scale of our study. Consequently, genuinely tolerant species will invariably be misclassified as urban or avoider by our assignment protocol.

Similarly, rather than attempting to assign each taxon unambiguously to either an urban or avoider state, to reflect the uncertainty inherent in our data we elected to specify tip states as prior probabilities that each species was in each of the two possible character states. We assigned these probabilities using a standardized protocol, described below, designed to capture our confidence that each species avoids or thrives in the urban environment.

To assign (prior) probabilities of being in the state "urban" or "avoider" to each species, we used reported locations from the GBIF database of museum specimen records (from 1980 to 2017; GBIF 2019), as well observations from the citizen science database "iNaturalist" (iNaturalist 2019). We (KMW and DLM) verified all iNaturalist records to confirm accurate species identification. Although these two sources represent opportunistically collected data, we strongly suspect that they are likely to be biased toward nonurban observations—particularly records in the GBIF data set that represent scientific collection. This is important in the context of our research because all anole species (even the most urbanophilic) also use nonurban environments.

In our assignment protocol, we started by treating tolerance status as unknown, and then we computed a score designed to measure the strength of evidence that a species is tolerant of urbanization (described in more detail in the Supporting Information Materials S1 and S2). In brief, our urban tolerance score takes into account the fact that even urbanophilic anoles use nonurban environments, and as such even a relatively small number of observations of a species in intensely urbanized sites suggest that it is at least tolerant of urbanization—regardless of how many nonurban records exist for the species. Likewise, many nonurban observations, absent a significant number of urban records, are required to conclude that a species is an urban avoider.

For both the GBIF and iNaturalist data sets, a single researcher (KMW) reviewed the reported location for each observation and classified it as urban or nonurban, while taking into account georeferencing accuracy by excluding any points for which the reported accuracy included both urban and forest habitat. We considered urban locations to be any habitat dominated by human structures and impervious surfaces ranging from small towns to large cities. We considered nonurban locations to be those in which there were two or fewer human structures within 0.1 km of the reported latitude and longitude and that were not dominated by impervious surfaces. This distance was chosen based on evidence that populations persisting in urban forest fragments experience habitat more similar to exurban forest habitats than to urban habitats and exhibit phenotypes consistent with exurban forest populations (e.g., Winchell et al. 2016, 2018b; Campbell-Staton et al. 2020). Using such a small buffer distance is likely to cause some urban observations to be misidentified as nonurban. However, since even the most urbanophilic anoles also use natural habitats, this type of misclassification will have a minimal impact on the urban score, so long as our data for the affected species consist of many observations. Critically, our chosen buffer distance is designed to minimize misidentification of nonurban observations as urban. This is a risk because our field work on anoles has taught us that forest-restricted, urban intolerant species can sometimes occupy forested habitat in close proximity to dense urbanization (e.g., in periurban forest or urban forest fragments), without using the urban habitat.

We supplemented these location-based data using information on rarity and habitat use from species accounts in Henderson and Powell (2009), because some relatively well-known species are nonetheless underrepresented in the GBIF and iNaturalist databases. Henderson and Powell (2009) provide detailed species descriptions and natural history information for nearly all currently described Caribbean *Anolis* species. If the species description by Henderson and Powell (2009) indicated that a species was known from just a single locality, absent from disturbed areas, or was restricted to a specific type of natural habitat, we considered this as evidence of urban avoidance, and assigned the species "avoider" points worth a specified number of equivalent nonurban "observations" (see Tables S1a and b for details). On the other hand, if the Henderson and Powell's

(2009) record indicated that a species used fences or buildings, was present in parks or modified human environments, or tended to be associated with humans, we considered this as evidence of urban tolerance, and we awarded "tolerance" points accordingly. Although this additional line of evidence is, in some ways, more subjective than our location-based data, we combined both sources of information using a standardized and reproducible protocol that we believe accurately captures the urban habitat use of species, while simultaneously maximizing species coverage in the *Anolis* phylogeny (Supporting Information Materials S1a). Furthermore, because our prior probabilities (procedure described below) are determined by multiple lines of evidence, Henderson and Powell (2009) is unlikely to strongly influence our resultant urban tolerance measure unless the species description included strong evidence of urban habitat use (e.g., a species is observed on buildings in urban environments).

The final result of our assignment procedure was an urban tolerance score for each species that took into account their presence or absence from urban areas in GBIF and iNaturalist, as well as details of their narrative species description in Henderson and Powell (2009). For simplicity, we refer to this tally as the "preliminary urban score." We provide more specific details about our assignment methodology in Supporting Information Materials S1. The scores that we computed from this protocol were not prior probabilities, and we wanted the latter to take into account not only our species description and database records but also the number of observations of a species in each habitat type. Our rationale for this is straightforward. First, logically, a small number of observations from urban sites should not give us as much confidence that a species tolerates this habitat type as would hundreds of records. This is because the former result could be due to spurious georeferencing, unaccounted-for misidentification, or the errant movement of some individuals. By contrast, a large number of urban observations cannot be explained absent genuine urbanophily. Second, the presence and absence from urban environments provide asymmetric information about tolerance. Even a modest number of reliable records of a species in urban habitats provides solid evidence that the species is urban tolerant, regardless of how many times it is has been recorded in natural environments. On the other hand, a species with relatively few records (due to rarity or lack of sampling), and none at all in urban areas, may plausibly be either urban tolerant or an avoider. (In other words, as the aphorism goes, the "absence of evidence is not evidence of absence.")

As such, to obtain our final prior probabilities of urban tolerance or avoidance from our data, we used a logistic model that was designed to take into account these considerations. We provide detailed methodology in Supporting Information Materials S2, but, in brief, we set two cutoffs: 12 urban observations to be confident of urbanophily, and 50 total observations to be confident of sampling effort. Under our model, a species with a preliminary urban score of at least 12 (which corresponds to 12 urban records in GBIF, iNaturalist, and/or evidence from Henderson and Powell 2009) was assigned a prior probability of 1 for the urban state if at least 50 total observations were recorded for the species. These cutoffs, although subjective, were chosen based on our experience with a subset of the species in our dataset with which we are very familiar. A higher cutoff than 12 for the urban score would result in species we know to be strong urbanophiles to be misclassified as possibly intolerant. Conversely, raising our sampling effort cutoff beyond 50 would result in increased uncertainty (i.e., closer to an uninformed probability of 0.5 for each state) for all but the most well-studied species, and lowering it would increase the risk of falsely classifying a species as either urban or nonurban confidently. Finally, if a species had no observations, we simply assigned it an equal (i.e., flat) prior probability of being in each of the two possible states. We did the same for any species found only on uninhabited islands (*Anolis desechensis*, *Anolis ernestwilliamsi*, *Anolis monensis*, and *Anolis nubilus* in this study) using the logic that each might tolerate or not tolerate urbanization if they encountered it.

We recognize that combining these disparate lines of evidence (georeferenced species records from GBIF and iNaturalist, written species accounts, and personal field experience) means that our final urban tolerance prior probabilities contain a degree of subjectivity. Nonetheless, we have strived to make our protocol reproducible and we are confident that our scores are correlated with urban tolerance, and that our prior probabilities accurately reflect the assignment ambiguity inherent in reconciling these different data sources.

TRAIT EVOLUTION AND PHYLOGENETIC SIGNAL

We used the Gamble et al. (2014) phylogeny of Caribbean anoles for all analyses. We removed any species from the tree that are not native to the Caribbean region. We added missing species (*Anolis agueroi*, *Anolis fairchildi*, *Anolis litoralis*, *Anolis roosevelti*, and *Anolis terraealtae*) next to their most likely sister taxon at 1/2 the terminal branch length for each taxon. A more recent phylogeny was published in 2017 by Poe et al.; however, the trees are largely congruent for Caribbean species, differing mainly in the relationships between a handful of sister taxa. Our results were qualitatively the same regardless of which tree we used (Supporting Information Materials S5).

We reconstructed ancestral and missing tip states for urban tolerance under the threshold model (Felsenstein 2005, 2012) and compared our results to continuous-time Markov chain models (also known as extended M*k* models; Lewis 2001; Harmon 2018). Under the threshold model, the state of a discrete character is determined by an unobserved continuous trait called the liability. When the liability crosses one or more threshold(s), the discrete character changes in state. The threshold model is derived from evolutionary quantitative genetics and dates to Wright (1934); however, it was more recently applied to the problem of analyzing trait evolution on phylogenies by Felsenstein (2005, 2012). Revell (2014) argued that the threshold model might not only be suitable as a model to approximate the evolution of threshold characters in a strict quantitative genetic sense, but also for ecological or life history characteristics in which the value of a discretely measured trait is likely to be influenced by many other discrete or continuously valued (measurable or unmeasurable) characteristics. Instead of instantaneous state changes from any state to another, the threshold model approximates trait evolution as incremental changes in one or many traits that cumulatively push the species closer and closer to a discrete character state change (the threshold), at which point the discrete character state flips. It also has the additional ancillary property (not shared by the M*k* model) that the more recently a state change has occurred, the more likely it is that a reversal of the character to its previous condition could result.

By contrast, the M*k* model is (by definition) memoryless and involves instantaneous transitions between states. For a two-state model, transitions might be symmetric or asymmetric, and if it is asymmetric, transitions can be reversible or irreversible. For instance, a symmetric model permits changes between avoiders and exploiters or the reverse, and backward and forward changes between adjacent states are assumed to occur at the same rate. An asymmetric model, by comparison, would be a model in which both forward and reverse changes are permitted to occur but in which these may occur at different rates. We fit four different variants of the M*k* model as follows: an asymmetric model, two irreversible models (one allowing transitions from avoid to urban and the other from urban to avoid), and a symmetric model in which both backward and forward transition rates were constrained to be equal (model summaries provided in Supporting Information Materials S3).

We reconstructed ancestral states under the threshold model with the function *ancThresh* in the R package "phytools" (Revell 2012) using Bayesian Markov chain Monte Carlo (MCMC), as in Revell (2014). We used Brownian motion as a model for the evolution of the liability, with 10,000,000 generations of MCMC sampled every 1000 generations and excluding the first 2,000,000 generations as burn-in. We ran four chains of this length with different starting values and combined all our post burn-in samples. We tested for convergence using Geweke's and Gelman's convergence diagnostics and computed effective sample sizes using the R package "coda" (Plummer et al. 2006).

In addition, we compared trait evolution under the aforementioned variations of the M*k* model using the function *fitMk* in "phytools." We compared M*k* models using AIC, and reconstructed ancestral states with the procedure of stochastic character mapping (Huelsenbeck et al. 2003) for the best-supported model using the function *make.simmap* with 500 stochastic maps in "phytools." We computed posterior probabilities of urban tolerance for internal nodes and tips under both the threshold model and the best-fitting M*k* model.

We tested for phylogenetic signal (i.e., whether urban-tolerant species tend to be closely related to other urban-tolerant species) by optimizing Pagel's (1999) λ tree transformation for our best-justified M*k* model to our data set of discrete state probabilities (i.e., for "avoid" and "urban") using the function *fitMk* in "phytools" and a custom numerical optimization routine in R. An optimized value of $\lambda = 1$ would correspond to similarity of related taxa proportional to their degree of shared ancestry, whereas a value of λ closer to 0 corresponds to an absence of phylogenetic signal. Consequently, we obtained a maximum likelihood estimate of λ and compared this fitted model to one in which λ was set to 0 using a standard likelihood-ratio test.

We tested the predictive value of the best-fit M*k* model and the threshold model using a leave-one-out cross-validation procedure. We compared the ability of each model to correctly predict tip states by changing the prior probability of each tip state (one by one) to be completely uninformative (i.e., 1/2 probability of being in each discrete state), then estimated urban tolerance projected tip states under an M*k* model (with 500 stochastic mapping simulations, as above) or the threshold model (with the same parameters as noted earlier). Thus, each model had only one tip state changed in each of the 131 iterations.

If the method is performing well we would expect it to be accurate in correctly predicting the values of our "missing" (but known) tip states. By contrast, if the model has no predictive value, we would expect it to predict each of the two discrete states with probabilities proportional to their equilibrium frequencies under the model. We measured predictive performance by simply multiplying the posterior probabilities computed in the leave-one-out analysis by the original tip state (prior) probabilities, and then computing the average across tips. We then divided this value by the mean maximum tip probability across all species in the tree. This quantity could thus vary on a scale of 0 through 1, in which 0 would suggest that the model confidently predicted the wrong state, and 1 indicates that the model confidently predicts the state whose tip probability was highest. We computed a *P*-value for the predictive value of the model by randomly permuting the tip (prior) probabilities among species a large number of times, and then each time recomputing the statistic. A *P*-value less than 0.05 would indicate significantly better prediction than picking either of the two possible states at random.

TRAIT CORRELATIONS

We tested for correlation between urban tolerance and several ecological and morphological traits using the estimated trait liability for urban tolerance underlying our discrete states. Specifically, the phenotypic traits we considered were as follows: body size (snout-vent-length [SVL]), fore- and hindlimb length, toepad lamella number from digit IV of both fore- and hind-feet (all from Mahler et al. 2013), ecomorph category, field body temperatures (sources in Supporting Information Materials S4), and dorsal and ventral scale counts (from Wegener et al. 2014). We also considered several emergent species traits that have been suggested to relate to ecological niche breadth in anoles: island of origin, range size, latitudinal range, number of congeners, and climatic niche.

In ArcMap (ESRI, version 10.4.1), we mapped species ranges (obtained from CaribHerp; Hedges 2019) and all 19 BIOCLIM climatic variables (WordClim, version 1; Hijmans et al. 2005). All data were set to geographic spatial reference WGS 1984 and projected to UTM Zone 20N. For each species, we calculated range size, number of congeners with overlapping ranges, and latitudinal range. We extracted BIOCLIM values for the range of each species in ArcMap and calculated species means for each of the 19 variables. We then performed a phylogenetic principal components analysis of all 19 BIOCLIM variables in R using the function *phyl.pca* in “phytools” (Revell 2009, 2012). We extracted principal components from the correlation matrix and retained components with eigenvalues greater than 1 for subsequent analyses.

To analyze trait correlations, we followed the approach outlined in Reynolds et al. (2016). Specifically, we treated the mean posterior liability from Bayesian MCMC analysis of the threshold model as our measure of species-specific urban tolerance to test for correlations between projected tip states and other traits that we hypothesized might influence success in urban areas. Unlike Reynolds et al. (2016), we also took uncertainty in the value of the liability into account by estimating the sampling variances of the species liabilities from the MCMC posterior sample.

For all of these analyses, we used phylogenetic generalized least squares (PGLS) as our estimation procedure with the function *pgls.SEy* as implemented in the package “phytools,” which fits the regression with sampling error (Revell 2012). We assumed that the correlation structure of the residual error was Brownian and calculated the sampling error as the standard deviation from the posterior distribution of liabilities with *summary.mcmc* implemented in the package “coda” (Plummer et al. 2006). We fit a total of five models analyzing correlation of the urban tolerance liability with island of origin, ecomorph, field body temperature, morphology, and ecology.

Our first two models address whether specific islands tend to have more or less urban tolerant species and whether specific ecomorphs are more likely to be tolerant of urbanization, the first of which could result from biological (e.g., shared environments) or nonbiological causes (e.g., if sampling in certain areas was inadequate). We first fit a model of the liability by island group. In this model, we assigned any species found natively in more than one island group (e.g., *Anolis sagrei*) to the largest of their native islands (e.g., Cuba instead of Bahamas), and all species from the Lesser Antillean islands were grouped together. Because island group was significant in this first model, we included it as a covariate in all subsequent models. We compared the marginal means of groups in each model with the *contrast* function with multivariate adjustment and used the function *CLD* to group significant responses based on marginal means comparisons with significance level of $\alpha = 0.05$. Both of these two functions are from the R package “emmeans” (Lenth 2016). We also fit a model of urban tolerance liability by ecomorph and island group, excluding species that do not fall into a specific ecomorphological class ($n = 91$ species included in the model).

Next, we analyzed field body temperature with a PGLS model of urban tolerance liability by mean field body temperature (sources in Supporting Information Materials S4) with island group as a covariate. We analyzed body temperature separately from other traits because we were only able to obtain information for 60 species for this trait. In our morphology model, we analyzed scale traits ($n = 111$ species), limb lengths, and lamella numbers ($n = 99$ species) for the 87 species shared between these two data sets. We fit a single multivariate PGLS model of urban tolerance liability by ln-transformed traits (dorsal and ventral scale count, front and rear lamella number, and fore- and hindlimb lengths) with ln-transformed body size (SVL) and island group as covariates. We performed stepwise model selection by AIC implemented in the package “MASS” (Venables and Ripley 2002) and retained body size as a covariate, as all other traits scale with body size.

Finally, in our ecological model, we asked if urban tolerance was correlated with climatic niche, range size, latitudinal span, and number of congeners under the assumption that ecological specialists should have smaller geographical range sizes (as in Bonier et al. 2007), span a smaller range of latitudes, and coexist with more congeners. We fit a single PGLS model of the urban tolerance liability by range size (ln-transformed), latitudinal range (ln-transformed), number of congeners, and significant principal components from the climate PCA along with island group as a covariate. Three species lacking climate data were excluded from this analysis (*A. ernestwilliamsi*, *A. desechensis*, *A. fairchildi*). We performed stepwise model selection by Akaike information criterion (AIC) to reduce the model complexity to a minimum set of explanatory variables.

All statistical and phylogenetic analyses were completed in R (R Core Team 2019). The R package “phytools” relies on the packages “ape” (Paradis and Schliep 2018), “phangorn” (Schliep 2011), and “nlme” (Pinheiro et al. 2019) for many of the functions that we used.

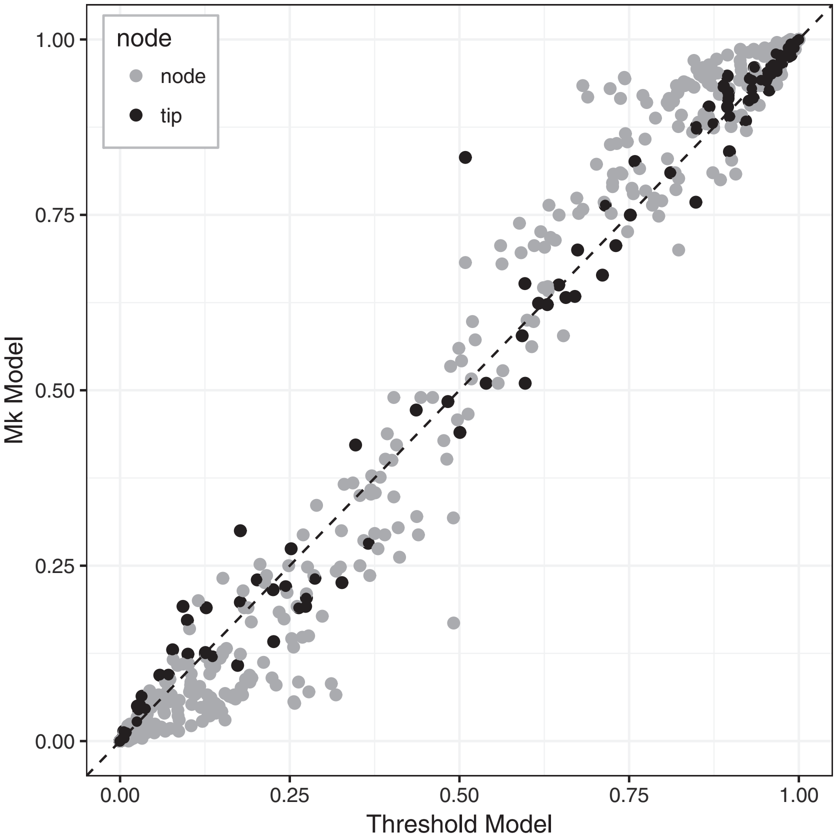

Figure 1. The threshold and Mk models yield similar results for posterior probabilities of tip (black) and node states (gray).

Results

TRAIT EVOLUTION

We assessed each post burn-in chain of the threshold model with Geweke's convergence diagnostic (Geweke 1992), which tests if the first and last samples of the chain are drawn from the same distribution. Geweke's convergence diagnostic showed convergence to the Bayesian posterior distribution after between 16.1 and 20.0% of samples in each chain. Gelman's diagnostic also indicated convergence for the combined chains (mean 1.073, range 1.001–1.920). Mean effective sample size for the combined chains was 1532.57 (range: 57.76–9479.46).

The best fit M*k* model was the model in which all rates were constrained to be equal (AIC: 172.138, Akaike weight: 0.434). This model was slightly better than the irreversible model permitting transitions from avoider to urban state, but not the reverse (AIC: 172.474, Akaike weight: 0.367). Both models were better supported than either the asymmetric ordered model (AIC: 173.795, Akaike weight: 0.190) or the irreversible model that permitted transitions from urban to avoider, but not the reverse (AIC: 179.761, Akaike weight: 0.010).

Posterior probabilities for nodes and tips from the threshold model were similar to those obtained from the best-fit M*k* model. The model predictions differed most one from the other for intermediate probabilities at nodes but were generally in agreement for tip states (Fig. 1; although this is perhaps unsurprising because both should resemble the priors at the tips of the tree). We found that urban tolerance was relatively common among anoles and our results suggest that the propensity to be an urban avoiding or exploiting species evolved independently in several different clades (Fig. 2). We also found strong phylogenetic signal in the evolution of urban tolerance (MLE(λ) = 0.955, $P = 0.001$), indicating that closely related species tend to have similar tolerances to urbanization.

PREDICTIVE PERFORMANCE

The M*k* model in the leave-one-out validation placed species in the correct category (the same category as in the full model) with a weighted frequency of 0.819, a value that was significantly greater than expected by chance ($P < 0.001$). The threshold model performed slightly better and correctly placed species in the correct urban tolerance category at a weighted frequency of 0.833 ($P < 0.001$). In the absence of any other information about a species, our phylogenetic models (on average) correctly predict the most probable state for urban tolerance significantly better

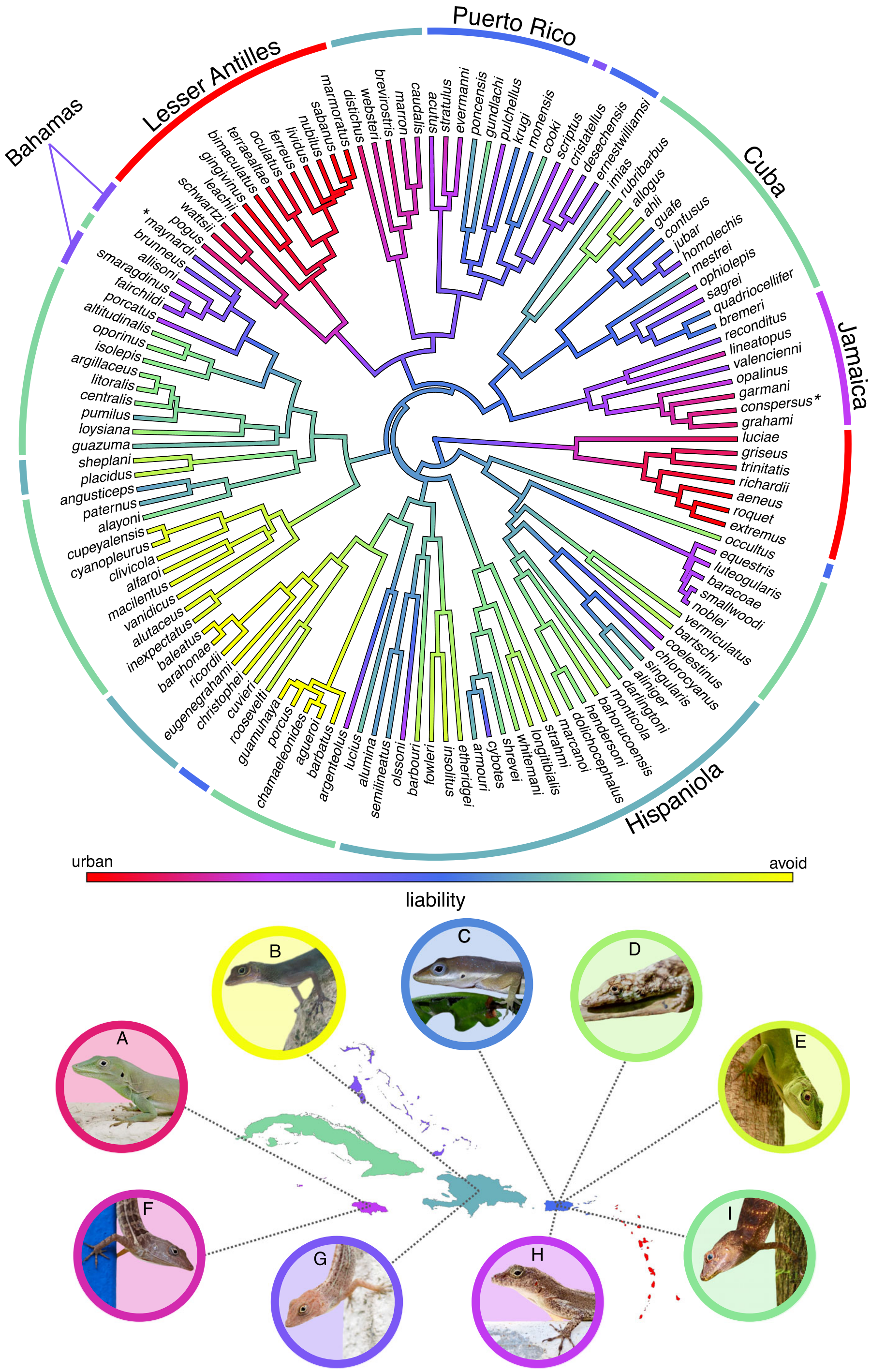

Figure 2. Top: Continuous-character map tree (Revell 2013) based on the threshold model of ancestral state reconstruction. As the evolution of anoles pre-dates anthropogenic habitats, ancestral state reconstruction of urban tolerance should be viewed as the evolution of many different traits cumulatively responsible for a predisposition to tolerate urbanization, and not the evolution of urban habitat use. Branches are colored depending on the liability of the urban tolerance trait, with higher values (red) indicating urbanophily and lower values (yellow) indicating urban avoidance. The outer ring is colored by island (or island group), with the color corresponding to the average urban tolerance liability for all species from that island. *Anolis maynardi* and *A. conspersus* (noted with asterisks) are found in the Cayman islands. Bottom: Caribbean anoles are ecologically diverse and differ widely in their urban tolerance: (A) *A. grahami*, (B) *A. eugenegrahami*, (C) *A. krugi*, (D) *A. occultus*, and (E) *A. cuvieri*. Even otherwise very ecologically similar species sometimes show a diverse range of urban tolerance, as seen in the trunk-ground ecomorph species: (F) *A. lineatopus*, (G) *A. cybotes*, (H) *A. cristatellus*, and (I) *A. gundlachi*. Islands are colored by the average liability of all species on the island (as in the top image labels) and circle colors for individual species correspond to their inferred urban tolerance. Images: KMW (A and C-I) and DLM (B).

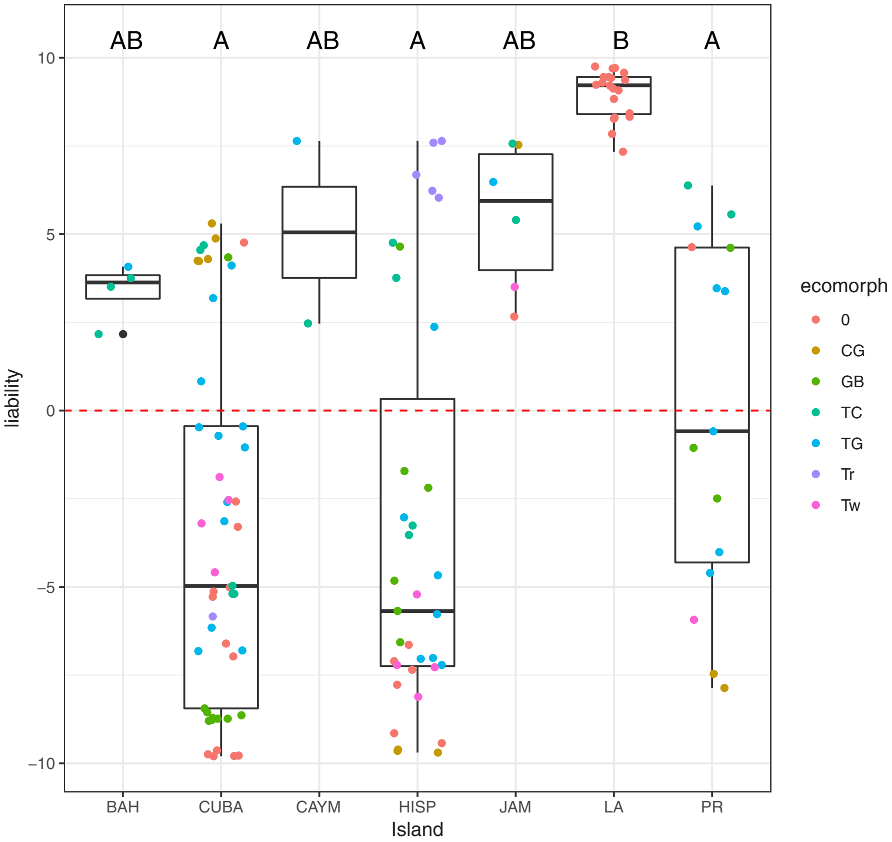

Figure 3. **Urban tolerance liability differed by island type, but not by ecomorph. Letters above each bar represent groupings based on PGLS marginal means comparisons at $\alpha < 0.05$. The dashed red line represents the threshold between urban and avoid states for trait liability. Island abbreviations: BAH, Bahamas; CUBA, Cuba; CAYM, Cayman Islands; HISP, Hispaniola; JAM, Jamaica; LA, Lesser Antilles; PR, Puerto Rico and Virgin Islands. Ecomorph abbreviations: 0, non-ecomorph; CG, crown-giant; GB, grass-bush; TC, trunk-crown; TG, trunk-ground; Tr, trunk; Tw, twig.**

than expected by chance, with the threshold model very slightly outperforming the M*k* model.

TRAIT CORRELATIONS

In our PGLS analysis of the mean tip-wise liability, we found correlations between the estimated liability and several ecological and morphological traits.

We found a correlation between urban tolerance and island group of origin ($F_{\mathrm{df}=6,124} = 3.349$, $P = 0.004$), but we did not find a correlation between urban tolerance and ecomorph category ($F_{\mathrm{df}=5,79} = 1.414$, $P = 0.228$; Figs. 2 and 3). Species from Cuba and Hispaniola, which also have the largest endemic anole communities of the Caribbean islands, had lower mean liability for urban tolerance compared to the other islands, whereas species from the Lesser Antilles tended to have higher liability.

We found a positive correlation between field body temperature and urban tolerance liability ($\beta = 0.528 \pm 0.216$, $t_{\mathrm{df}=52} = 5.971$, $P = 0.018$), indicating species that experience higher body temperatures in their natural (nonurban) environments have higher average urban tolerance. We also found several morphological traits (relative to body size) to be significantly correlated with urban tolerance liability: number of ventral scales ($\beta = -4.632 \pm 1.474$, $t_{\mathrm{df}=78} = -3.142$, $P = 0.002$), rear lamella number ($\beta = 13.480 \pm 3.680$, $t_{\mathrm{df}=78} = 3.663$, $P < 0.001$), and hindlimb length ($\beta = -9.931 \pm 4.895$, $t_{\mathrm{df}=78} = -2.029$, $P = 0.046$). Forelimb length and SVL were also retained in the reduced model, but neither was statistically significant (forelimb: $\beta = 7.862 \pm 5.752$, $t_{\mathrm{df}=78} = 1.367$, $P = 0.178$; SVL: $\beta = -4.879 \pm 4.067$, $t_{\mathrm{df}=78} = -1.200$, $P = 0.234$). Island group of origin was not a significant covariate but was retained during model selection (analysis of variance [ANOVA], $F_{\mathrm{df}=3,78} = 1.935$, $P = 0.131$).

In our ecological traits model, we found that the liability for urban tolerance was positively correlated with PC1 ($\beta = 0.036 \pm 0.015$, $t_{\mathrm{df}=118} = 2.434$, $P = 0.016$) but not PC2 ($\beta = 0.031 \pm 0.019$, $t_{\mathrm{df}=118} = 1.571$, $P = 0.119$). Principal component 1 is loaded on several temperature and precipitation variables, with larger values of PC1 corresponding with warmer temperatures and drier climates (Table 1). Principal component 2 is loaded

Table 1. Principal component loadings from the phylogenetic PCA of 19 BioClim climate variables.

		PC1	PC2	PC3	PC4
BIO1	Annual mean temperature	**0.903**	0.328	0.229	−0.153
BIO2	Mean diurnal range	−0.239	**−0.656**	0.160	**−0.632**
BIO3	Isothermality	−0.217	−0.156	−0.411	**−0.855**
BIO4	Temperature seasonality	0.075	−0.215	**0.738**	0.501
BIO5	Max temp. of warmest month	**0.868**	0.121	0.380	−0.245
BIO6	Min temp. of coldest month	**0.826**	0.549	0.004	−0.015
BIO7	Temperature annual range	−0.158	**−0.699**	0.489	−0.296
BIO8	Mean temp. of wettest quarter	**0.881**	0.194	0.404	−0.092
BIO9	Mean temp. of driest quarter	**0.870**	0.429	0.059	−0.222
BIO10	Mean temp. of warmest quarter	**0.895**	0.285	0.332	−0.062
BIO11	Mean temp. of coldest quarter	**0.884**	0.384	0.066	−0.241
BIO12	Annual precipitation	**−0.747**	0.482	0.398	−0.173
BIO13	Precipitation of wettest month	**−0.789**	0.331	0.399	−0.078
BIO14	Precipitation of driest month	−0.529	**0.798**	−0.030	−0.108
BIO15	Precipitation seasonality	0.180	**−0.765**	0.379	0.020
BIO16	Precipitation of wettest quarter	**−0.728**	0.287	0.531	−0.138
BIO17	Precipitation of driest quarter	−0.572	**0.794**	0.044	−0.050
BIO18	Precipitation of warmest quarter	−0.572	0.035	**0.716**	−0.137
BIO19	Precipitation of coldest quarter	−0.513	**0.809**	−0.036	−0.052
Eigenvalue		8.349	4.798	2.716	1.762
Percentage variance		44.418	25.251	14.297	9.279

We retained all principal components with eigenvalues greater than 1. Loadings ≥0.6 are given in bold for each component. PC1, which corresponds to warmer temperatures and less precipitation, was positively correlated with urban tolerance. PC2, which corresponds to reduced annual and daily temperature ranges, increased precipitation, and reduced seasonality in precipitation was positively correlated with urban tolerance.

on diurnal and annual temperature ranges as well as several precipitation variables, with larger values of PC2 indicating less annual and diurnal temperature variation, more precipitation in cold and dry periods, and less seasonality in precipitation. This model thus suggests that anoles whose native ranges include warmer and drier conditions (PC1) are more likely to be tolerant of urban environments. In addition, liability for urban tolerance was positively correlated with total native range size ($\beta = 0.358 \pm 0.089$, $t_{\mathrm{df}=118} = 4.038$, $P < 0.001$), indicating that species with more widespread distributions are more likely to be tolerant of urbanization. Island group of origin was a significant covariate in this model only (ANOVA, $F_{\mathrm{df}=6,\,118} = 3.874$, $P = 0.001$).

Discussion

As urbanization continues to mount throughout the Caribbean, the species that occupy and adapt to cities will likely be nonrandom. We found that tolerance to urban areas is indeed nonrandom in *Anolis* lizards, exhibiting a relatively high degree of phylogenetic signal in our data. We also found that species adapted to warmer and drier climates in their natural range may be predisposed to tolerate urban life. Such filtering could reduce local biodiversity and destabilize populations of urban avoiding species as urbanization expands and fragments natural forest environments. Finally, we found that species tolerant of urbanization tend to have morphological attributes important for locomotor function in the urban setting. These traits may be key preadaptations in anoles that help enable urban colonization and niche expansion onto anthropogenic structures where novel selective pressures may then drive phenotypic evolution on different morphological or physiological trajectories.

THE EVOLUTION OF URBAN TOLERANCE

We found that urban tolerance in anoles has strong phylogenetic signal, indicating that closely related species are more likely to respond similarly to urbanization. The few studies that have measured phylogenetic signal of urban tolerance in other taxa have found mixed results, in some cases showing strong phylogenetic signal (e.g., Sol et al. 2014) and in others finding weak or no signal (e.g., Cardoso 2014). In both cases, these studies also found urban tolerance to be relatively rare. In contrast, and consistent with our experience, we found urban tolerance to be widespread among Caribbean anoles, although we identified a number of species with low liability scores indicating strong urban avoidance (e.g., members of the Cuban "*Chamaeleolis*" clade). We suggest that these species should be of conservation priority where their natural habitat is threatened, which may be particularly useful for species that are less well known. That closely related species tend to have similar vulnerability to anthropogenic change also suggests that entire clades may be lost as urbanization transforms natural areas, resulting in a disproportionate loss of phylogenetic diversity (Isaac et al. 2007; Frishkoff et al. 2014). An important caveat to our finding of strong phylogenetic signal, however, is that phylogenetic signal does not necessarily mean that a trait is inherited. The pattern of urban tolerance evolution we find could also arise by other nongenetic causes, such as shared environmental conditions among closely related lineages.

In recent years, researchers have begun to investigate factors determining urban tolerance across a variety of taxa (e.g., Ducatez et al. 2018), especially in birds (Sol et al. 2013). These studies measure urban tolerance as a discrete trait, mainly as physical presence or observed breeding in urban environments. A common criticism of treating urban tolerance as a discrete character is that doing so effectively assumes that all species with the same state are equally tolerant of urbanization (Evans et al. 2011; Sol et al. 2013). Here, we take an alternative approach using a probabilistic state assignment and phylogenetic comparative methods. Our threshold approach adds nuance by using phylogenetic information to estimate the propensity for tolerance on a continuous rather than a discrete scale. Under the threshold model, for instance, we might predict that urban exploiting species found deeply nested within a clade of other exploiters are likely more tolerant (i.e., they likely have higher values of tolerance liability) than species that more recently evolved the traits that are associated with urban exploitation and that are closely related to urban avoiders.

We considered two models of trait evolution: the threshold model (Felsenstein 2005, 2012; Revell 2014) and the simpler, but consequently highly tractable, M*k* model (Lewis 2001). When we compared the threshold model to our best-fitting M*k* model, we found that posterior probabilities for node and tip states were quite strongly correlated, but not identical (Fig. 1). Unfortunately, the models are difficult to compare directly. This is because computing the likelihood under our threshold model would involve calculating integrals of very high dimensional Gaussian probability densities that are (so far as we know) not possible to compute (Revell 2014). Nonetheless, we contend that the threshold model may be more biologically appropriate for our data in that urban tolerance is not likely to be attributable to a single trait but rather to a combination of traits. This contention finds support from the fact that we found that multiple ecological and morphological variables were correlated with urban tolerance, a finding concordant with studies in birds (e.g., Kark et al. 2007; Evans et al. 2011).

PREDICTING RESPONSES TO URBANIZATION

Our phylogenetic models successfully predicted the observed tip tolerances for >82% of cases in leave-one-out analyses, suggesting that our methods can be used (albeit with considerable caution) to predict how species are likely to respond to increased urbanization. For example, Desecheo and Mona are two uninhabited islands off the west coast of Puerto Rico and are home to *A. desechensis* and *A. monensis*, respectively. According to our model, if either islands were to be developed (although not expected as both are government-owned nature reserves), we would expect *A. desechensis* to be more tolerant of urbanization than *A. monensis*. This finding makes evolutionary sense because *A. desechensis* is very closely related to the highly tolerant urban exploiter, *Anolis cristatellus*, whereas *A. monensis* is most closely related to the tropical dry forest specialist *Anolis cooki*, which appears to be intolerant of urbanization (based both on the personal experience of the authors and our model). The ability to predict tolerance in species that have not yet been extensively exposed to urbanization is particularly relevant as development progresses throughout the Caribbean.

We caution that high liability scores should not be taken as evidence that natural habitat elements are not necessary for persistence. For example, *Anolis stratulus* scores higher on our urban tolerance scale than the syntopic congener *A. cristatellus*, but it has been previously shown that despite its commonness in urban habitats, *A. stratulus* predominantly uses vegetative elements and does not exploit anthropogenic structures in the same way as *A. cristatellus* (Winchell et al. 2018a). Similarly, without demographic information we cannot know if a species that appears to be an urban exploiter is truly an urbanophilic species and not reliant on nearby forested areas as a source for urban sink populations, a distinction of considerable conservation significance.

This lack of resolution at the upper end of the urban tolerance scale is likely a consequence of our methodology: for practical reasons (primarily due to data availability), we initially scored species mainly based on presence and absence in urban areas and did not consider whether species exploit urban habitat by using anthropogenic structures (although any species could additionally receive "urban points" if the use of such structures was documented) or whether they are transient occupants of urban areas or demographically stable populations. More generally, we stress that the approach we have presented should be used to guide future direct study of sensitivity to urbanization in clades of interest, and that predictions from our model are not sufficient to assess the true sensitivity of individual species to urbanization. Detailed assessments of individual species responses require a spatially explicit framework that takes into account ecological (e.g., behavior, microhabitat use, demography) and anthropogenic factors (e.g., patterns, pace, and characteristics of urban intensification) that have not been taken into consideration here.

Nevertheless, our approach provides a starting point for future studies of urban tolerance by identifying species that may be likely to persist or perish in urban sites.

ECOLOGICAL AND PHENOTYPIC PREDICTORS OF URBAN TOLERANCE

Our investigation of the relationships between estimated liabilities for urban tolerance and ecological and morphological traits revealed a syndrome of attributes that generally characterize urban-tolerant anoles. Several key patterns emerge from these relationships.

First, we found at best mixed support for the hypothesis that a generalist ecological niche facilitates urban habitat use. On the one hand, species from smaller islands and with larger geographic ranges appear to be more likely to succeed in urban environments. Both of these emergent traits have been linked in past work to a broad ecological niche on the assumption that wide-ranging species experience more diverse ecological conditions and that smaller, more depauperate islands are home to more ecologically generalized species (e.g., Hayes and Barry 2008). In anoles, species from the two largest Greater Antillean islands (Cuba and Hispaniola) had the lowest mean urban tolerance liability, where species from the comparatively small Lesser Antillean islands had the highest mean urban tolerance liability (Figs. 2 and 3). Cuba and Hispaniola are the most species rich (Cuba, $n = 64$ anole species; Hispaniola, $n = 57$ anole species) and ecologically diverse (i.e., containing many habitat specialists) Caribbean islands (Losos 2009), whereas the islands of the Lesser Antilles are home to just one or two species (although whether these species are ecological generalists is debatable; Losos and de Quieroz 1997). Likewise, anole species that were more widespread tended to have higher urban liability scores. These results are in accord with studies of other taxa, particularly birds, that have found urban tolerance to correlate with tolerance of diverse conditions and large geographical range size (Bonier et al. 2007; Evans et al. 2011; Sol et al. 2014; Ducatez et al. 2018; Callaghan et al. 2019). An alternative explanation for this pattern may be that wider ranging species and species from the smaller Lesser Antillean islands are simply more likely to encounter urban habitats.

However, we found little support for the generalist success hypothesis for climate niche traits. Instead, we found that for climate traits, higher urban liability was correlated with high average field body temperatures, fewer ventral scales, and the use of hot, dry habitats. Together, these results suggest that specialization for warm temperatures, rather than a generalist thermal niche, may preadapt species to tolerate urbanization, and we discuss each of these results in turn.

High average body temperatures may indicate a predisposition for warmer environments, a tolerance of high temperatures, or plasticity in thermal physiology, all of which are likely to be favorable in the urban environment. Ventral scale number is also related to thermal and hydric climate (reviewed in Losos 2009), and generally species with fewer (and thus typically larger) scales tend to occupy drier and warmer climates (Lister 1976; Calsbeek et al. 2006; Wegener et al. 2014). Variation in scale size and density is related to evaporative water loss via interscale integument and heat dissipation by larger scales (Soulé 1966; Horton 1972; Oufiero et al. 2011). Species with fewer and larger scales should experience less evaporative water loss and would dissipate heat at a greater rate in the hotter and drier conditions of urban environments. Importantly, average body temperature and scale density have both been found to differ between urban and forest populations of lizards. Urban *A. cristatellus* experience elevated field body temperatures along with shifts in thermal tolerance and urban *Sceloporus occidentalis* have fewer dorsal scales compared to nonurban conspecifics (Winchell et al. 2016; Putman et al. 2019; Campbell-Staton et al. 2020). Together these traits may enable species to tolerate the year-round elevated temperatures typical of urban habitats.

Likewise, we found that species from warmer and drier climates (climate PC1) are more likely to be urban tolerant. This finding echoes Frishkoff et al. (2019), who found that Dominican warm-climate specialist anoles were more tolerant of anthropogenically modified habitats (cleared forest). The association between urban tolerance and these climatic traits seems reasonable as urban environments tend to be warmer and drier than nearby forested habitats and experience reduced seasonality and lower daily temperature variability (Oke 1982; Adeyabo 1991). Urban areas maintain average air temperatures as much as 10°C greater than nearby natural habitats, including elevated nighttime and winter temperatures (Oke 1973). Caribbean islands are no exception to this pattern, and the magnitude of this effect is expected to increase in coming years (Velazquez-Lozada et al. 2006). The positive correlation we detected between urban tolerance liability and climate PC1 suggests that species whose natural ranges are warmer and drier would find urban climatic conditions to be well matched to their physiological tolerances. We hypothesize that the predisposition to tolerate the urban climate plays a major role in filtering which species colonize and persist in urban environments. In the future, this kind of filtering effect could contribute to increased biotic homogenization of urban areas and regional destabilization of urban intolerant species (McKinney 2006; Devictor et al. 2007).

We also investigated whether prior adaptation to particular structural microhabitats might predict present-day urban tolerance. We found no indication that certain ecomorphs, which are specialized for various natural structural habitats, are more or less tolerant of urbanization. This was initially surprising to us considering that the few studies of urban ecology and evolution in anoles (e.g., Perry et al. 2008; Marnocha et al. 2011;

Winchell et al. 2016, 2018a) had led us to predict that trunk-ground or trunk-crown anoles may be more likely to be urban exploiters than the other ecomorphs. This prediction was not supported in large part because of the great range of variability in tolerance within each ecomorph. For instance, several species in the crown-giant ecomorph have very low liability for urban tolerance, whereas others such as the Jamaican *Anolis garmani* and Cuban *Anolis equestris* show liabilities that are relatively high. Indeed, both of these latter species can readily be found in major cities within their native and introduced ranges. Similarly, though trunk-ground anoles such as *A. cristatellus* and the Jamaican species *Anolis lineatopus* are among the most tolerant of urbanization, some trunk-ground species showed very low liabilities for urban tolerance, such as *Anolis gundlachi*, a cool-climate forest interior specialist.

Finally, we found urban tolerance to be correlated with traits related to locomotor performance: rear lamella number and hindlimb length, but not with front lamella number or forelimb lengths. This is intriguing as all four of these traits have been shown to shift in urban populations of *A. cristatellus*, presumably because of differences in structural habitat between urban and forest environments (Winchell et al. 2016, 2018b). The finding of relatively shorter hindlimbs is also puzzling as it has previously shown that urban *A. cristatellus* have longer hindlimbs and that this trait confers a performance benefit (Winchell et al. 2016, 2018b). However, the benefit of longer hindlimbs is negated on smooth flat vertical surfaces, such as painted walls, unless the species also possesses large toepads (Winchell et al. 2018b). Thus, long limbs by themselves may not be conducive to urban colonization. Lamellae, which are specialized scales on the toepad used for adhesion to smooth surfaces, are positively correlated with clinging ability (Zani 2000). Lamellae may be particularly important in urban areas where the majority of surfaces are smooth anthropogenic substrates such as metal, painted concrete, and glass. It is possible that having more rear lamellae enables use of anthropogenic structures in urban areas, allowing niche expansion into this unique habitat space. Limb length and front lamella number may then be acted on by natural selection in some species but are not prerequisites to urban colonization.

Although we identified several ecological and morphological correlates of urban tolerance, others may have been overlooked. For example, our analyses do not consider the role of behavior, which is undoubtedly significant in determining urban tolerance. Behavioral flexibility and innate differences in risk-taking behavior could be very important for determining which species enter and thrive in urban environments (Lowry et al. 2012; Sol et al. 2013). Indeed, behavior has been examined in urban tolerance studies of other taxa, particularly birds. For example, Carette and Tella (2011) found that bird species with large standing variation in behavioral responses to humans were more likely to be successful in cities. Prior studies on a small number of *Anolis* species have found behavioral shifts in risk-taking behavior in urban populations (e.g., Lapiedra et al. 2016; Avilés-Rodriguez and Kolbe 2019). However, a comprehensive study of behavioral traits relevant to urban tolerance has not been undertaken for the phylogeny of anoles and so we were unable to include behavioral phenotypes in our analyses at this time. Future studies examining behaviors such as flight initiation distance or neophobia across a large number of anole species could help to shed light on this important and understudied aspect of urban tolerance.

Conclusions

The Caribbean islands have experienced some of the highest rates of urbanization globally. Using a novel analytical approach, we show that for one of the region's most ecologically important clades, the *Anolis* lizards, tolerance of urbanization exhibits a phylogenetic signal. Even though urbanization has only emerged as a potent threat in the very recent past, we believe that a phylogenetic perspective holds great potential for helping to identify the mechanisms underlying urban tolerance and sensitivity, and in turn for guiding future conservation and sustainable development initiatives in a rapidly changing world.

AUTHOR CONTRIBUTIONS

KMW and LJR conceived of the idea. LJR and KPS developed the necessary computational resources. KMW, DLM, and KPS developed the methodology for assessing urban tolerance from species occurrences. KMW and DLM verified species identities of occurrences reported in iNaturalist and KMW characterized occurrences from iNaturalist and GBIF as urban or nonurban. KMW and LJR analyzed the data with input from KPS and DLM. All authors participated in the writing of this manuscript.

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DATA ARCHIVING

All data including R scripts needed to replicate this study are archived with Data Dryad: https://doi.org/10.5061/dryad.kh189322k.

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Supplementary Materials