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Climate, predation, and the controls of island lizard abundance and community structure

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Abstract

Alternative ecological theories make divergent predictions about the relationship between predators and their prey. If predators exert top-down ecosystem control, increases in predation should diminish prey abundance and could either diminish or enhance community diversity of prey species. However, if bottom-up ecosystem controls predominate, predator populations should track underlying variation in prey diversity and abundance, which ultimately should reflect available energy. Past research, both across islands and comparing islands with the mainland, has frequently invoked the importance of predation in regulating lizard abundance and diversity, suggesting an important role of top-down control when predators are present. However, others have posited a stronger role of food limitation, via competition or bottom-up forces. If top-down control predominates, then negative correlations between prey abundance and predator occurrence should emerge within and among islands. Using data from eBird, we inferred landscape-level presence data for bird species on the islands of Jamaica and Hispaniola. By summing occurrence probabilities of all known anole-predator birds, we estimated total avian predation pressure and combined these estimates with anole community data from a mark-recapture study that spanned spatial and climatic gradients on both islands. Avian predators and anole lizards were both affected by climate, with total predator occurrence, anole abundance and anole species richness increasing with mean annual temperature. Anole abundance and predator occurrence showed a curvilinear relationship, where abundance and predator occurrence increased together until predator occurrence became sufficiently high that anole abundance was negatively impacted. This indicates that bottom-up ecosystem controls drive richness of both anoles and their predators, mitigating the negative effects predators might have on their prey, at least until predator occurrence reaches a threshold. We did not detect consistent evidence of predator occurrence reducing anole community richness. These findings support past research showing that islands with more predators tend to have lower prey abundances, but it does not seem that these top-down forces are strongly limiting species coexistence. Instead, bottom-up forces linked with climate may be more important drivers of diversity in both lizards and their avian predators on these islands.

KEYWORDS
Anolis, birds, eBird, predation, species richness, trophic ecology

INTRODUCTION

Population sizes and total community diversity are regulated by an array of forces, ranging from long-term climatic conditions and energy availability, to diminished survival due to antagonistic interactions from predators or parasites, to extreme climatic events, to resource depletion due to competition. Such forces are often divided into those related to restrictions on energy acquisition (e.g., food availability), in which case the population is regulated from the "bottom up," versus forces imposed from the "top down" by higher trophic levels (e.g., through consumption of individuals by predators). The potential for top-down forces to establish ecosystem structure has become increasingly clear over time (Estes et al., 2011; Hairston et al., 1960; Pringle et al., 2019; Ripple & Beschta, 2012), but the relative strengths of top-down versus bottom-up forces vary depending on the individual ecosystem and focal trophic level within it, making generalization difficult so far (Denno et al., 2005; Hairston et al., 1960; Hunter & Price, 1992). Current evidence suggests that at global and regional scales, species richness is linked closely to climate such that areas with more available energy (warmer temperatures and greater precipitation) generally possess more species (Evans et al., 2005). But the relative importance of bottom-up versus top-down influences at local scales is less clear (Gripenberg & Roslin, 2007).

Complicating matters, top-down forces such as predation, parasitism, and disease can either promote or limit diversity, depending on the circumstances (Sih et al., 1985, Sinclair & Krebs, 2002). The addition of predators to a community generally has a negative impact on prey populations (Sih et al., 1985), which then scales up to impact prey community structure. But how this scaling works depends on food web structure. Over-consumption of a species can cause it to go extinct, thereby reducing diversity (Doherty et al., 2016; Medina et al., 2011). Additionally, predation may decrease coexistence by increasing competitive pressure for resources like refuges, or foraging availability in predator-free space (Hixon & Menge, 1991; Pringle et al., 2019). Indeed, in some cases, coexistence between multiple species is maintained in the absence of predation but collapses when a predator is added to the system, resulting in species loss (Pringle et al., 2019).

Alternatively, however, ecological theory suggests that, in some circumstances, predation can instead increase diversity (Paine, 1966). By reducing population sizes of superior competitors, predators can alleviate competition between species and facilitate coexistence, thereby increasing the species richness of a community (Canter et al., 2018; Gurevitch et al., 2000). Because such predation decreases the abundance of otherwise-dominant species, it can also increase evenness among prey species. In this case, total prey community abundance may either decrease or stay the same, depending on how predation directly affects the other species. Total abundance might not change if predation is focused on the dominant competitor. In such a circumstance lesser competitors can undergo compensatory population growth with the decline of the dominant competitor. However, if subordinate competitors are themselves also prey of a generalized predator, then overall prey community abundance would decline with increasing predation.

In contrast to the multidirectional predictions elicited from top-down forcing on prey communities, the effects generated from the bottom up are generally positive. In such cases, abundances tend to follow the total energy resources available in the system, as dictated by seasonal and climatological forces. If this is the case, we would see patterns where predator and prey abundance increase together, and indeed studies have often shown positive associations between the abundances of species and their prey (Fisher et al., 2002). Further, pulses of resources, such as those caused by rainfall, have been observed to cascade through the food web, providing greater energy availability in the environment and thus resulting in an increase in abundances of producers and consumers at higher trophic levels (Báez et al., 2006; Meserve et al., 2003). This work suggests that when food availability is high, consumer abundance will also be high (Guyer, 1988; Wright et al., 2013, 2020).

Island lizards—and insular *Anolis* lizards in particular—provide an attractive system for asking questions about the drivers of community diversity, because islands are isolated systems where communities are relatively simple with independent and bounded regional pools. Anoles are a highly diverse genus of neotropical arboreal lizards that have adaptively radiated on islands in the Caribbean. The larger islands of the Caribbean each harbor an evolutionarily distinct anole fauna, with members that sort ecologically into communities across various biogeographic regions of each island (Frishkoff et al., 2022; Losos, 2009; Muñoz et al., 2023). But the role of predation, rather than competition or food limitation, in controlling such insular anole communities has confounded ecologists for decades. Andrews (1979) initially proposed that top-down forces were of paramount importance for structuring anole communities, but only on the mainland, where predators are diverse. On the islands of the Caribbean, where predators are much less common, and anoles reach higher abundances, the supposition was that bottom-up forces dominate. This view was embraced by Wright (1981), who envisioned predation playing at best a minor role in the islands of the Caribbean, and where a dearth of avian competitors allowed high lizard abundances. However, Wright's interpretation of island diversity was vigorously contested by Waide and Reagan (1983) who noted a strong negative correlation between predator species richness and anole abundances across Caribbean islands. This negative correlation between predator diversity and abundance of their prey is supported by Buckley and Jetz (2007) who showed that on a global scale, lizard populations on small islands are denser than on larger islands, which in turn had denser populations than on the mainland. These trends were well explained by the number of predator species that occurred on the islands in question (although the effects of competition could not be ruled out).

Such broad-scale cross-island findings have been mirrored by population studies and experimental predator introductions on small islands in the Bahamas. In comparing islands of different sizes with different numbers of predatory birds, Schoener and Schoener (1978) found lower abundances and lower survival rates in anole populations where predators were more common, without a diminishment of body condition (as would be expected if competition were the driving mechanism). Likewise, introduction of predators on small experimental islands decreased the abundance of their anole prey, and even pushed populations toward extinction (Pringle et al., 2019; Schoener et al., 2005). Nevertheless, on similar small islands in the Panama canal, Wright (1979) and Wright et al. (1984) noted that variation in predator number seemed uncorrelated with anole survival. As a result of these conflicting findings to date, there is no consensus about the relative roles of predation, competition, and resource availability in structuring anole communities. However, when links between predator occurrence and lizard abundance have been investigated, findings of both macroecological and experimental studies have generally indicated a negative correlation between the two. Further, some experimental studies suggest a plausible role for anole predators in limiting species diversity, by pushing individual species toward local extirpation (Pringle et al., 2019).

Issues of scale, however, complicate the extension of these findings to communities more generally. Macroecological approaches typically compare estimates of lizard abundances taken at specific areas within an island to the number of predator species that occur on island-wide lists (or habitat-specific lists). Such an approach makes sense on small islands that effectively constitute a single "site" but could break down on larger ones, where environmental heterogeneity and spatial distance beget multiple ecologically independent predator and prey communities. As a result, in such macroecological studies, there is no direct causal link between predator number and lizard abundance, given that the full complement of predators need not occur at the specific location(s) where abundance was measured. This lack of connection in scale of observations casts some doubt on the pattern of negative correlation between predator richness and prey abundance documented in cross-island comparison studies, since larger islands will have more species (predator and otherwise) regardless of how many occupy local communities, and may also have higher lizard abundances due to some reason unrelated to predation.

Likewise, mechanistic studies on small islands (Calsbeek & Cox, 2010; Lapiedra et al., 2018; Piovia-Scott et al., 2019; Pringle et al., 2019; Schoener & Spiller, 1996) may not translate well to more diverse and non-bounded communities. These experimental islands' areas are typically less than 0.2 ha and tend to be extremely depauperate in comparison with communities on larger islands or the mainland—the types of communities where most lizards occur and interact with predators. Simplified vegetation, lack of refugia, and small populations may all make abundance declines and extirpations more likely on such islands in comparison to less severely bounded environments.

What is currently lacking is an understanding of the effects of predation on local diversity across large, multi-community landscapes that better exemplify the types of communities in which most organisms dwell. A finding that predator abundance negatively correlates with prey abundance across communities within islands would lend credence to top-down forcing of prey communities.

To fill this gap, we used fine-scale mark-recapture data on *Anolis* lizard communities conducted broadly across the large Caribbean islands of Hispaniola and Jamaica. We combined this with an eBird dataset spanning 10 years to quantify predatory bird occurrence across these islands to ask questions related to top-down versus bottom-up forcing between birds and lizards. Although anoles experience predation from snakes and mammals, they are primarily preyed upon by birds (Mclaughlin & Roughgarden, 1989; Poulin et al., 2001; Waide & Reagan, 1983; Wunderle, 1981). These birds range from specialists, such as lizard-cuckoos, to more generalist predators such as hawks and falcons, to opportunistic feeders such as kingbirds. We first assessed whether bird and lizard communities within islands show evidence of being driven by bottom-up energy availability such that features of the community correlate with aspects of climate that drive total energy availability. We next asked whether top-down effects of avian predators are apparent on anole community abundance within islands and, relatedly, whether predator occurrence promotes or limits species diversity. If predators play a large role in structuring lizard communities, as suggested by past macroecological work looking across islands, we expect that greater predation pressure would be associated with lower anole abundances. If such predation pressure affects all prey species similarly, it could push some to local extinction, decreasing diversity. Alternatively, if predation modulates dominant competitors, diversity should positively correlate with predation pressure, and prey community evenness should increase (Table 1).

TABLE 1 Summary of predicted correlations that would suggest effects of bottom-up and top-down ecosystem control.

Predictor	Lizard community trait	Association if bottom-up drivers are supported	Association if top-down drivers are supported
Predators	Abundance	Positive	Negative
	Species richness	Positive	Positive or negative
	Community evenness	Positive	Positive or negative
	H (Shannon index)	Positive	Positive or negative

METHODS

Lizard abundance

Between 2016 and 2018, we conducted mark-resight surveys across 40 plots spanning seven total sites in Jamaica, and 58 plots spanning 13 total sites in the Dominican Republic (on the island of Hispaniola), as described in Frishkoff et al., (2019, 2022). Plots were located either in forest or human-modified habitat, and sites varied in elevation and forest type within each island so as to broadly represent the full range of communities present. At each location, we surveyed multiple 15-m radius plots for all anole species for 2 h during the day and 2 h at night for three consecutive days. During each survey, an observer conducted a standardized survey walk covering the full area of the plot and recorded species identity of all observed *Anolis* individuals. Over the course of the six survey sessions in each plot, all lizards observed were marked with diluted, nontoxic, latex-based paint using an Idico "Duz-All" paint sprayer, allowing observers to identify resighted versus new individuals (Heckel & Roughgarden, 1979).

We estimated the species richness and abundance of the anole community in each plot in the Dominican Republic and Jamaica using a mark-resight model, which accounts for variation in detection probability, differences in observers, and the time of day that the surveys were conducted (Frishkoff et al., 2019, 2022). When estimating abundance, the model also incorporated the effects of mean annual temperature, mean annual precipitation, canopy cover, and interaction terms. Independent models were run to estimate anole community abundance on Jamaica, and in the Dominican Republic. The mark-resight model was fit using a Bayesian framework with JAGS (v 4.2.0) in R (v 3.4.4). For more detailed model descriptions see Frishkoff et al. (2019, 2022).

Plot-level abundance was obtained by summing the estimated number of individuals for each anole species along each iteration of the posterior, and then using the posterior mean to summarize the distribution. Likewise, species richness was obtained by summing the number of species present in the plot along each iteration of the posterior (all species with abundance of 1 or greater) and again taking the mean of the posterior as a point estimate.

Predation pressure

To quantify bird predator occurrence, we used observation data from checklists submitted to eBird for species that are known to prey on lizards (eBird, 2021). All potential lizard predators were species that opportunistically feed on anoles and were determined by considering the diet of the bird species listed by the Cornell Lab of Ornithology's research platform Birds of the World (Billerman et al., 2022). Dominican naturalist Miguel Landestoy also provided insight into the importance of certain Dominican species as predator of anoles, based on personal observation.

We looked at all eBird checklists for Jamaica and the Dominican Republic from August 2010 to August 2020, filtered to include both stationary and traveling checklists (omitting incidental observations), with a maximum of 5 h duration, 10 observers, and 10 km distance. All data were accessed in September of 2020. These checklists were treated as presence–absence data (i.e., we assumed that all species not listed were not observed).

We then used a general additive model with a binomial error distribution to model the probability of each bird species being present throughout Jamaica and the Dominican Republic, granting us the ability to predict presence probability in the vicinity of each lizard plot location. Specifically, we modeled bird presence based on the WorldClim variables of mean annual temperature (bio1), temperature seasonality (bio4), annual precipitation (bio12), and precipitation seasonality (bio15) (Fick & Hijmans, 2017). We also included effects of checklist duration, location, number of observers, distance traveled, day of year the checklist was recorded on, and time of day at which observations began. All continuous variables were implemented with thin-plate splines, allowing the model to flexibly estimate the degree of curvature in the relationship between the variable and bird occurrence. In addition, we incorporated a two-dimensional thin-plate spline based on the latitude and longitude of the checklist to both account for spatial autocorrelation, and to incorporate any unmeasured environmental factors that correlate with space into predictions. Predictions of probability of occurrence were then made for each bird species at the plot locations where lizards were surveyed, at a grid cell resolution of approximately 1 km^2. To obtain standardized estimates of predation pressure, we considered a hypothetical eBird transect conducted by a single observer, lasting for 60 min, and spanning 1 km. Because bird occurrence varies between time of day and day of year, we made an ensemble of predictions for each plot location, evaluating hypothetical transects every hour on the hour between 4:00 am and 3:00 pm, for all days of the year. To summarize per-species predation pressure at each plot location, we considered the maximum probability of occurrence across all hours and across the entire year, under the theory that this value best represents true occurrence probability (whereas lower values may be primarily influenced by detection probability from nonideal times of day for sighting the species in question). In addition to using maximum summed predator occurrence, we also considered mean occurrence, but downstream results were qualitatively similar, and so we present only the maximum. These summed predator occurrence values can essentially represent the expected species richness of avian predators along a hypothetical 1 km transect, and we refer to our measures of predation as predator occurrence. While we use data from the Dominican Republic, we discuss our results in the context of the entire island of Hispaniola.

We used four complimentary sets of bird species to analyze predator occurrence (Appendix S1: Tables S1 and S2). First, we considered all potential lizard predators, second all specialized lizard predators, third all birds of prey, and fourth all pigeon species. Our first category comprised all potential lizard predators, including opportunistic feeders. The specialized predatory bird category was a subset of the first, including only species for which lizards are likely a main dietary component. We then created a subset of this category which only included specialized predator species that are also birds of prey. This taxonomically restricted set was chosen to represent a group that is known to prey on vertebrates and may impose especially clear signatures on community structure. In contrast, our final category included all pigeons, which are not predators (or competitors) with anoles and thus serve as a neutral "control" group, for which we would not expect to observe any signal from either top-down or bottom-up forces. Analysis of pigeons thus allows us to more accurately interpret whether any observed effects are due to predator species per se, or just correlation with general bird presence. To obtain total predator occurrence, we summed the individual occurrence values for all bird species in each category (i.e., all potentially predatory birds, all specialized predatory birds, all birds of prey, and all pigeons [non-predatory control]). These probabilities of predatory bird occurrence provided us with quantitative estimates of predation at a comparable spatial and temporal scale as the lizard community data.

We first evaluated the effects of climate on both predatory bird occurrence and anole community richness. To do this, we fit a linear mixed-effects model for anole species richness, as well as total predator occurrence. For these models, we included mean annual temperature and mean annual precipitation as fixed effects, with site (where three to six plots were grouped) as a random effect.

To identify differences between islands for our species groups, we first compared anole community metrics and predator occurrence between Jamaica and Hispaniola. We assessed the difference between mean estimates using mixed-effects models with island identity as a fixed effect and site as a random effect. We used this same method to test for differences in anole abundance and species richness between forest and human-modified habitats, substituting habitat type for island identity as the fixed effect.

To evaluate whether greater predator occurrence is associated with increased or decreased lizard community metrics, we fit linear mixed-effects models for anole abundance, species richness, evenness, and Shannon diversity (H). Abundance was square-root-transformed to fulfill model assumptions of residual normality. Since all other community metrics were normally distributed, they were not transformed. Predictor variables included our metric of predator occurrence, habitat type (i.e., forest or human-modified), and island identity as fixed effects, with site as a random effect. Predator occurrence was included as a quadratic fixed term to allow for the possibility of a curvilinear relationship. We also included two fixed interaction terms. One accounted for potential interactions between habitat type and island, thereby allowing the effect of deforestation on anole community structure to differ between Hispaniola and Jamaica. The second was an interaction effect examining differences in the way predation pressure affected anole communities on the two islands. Hispaniola is larger than Jamaica, reaches higher elevations, and has a larger regional species pool of both lizards and birds. While we do not specifically test for these effects on the bird-lizard relationships, we include this term to allow us to control for any such differences. We also included mean annual temperature and mean annual precipitation to control for climate. Although we used these same climate variables to predict the presence of our predator species as well as anoles, we modeled each species individually, allowing for differences in how each species responds to climate. As a result, when summed together, species occurrence/abundance patterns should not correlate with climate unless there is a real biological signal that emerges because of the independent associations of many species together. Including climate variables in our secondary mixed-effects model ensured that we control for biologically relevant climate effects when testing for a relationship between summed predator occurrence and anole community diversity. Failing to do so would risk spuriously reporting predation effects on characteristics of the anole community, when in fact climate is ultimately driving such trends. We conducted backward model selection, dropping each term until only significant ones remained. The p values reported are those comparing model fitness with and without the relevant term using a likelihood ratio test (evaluated against a χ^2 distribution using the "drop1" function in R (R Core Team, 2023). Model estimates reported are the slope coefficients of terms from the mixed-effects model. In addition to plotting trends based on our full models, we also visualized the marginal effect of each bird category, using partial dependence plots created with the "effects" package in *R* (Fox and Weisberg, 2018; Fox and Weisberg, 2019). All modeling was done in R 1.4.1103 and marginal r^2 values for all models were calculated using the partR2 package (Stoffel et al., 2021).

RESULTS

Across the surveyed plot locations in Jamaica and Hispaniola, total predator occurrence ranged from 1.84 to 7.53 predators/plot (Figure 1). This range was driven by variation on Hispaniola, whereas Jamaica showed nearly a third less total variation in total predator occurrence (3.22–7.17 predators/plot). On average, total predator occurrence was similar in Jamaica (5.42 ± 0.20 predators/plot; mean ± SE) and Hispaniola (4.62 ± 0.21 predators/plot, $p = 0.21$), despite Hispaniola having 31 predator species regionally and Jamaica only 23 (Appendix S1: Tables S1 and S2). For mapped distributions of bird occurrence for our other bird categories, see Appendix S1: Figures S1–S3.

When considering only specialized predators, occurrence of these species ranged from 0.35 to 3.15 on Jamaica, and from 0.37 to 2.88 on Hispaniola. Like our measure of predation pressure that included opportunistic species, Jamaica was similar to Hispaniola not only in average predator occurrence (1.50 ± 0.12 vs. 1.18 ± 0.08, respectively, $p = 0.29$) but also had similar regional predator occurrence (10 species in Jamaica and 11 on Hispaniola). We found no difference between islands when only considering birds of prey, with average bird of prey occurrence being 0.51 ± 0.04 birds of prey/plot on Hispaniola, and 0.53 ± 0.04 birds of prey/plot in Jamaica ($p = 0.91$).

Across all plots, lizard abundances and community richnesses were similar between islands. In our 15-m radius (706 m^2) plots in Jamaica, the mean abundance was 65.39 ± 9.19 lizards/plot, compared with 53.95 ± 6.13 lizards/plot in Hispaniola ($p = 0.44$). The islands also did not differ when comparing species richness of local communities. Species richness in both Jamaica and Hispaniola was slightly less than four species (3.55 ± 0.29 species/plot and 3.63 ± 0.20 species/plot, respectively, $p = 0.63$).

Mean species richness of anole communities also did not differ between human-modified and forested plots (3.34 ± 0.27 species/plot and 3.76 ± 0.21 species/plot, respectively, $p = 0.08$), but anole abundance was significantly higher in forested plots (71.92 ± 7.58 anoles/plot) than in plots that were human-modified (40.40 ± 5.68 anoles/plot, $p < 0.01$).

We assessed the relationship between climate and the presence of both anoles and bird predators independently. Species richness of anoles was positively associated with mean annual temperature (slope coefficient = 0.24, $p < 0.01$; Figure 2A) and negatively associated with precipitation (slope coefficient = −0.001, p-value < 0.01). Similar patterns were found for anole abundance: a positive relationship with temperature (slope coefficient = 0.42, $p < 0.01$) and a negative relationship with precipitation (slope coefficient = −0.002, $p = 0.03$). Likewise, total

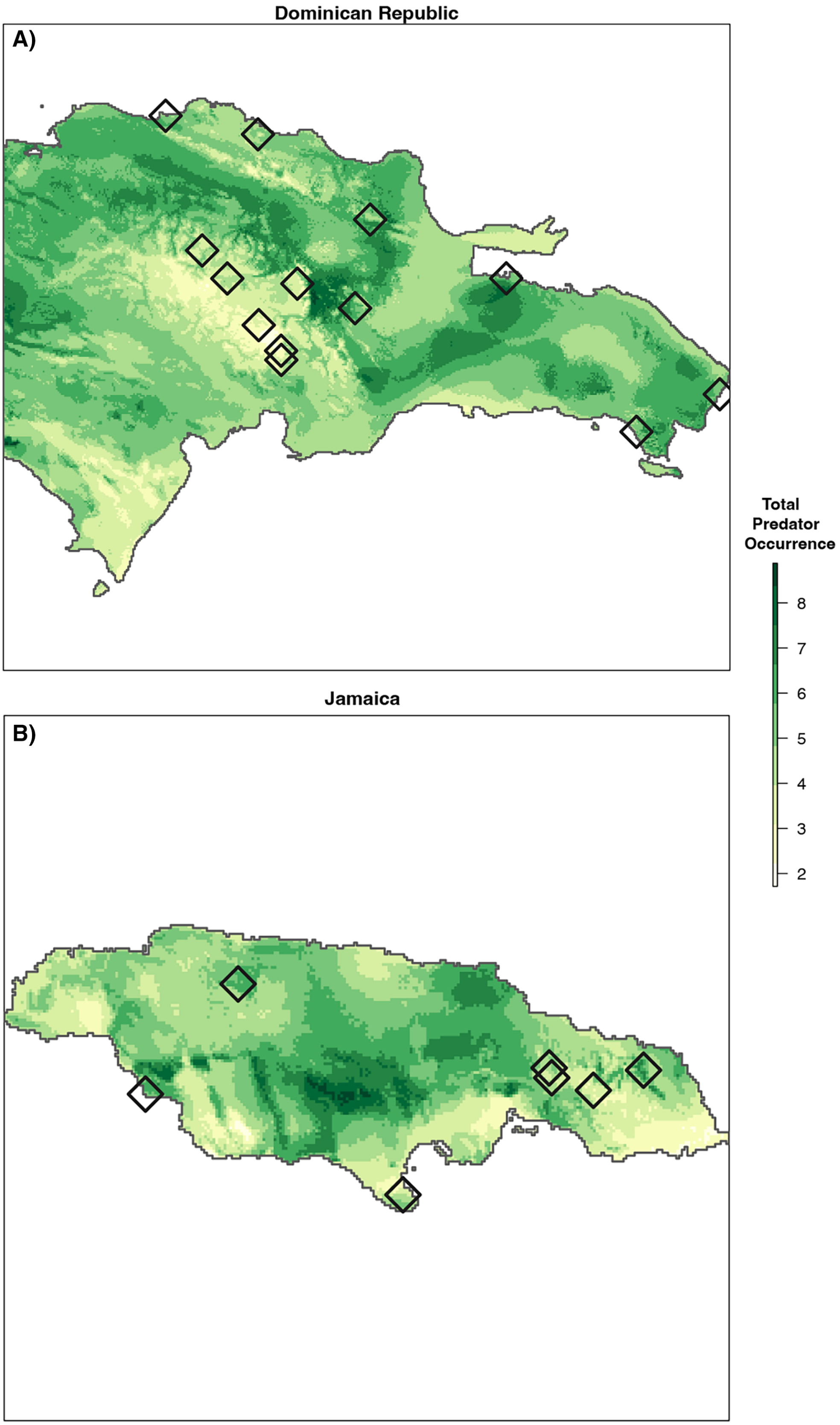

FIGURE 1 Within-island variation in total predatory bird occurrence on (A) Hispaniola and (B) Jamaica. Occurrence is modeled as the sum of the probabilities of presence of all predatory birds. For the island of Hispaniola, only the Dominican Republic is shown here, as birds found only in Haiti were not included in our study. Darker shades show higher estimated values of predator occurrence, and diamonds represent our study locations.

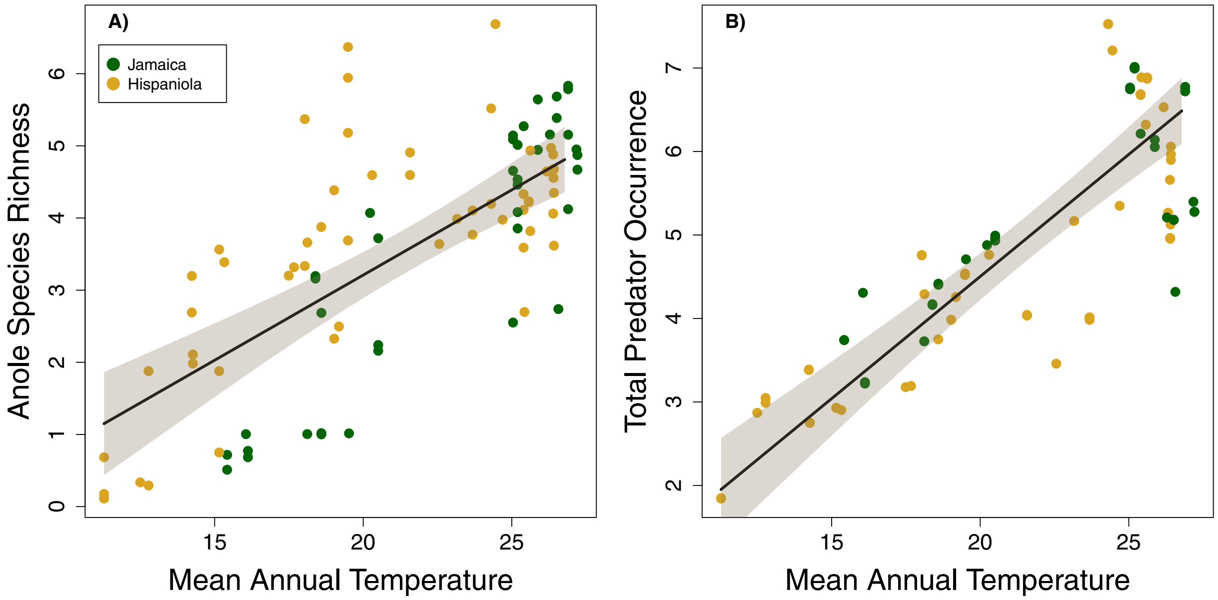

FIGURE 2 The correlation between mean annual temperature and (A) anole species richness and (B) total predator occurrence. The trendlines are predicted using mixed-effects models from data across both islands, and confidence intervals are represented by the area in gray.

predatory bird occurrence was also positively correlated with mean annual temperature (slope coefficient = 0.29, $p < 0.01$; Figure 2B) and its relationship with mean annual precipitation trended positive (slope coefficient = 0.001, $p < 0.01$). While total predator occurrence correlated with macroclimate temperature, there was still substantial residual variation in the relationship, allowing for the potential to detect independent effects of predation and climate on lizard communities.

Predation and anole abundance

We found a curvilinear relationship in which anole abundance was low in areas with low total predator occurrence, then increased as the number of predator species increased, and then decreased after crossing a threshold of predator occurrence (predator slope coefficient = 5.50, $p = 0.02$; predator^2 slope coefficient = −0.56, $p < 0.01$; island × predator slope coefficient = 1.10, $p = 0.02$; Figure 3A). This initially positive relationship became negative after a total predator occurrence of 5.84 on Jamaica, and 4.94 on Hispaniola. In terms of island area, 27% of Jamaica and 58% of Hispaniola fell above their corresponding predator diversity thresholds, indicating that the negative consequences of predation were more prevalent on Hispaniola. Anole abundance had similar quadratic relationships with specialist predator occurrence as with total predator occurrence; however, we found a steeper decline at higher specialist predator occurrence (predator slope coefficient = 10.11, $p < 0.01$; predator^2 slope coefficient = −2.60, $p < 0.01$; Table 2; Figure 3B) than when considering total potential predators (seen in the relative strengths of the predator^2 slope coefficients). A decrease in abundance at higher predator occurrence was especially clear when the predators were birds of prey. Occurrence of birds of prey was a monotonically negative predictor of anole abundance (predator slope coefficient = −2.50, $p = 0.01$; Table 2, Figure 3C) such that sites with more birds of prey were always associated with lower abundances of anoles. When considering pigeons, we found a similar curve-shaped relationship to that between total predator occurrence and abundance of anole communities (pigeon slope coefficient = 5.24, $p < 0.01$; pigeon^2 slope coefficient = −0.75, $p < 0.01$; Table 2, Figure 3D), but with less downward curvature than the responses to true predators. In other words, as the number of pigeons in a region increases, anole abundance stabilizes but does not actually begin to decline like it does with predator occurrence.

Predation and anole species richness

Areas with greater total predator occurrence were associated with more anole species (predator slope coefficient = 2.45, $p = 0.01$; predator^2 slope coefficient = −0.19, $p < 0.01$; island × predator slope coefficient = 0.48,

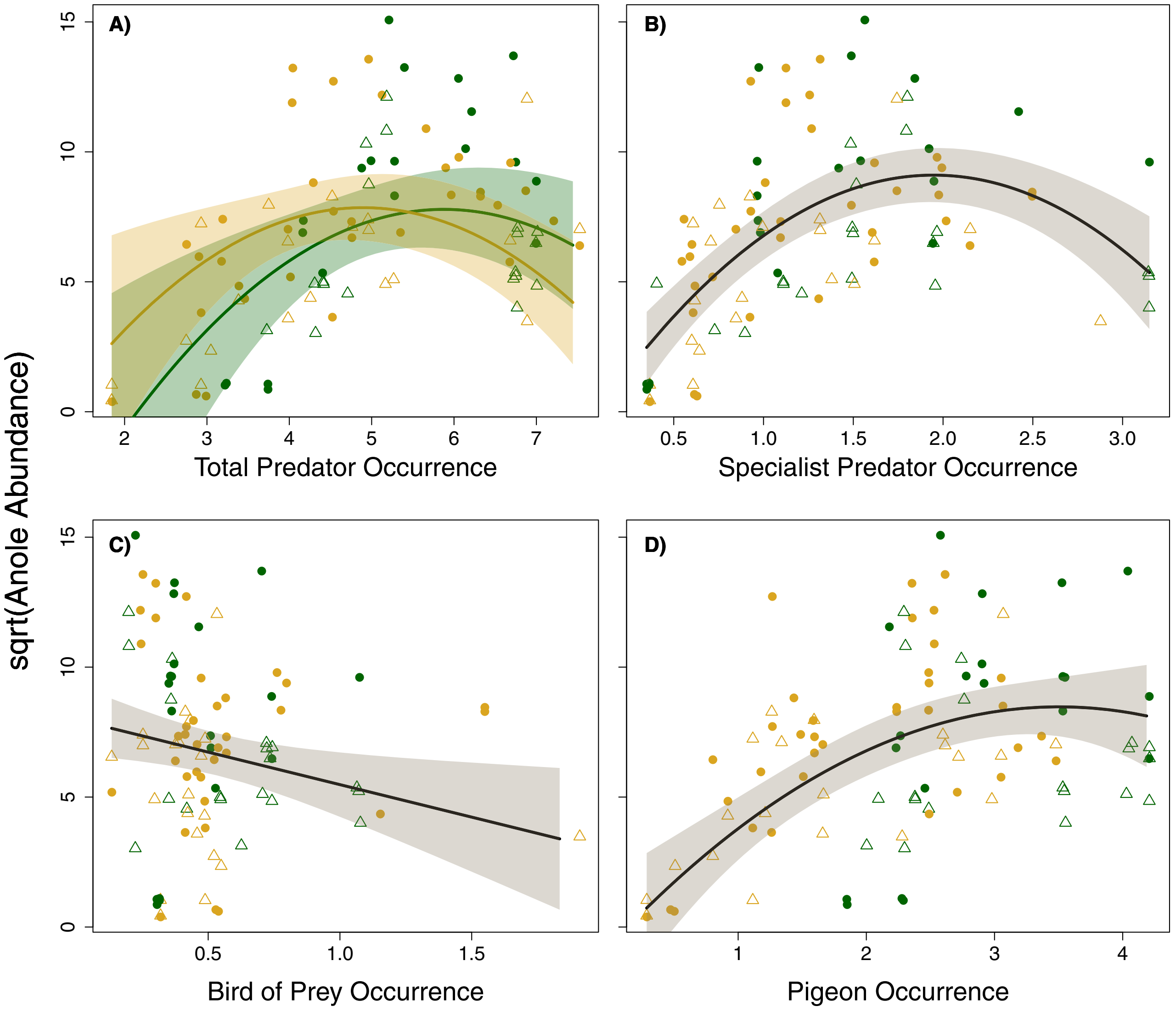

FIGURE 3 Changes in anole abundance as a function of increasing occurrence of (A) total predators, (B) specialized predators, (C) birds of prey, and (D) pigeons. Solid circles represent forested plots, and open triangles represent human-modified plots. Jamaica and Hispaniola are shown in green and gold, respectively. In (A), the different islands showed different relationships between the occurrence of all predators and anole abundance. The shaded area displays the confidence intervals of the modeled relationships. Trend lines are modeled using linear mixed-effects models. For trend lines representing the effects of our bird categories only, see partial dependence plots in Appendix S1: Figure S6.

$p = 0.01$; Table 2), but as with abundance, this relationship began to level off at higher total predator occurrence (Figure 4A). Anole species richness also increased as specialized predator occurrence increased, but this relationship was slightly different between islands (Figure 4B). In Jamaica, the point at which species richness begins to decline is higher than in Hispaniola (predator slope coefficient = 1.45, $p < 0.01$; predator^2 slope coefficient = −0.59, $p = 0.01$; island × predator slope coefficient = 1.33, $p < 0.01$; Table 2). We did not find a relationship between anole species richness and occurrence of birds of prey ($p = 0.15$; Table 2, Figure 4C), or pigeon occurrence ($p = 0.07$; Table 2, Figure 4D).

Predation and anole community evenness

Anole community evenness increased with total predator occurrence, but this relationship leveled off at higher total occurrence of predators (predator slope coefficient = 0.41, $p < 0.01$; predator^2 slope coefficient = −0.03, $p < 0.01$; island × predator slope coefficient = 0.11, $p < 0.01$; Table 2; Appendix S1: Figure S4a). Specialized bird predators showed a curvilinear relationship with evenness as well (predator slope coefficient = 0.19, $p < 0.01$; predator^2 slope coefficient = −0.09, $p = 0.04$; Table 2; Appendix S1: Figure S4b), but this differed between islands, in a similar way to when we considered

TABLE 2 All model summary outputs for linear mixed-effects models, including marginal r^2 values for each full model, calculated using the partR2 package in R.

Lizard community trait	Predator group	r^2 marginal	Intercept	Jamaica	Forest	Forest × Jamaica	Predator group	(Predator group)^2	Predator × Jamaica	MAT	MAP
AB	All pred. birds	0.51	−12.78	−6.01	1.90	…	5.50	−0.56	1.10	0.29	…
SR	All pred. birds	0.66	−1.89	−2.84	0.42	…	2.45	−0.19	0.48	…	−0.001
EV	All pred. birds	0.53	−0.24	−0.79	−0.19	0.28	0.41	−0.03	0.11	…	−0.0001
H	All pred. birds	0.61	−0.25	−0.95	−0.18	0.32	0.53	−0.04	0.14	…	−0.0003
AB	Specialized pred. birds	0.56	1.88	1.45	1.89	…	10.11	−2.60	…	…	−0.003
SR	Specialized pred. birds	0.66	−2.06	−2.33	0.42	…	1.45	−0.59	1.33	0.23	…
EV	Specialized pred. birds	0.50	−0.04	−0.53	−0.19	0.27	0.19	−0.09	0.21	0.03	…
H	Specialized pred. birds	0.60	−0.45	−0.77	−0.18	0.31	0.24	−0.13	0.35	0.06	…
AB	Birds of prey	0.48	−3.10	…	3.73	…	−2.50	…	…	0.47	…
SR	Birds of prey	0.61	−0.25	…	0.37	…	…	…	…	0.24	−0.001
EV	Birds of prey	0.44	−0.19	−0.27	−0.20	0.28	0.49	−0.30	…	0.04	…
H	Birds of prey	0.56	−0.70	−0.33	−0.20	0.31	0.75	−0.52	…	0.07	…
AB	Pigeons	0.48	3.86	…	1.71	…	5.24	−0.75	…	…	−0.003
SR	Pigeons	0.61	−0.25	…	0.37	…	…	…	…	0.24	−0.001
EV	Pigeons	0.55	0.52	−0.88	−0.19	0.26	0.39	−0.06	0.23	…	−0.0002
H	Pigeons	0.62	0.97	−0.32	−0.17	0.28	0.32	…	…	…	−0.0005

Note: Models show the effects of our predatory (pred.) bird groups as well as pigeons on lizard community abundance (AB), species richness (SR), evenness (EV), and Shannon diversity (H). We include mean annual temperature (MAT) and mean annual precipitation (MAP) to control for the varied effects of climate on all species considered. Final models were obtained using backward model selection until all terms were significant.

the effects of these predators on anole species richness. In Jamaican communities, evenness tended to decrease at much higher specialized predator occurrence than on Hispaniola (predator × island slope coefficient = 0.21, $p < 0.01$; Table 2). On the other hand, bird of prey occurrence had similar effects on both islands, with anole community evenness increasing initially and then decreasing at higher bird of prey occurrence (predator slope coefficient = 0.49, $p = 0.04$; predator^2 slope coefficient = −0.30, $p = 0.03$; Table 2; Appendix S1: Figure S4c). Pigeon occurrence showed a positive but curved relationship with evenness (pigeon slope coefficient = 0.39, $p = 0.01$; pigeon^2 slope coefficient = −0.06, $p = 0.03$; island × pigeon slope coefficient = 0.23, $p = 0.01$; Table 2; Appendix S1: Figure S4d).

Predation and anole Shannon diversity (H)

The relationships between our bird occurrence measures and Shannon diversity were similar to those of bird occurrence and community evenness. Total predator occurrence was generally correlated with higher H values, and this effect was strongest in Jamaica, which experienced a steeper increase in diversity with total predator occurrence (predator slope coefficient = 0.53, $p = 0.01$; predator^2 slope coefficient = −0.04, $p = 0.01$; island × predator slope coefficient = 0.14, $p = 0.01$; Table 2; Appendix S1: Figure S5a). Specialized predator occurrence had a similar effect on H in Jamaican communities (predator slope coefficient = 0.24, $p < 0.01$; predator^2 slope coefficient = −0.13, $p = 0.04$; Table 2; Appendix S1: Figure S5b), but Hispaniolan communities began experiencing decreasing H at lower specialized predator occurrence (island × predator slope coefficient = 0.35, $p < 0.01$). The effects of bird of prey occurrence on H also showed a quadratic relationship but began to decrease more rapidly than in our other predatory bird categories (predator slope coefficient = 0.75, $p = 0.03$; predator^2 slope coefficient = −0.52, $p = 0.01$; Table 2; Appendix S1: Figure S5c). Pigeon occurrence was linearly and positively correlated with anole diversity on

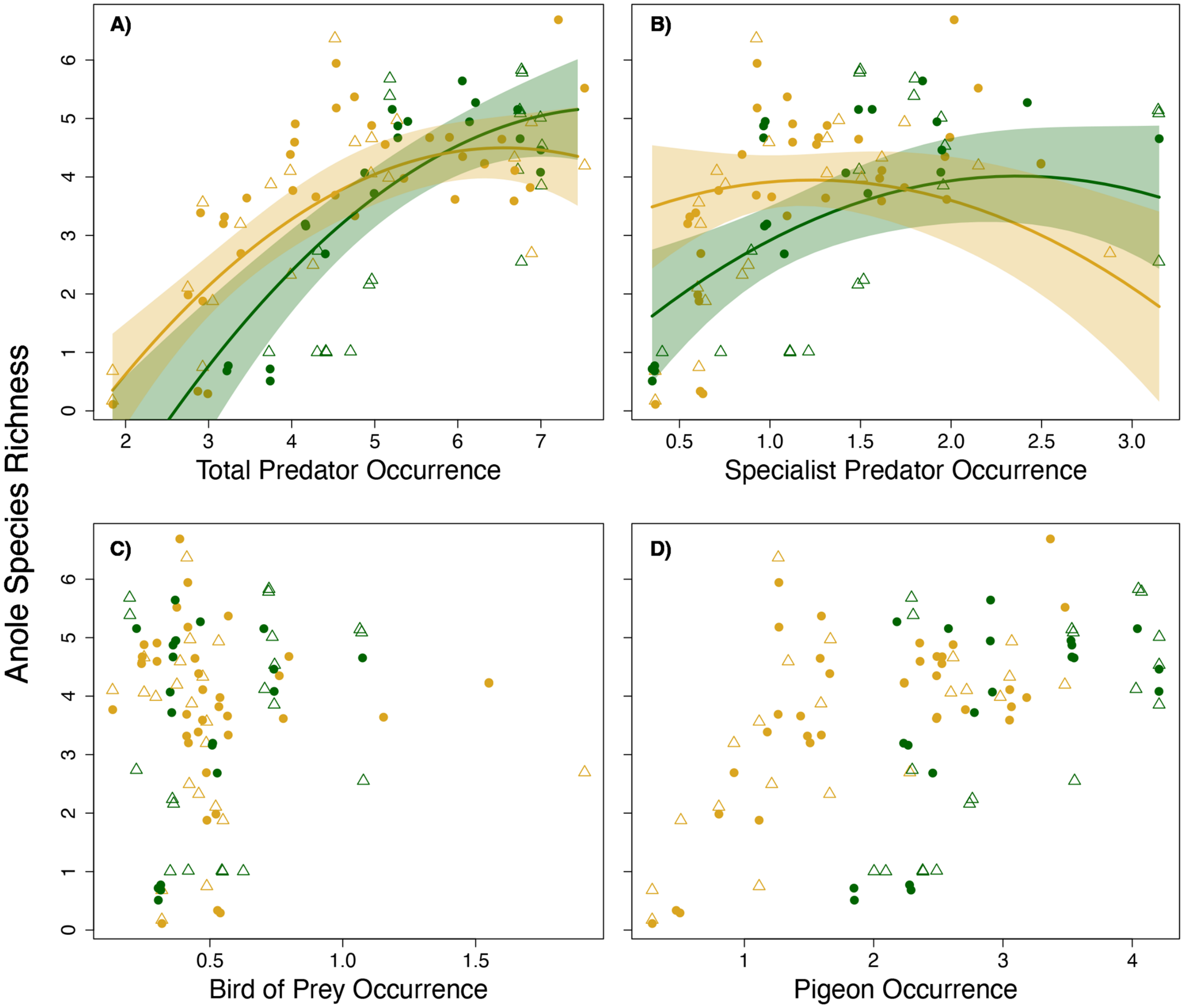

FIGURE 4 Effects of avian predator categories (and pigeons) on anole species richness. Plot attributes are the same as those in Figure 3. Trend lines are not shown in (C) and (D) due to the nonsignificant effect of bird of prey or pigeon occurrence on anole species richness. Partial dependence plots can be found in Appendix S1: Figure S7.

both islands (pigeon slope coefficient = 0.32, $p < 0.01$; Table 2; Appendix S1: Figure S5d).

Partial dependence plots showing the individual effect of each bird category on each anole community metric can be found in the supplemental material (Appendix S1: Figures S6–S9). These plots show the effect of each bird category while holding other model variables constant.

DISCUSSION

Our findings suggest that climate plays a major role in dictating anole community diversity and that bottom-up forces predominate on the islands of Jamaica and Hispaniola such that both bird and anole richness are strongly correlated with mean annual temperature (a proxy for ecosystem productivity). Further, bird occurrence, and lizard abundance lizard diversity all generally increased together, suggesting that more lizards are likely present in areas with more bird predators because of environmental suitability. Climate variables were consistently strong predictors of anole abundance and diversity in all models. Forested habitats were also always associated with higher abundance of anoles, suggesting again that climate and resource availability play a key role for diversity and that bottom-up drivers are prevalent within these islands. Interestingly, however, abundance and species richness tended to decline at very high predator levels, whereas with pigeons these values only stabilize. This suggests that while many of the effects of top-down forces are overwhelmed by bottom-up ones, abundance and species richness are lower than would otherwise be expected when predator incidence is very high.

Our observation that more lizard individuals and more bird species are present in areas where there is higher resource abundance is consistent with the hypothesis that bottom-up forces drive diversity. Favorable environmental conditions promote abundance at lower trophic levels, which thus allow for greater abundance and diversity of consumer species. Indeed, productivity has been used as an indicator of resource availability in community ecology (Evans et al., 2005; Novosolov et al., 2016). Higher temperature and precipitation are tied to ecosystem productivity and are shown to drive an increase in plant biomass and can also sustain a larger arthropod population (Bragazza et al., 2015; Haddad et al., 2001; Siemann, 1998; Wenninger & Inouye, 2008). Lizards rely on vegetation for microhabitat and arthropods for food. A greater abundance of these resources would therefore support a greater abundance of anoles (Higgins et al., 2021). Under bottom-up control, this higher resource availability would also allow for greater abundances of bird species (both lizard predators and insectivorous competitors, as well as granivores and frugivores that do not interact with lizards).

While our findings suggest that diversity is driven by bottom-up forces, we also see some potential signatures of top-down effects on abundance. As predator occurrence increased, so did anole abundance, but only up to a point. As predator occurrence became higher still, we began to see a negative relationship with increasing predator occurrence and abundance. This relationship was evident when opportunistic predators were included in our measure of predation but was more pronounced when we considered only specialized predators. Most opportunistic feeders of anoles are insectivores, so when these species were included in our measure of predation pressure, the negative effects of predator occurrence on anole abundance were still evident, but not as distinct. As we limited predator species further to birds of prey, anole abundance and occurrence of birds of prey showed a strong negative correlation, with no signature of bottom-up control. Birds of prey may have especially strong effects on anole communities due to natural histories that are specialized for preying on vertebrates. This effect on abundance likely explains the mechanism behind the observed reductions in evenness and overall diversity at sites with more birds of prey.

Interestingly, Hispaniola had a much greater proportion of area that showed negative effects of predation on anole abundance (58% compared with 27% of Jamaica). Yet on average, Hispaniola and Jamaica did not differ in modeled predator occurrence at individual sites. A possible explanation for this could be that Hispaniolan predators are more efficient at prey capture and consumption. Hispaniola is also a much larger island than Jamaica. Previous studies have suggested that larger islands more closely approximate the mainland and that mainland communities are more strongly governed by top-down predator controls (Andrews, 1979; Schoener & Schoener, 1978). Our finding that Hispaniola has more land area where abundance has a negative relationship with predator occurrence is consistent with this hypothesis.

Although abundance was impacted by high predator occurrence, this did not necessarily always have a negative impact on community diversity. Species richness, evenness, and overall diversity (H) tended to increase and then level off with increased predator occurrence (as with abundance), or show no relationship with predator occurrence at all. The abundance of anoles was always lower at sites with more birds of prey, yet bird of prey occurrence did not seem to be affiliated with lower or higher species richness values. This suggests that even when considering species that reduce anole abundance the most, these effects may still not be strong enough to prevent or promote species coexistence on these islands.

While our study focuses on patterns regarding birds, there are also other species that prey on anoles. Snakes, bats, and introduced mammals such as rats and mongooses all prey on lizards and were not considered in this study. Other potential predators include large spiders and *Solenopsis* ants which feed on anole eggs (Andrews & Rand, 2022; Reyes-Olivares et al., 2020). While lists of mammal and snake occurrence on these islands as a whole exist, our study focused on birds because they are often considered primary predators of anoles (Mclaughlin & Roughgarden, 1989; Poulin et al., 2001; Waide & Reagan, 1983; Wunderle, 1981). In addition, the eBird platform provides timed and tracked presence–absence surveys of bird communities at a local scale. As a result, our measures of bird predation may be lower overall than what lizards likely experience from all predator sources. Hispaniola has more species of potentially lizard-consuming snakes than Jamaica (18 and 8 respectively; Caribherp, 2024; Landestoy, 2023), but fine-scale data on local coexistence are limited, so this does not necessarily guarantee that snake occurrence is greater at individual sites. Our analytical approach represents an improvement over previous whole-island predator lists in that it estimates probability of predator occurrence at the local scale. However, the ideal metric of predation pressure would incorporate local predator abundance and then further integrate information on per capita predator effects on prey. Unfortunately, our preliminary examinations of eBird data with abundance-based models resulted in convergence issues, or extreme predictions, potentially due to high variance in observed abundance in some checklists. As such, eBird and similar databases at best represent an imperfect substitute for broad-scale time and area-standardized ecological surveys.

Our results support previously reported negative correlations between anole abundance and predation pressure (Buckley & Jetz, 2007; Calsbeek & Cox, 2010; Pringle et al., 2019; Waide & Reagan, 1983). However, we found no evidence that predation pressure reduces anole community diversity or leads to local extirpation or declines in species richness. Previous work has shown reduced coexistence between species in the presence of predators, contrary to our findings (Pringle et al., 2019). The reason for this divergence is likely in part due to the differences in focal scale between past studies and our own analyses. Many past studies focused on small, bounded, experimental islands, often finding that predation may quickly lead prey to go locally extinct (Pringle et al., 2019; Schoener & Spiller, 1995). On much larger islands, however, there are more opportunities for species to find refuge, which may mitigate a predator's impact on prey abundance and therefore extinction (MacArthur & Wilson, 1967).

CONCLUSION

Our study utilized a large dataset of bird detections spanning several years and combined this with local *Anolis* community surveys in a variety of habitat types on two large Caribbean islands. This method allowed us to examine community properties across individual islands, at a scale in which individual species co-occur. We discovered a curvilinear relationship in which anole abundance and predator occurrence increase together, suggesting bottom-up ecosystem control at low to moderate diversities of predators. As predator occurrence increases further, we begin to see negative effects of predators on anole abundance such that lower abundances of anoles occur at sites with increasingly more predators. Despite the large sample size of predator and lizard observations across these islands, we failed to detect a strong or consistent signal of predators diminishing lizard species richness. Instead, correlations between predator occurrence and lizard community diversity tended to be positive, suggesting that bottom-up ecosystem controls drive the presence of both anoles and their avian predators, mitigating the negative effects they might have on their prey, until predator occurrence reaches high levels. While bottom-up forces appear to be the dominant driver of anole diversity, birds of prey specifically may have especially negative consequences for anole community abundance, although they did not have an effect on species coexistence—perhaps because they predominantly prey on abundant species. These findings point to an important knowledge gap related to the way that predation pressure manifests at different scales. Irrespective of predation, climate repeatedly emerges as a significant predictor of diversity, suggesting that bottom-up control of communities is the primary driver of variation in diversity on these islands. While species interactions may play a role in structuring some aspects of communities, our data suggest that ultimately resource availability is required for high levels of biodiversity.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Folfas et al., 2024) are available from Figshare: 10.6084/m9.figshare.27183549.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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