# Lizard species evenness but not abundance tracks with avian predator occurrence across island communities

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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, but can alternatively diminish or enhance community diversity of prey species. But if bottom-up ecosystem controls predominate, variation in predation 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 have frequently invoked the importance of predator occurrence 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, either by way of competition or bottom-up forces. If top-down control predominates generally, then negative correlations between prey abundance and predator occurrence should emerge within islands, as well as across islands. Using survey data from eBird, we inferred landscape-level bird presence for all species on the islands of Jamaica and Hispaniola. By summing occurrence probability of 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 predation pressure, as well as anole abundance and species richness increasing with mean annual temperature. While predator occurrence was uncorrelated with anole abundance, it was positively correlated with anole species richness. These findings suggest that despite past research showing that islands with more predators tend to have lower abundances of prey, within islands, top-down forces of predation may not be strongly limiting community diversity. Instead, bottom-up forces linked with climate may be more important drivers of diversity in both lizards and their avian predators.

#### 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, or resource restriction due to competition. Such forces are often divided into those related to restriction in 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 the focal population by predators). The potential for top-down forces to establish ecosystem structure has become increasingly clear over time (Hairston et al. 1960, Estes et al. 2011, Ripple and Beschta 2012, Pringle et al. 2019), but the relative strengths of top-down versus bottom-up forces varies depending on the individual ecosystem and focal trophic level within it making generalizations difficult so far (Hairston et al. 1960, Hunter and Price 1992, Denno et al. 2005). Current evidence suggests that at global and regional scales, species diversity 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 and Roslin 2007).

Complicating matters, top-down forces such as predation, parasitism, and disease can both promote and limit diversity (Sih et al. 1985, Sinclair and Krebs 2002). The addition of predators to a community generally has a negative impact on the population size of its prey (Sih et al. 1985), which then scales up to impact prey community structure. But how this scaling works varies depending on food web structure. Over-consumption of a species can cause it to go extinct, thereby reducing diversity (Medina et al. 2011, Doherty et al. 2016). Additionally, predation may decrease coexistence by increasing competitive pressure for resources like refuges, or foraging availability in predator-free space (Hixon and 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 species richness of a community (Gurevitch et al. 2000, Canter et al. 2018). Doing so often decreases the species that would otherwise be most abundant, thereby increasing evenness between 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. On the one hand 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 increased predation.

In contrast to the multidirectional predictions elicited from top-down forcing on prey communities, the predictions generated from the bottom-up are relatively straight forward. In such cases, abundance and diversity would simply 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, 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 (Meserve et al. 2003, Báez et al. 2006). This work suggests that when food availability is high, consumer abundance will also be high (Guyer 1988, Wright et al. 2013, Wright et al. 2020).

Island lizards—and insular Anolis lizards particularly—provide an attractive system for asking questions about the drivers of community diversity, particularly because islands are isolated systems where communities have assembled independently and can thus be easily compared. 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 harbors an evolutionarily distinct anole fauna, with members that sort ecologically into communities across various biogeographic regions of each island (Losos 2009, Frishkoff et al. 2022). But the role of predation, rather than competition or food limitation, in controlling such insular communities has beguiled 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 more dense 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 abundance of their anole prey, and even pushed populations towards extinction (Schoener et al. 2005, Pringle et al. 2019). Nevertheless, on similar small islands in the Panama canal, Wright (1979, 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 predator, 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 towards local extirpation.

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). As such, there is no causal link between predator number and lizard abundance, given that the full complement of predators may 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.

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

Because macroecological studies and studies restricted to very small islands are the two primary research avenues used to assess predation in anoles, our knowledge of predation's role thus largely pertains to both very large scales (often with a mismatch in resolution of predator data and prey abundance data) and very small ones (with environmental characteristics that may be non-generalizable to non-bounded communities). What is then 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 use fine-scale mark-recapture data on *Anolis* lizard communities conducted broadly across the islands of Hispaniola and Jamaica in the Caribbean. We combine this with an eBird dataset spanning 10 years to quantify predatory bird presence across these islands in order to assess 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 predatory birds (Wunderle Jr. 1981, Waide and Reagan 1983, Mclaughlin and Roughgarden 1989, Poulin et al. 2001). These range from specialist species, such as lizardcuckoos, to more generalist predators such as hawks and falcons, to opportunistic feeders such as kingbirds. We first assess whether bird and lizard communities within islands show evidence of being driven by bottomup energy availability, such that these features of the community correlate with aspects of climate that drive total energy availability. We next ask whether top-down effects of avian predators are apparent on anole community abundance within islands, and relatedly, whether predator presence promotes or limits species diversity. If predators play a large role in structuring lizard communities as suggested by past macroecological work looking across islands, then we would expect that greater predation pressure would be associated with lower anole abundances. If such predation pressure is borne equally among prey species it could push some to local extinction, decreasing diversity. Alternatively, if predation modulates dominant competitors diversity would positively correlate with predation pressure, and prey community evenness would increase.

### Methods

# $Lizard \ abundance$

Between 2016-2018, mark-resight surveys were conducted across 40 plots spanning 7 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, Frishkoff et al. 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, multiple 15m radius plots was surveyed for all anole species for two hours during the day and two hours at night for three consecutive days. During each survey, an observer conducted a standardized survey walk around the plot and recorded species identity. Over the course of the six survey sessions in each plot, all lizards observed were marked with diluted, non-toxic, latex-based paint using an Idico "Duz-All" paint sprayer, allowing observers to identify resignted versus new individuals (Heckel and Roughgarden 1979).

We estimated 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, Frishkoff et al. 2022). When estimating abundance, the model also incorporated the effects of temperature, precipitation, canopy cover, and interaction terms. The mark-resight model was conducted 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 and Frishkoff et al. 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 presence, we used observation data from checklists submitted to eBird for species that are known to prey on lizards. All potential lizard predators included species that opportunistically feed on anoles, and were determined by considering the diet of the bird species listed by the Cornell Lab of Ornithology (https://birdsoftheworld.org/bow/home), or National Audubon Society (https://www.audubon.org/bird-guide). Miguel Landestoy also provided insight into the importance of certain Dominican Republic species as predator of anoles, based on personal observation.

We looked at all eBird checklists for Jamaica and the Dominican Republic from August 2010 – August 2020 and filtered to include both stationary and travelling checklists (omitting incidental observations), with a maximum of 5 hours 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 using 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, modeled bird presence was based on mean annual temperature (bio1), temperature seasonality (bio4), annual precipitation (bio12) and precipitation seasonality (bio15) obtained from WorldClim (Fick and Hijmans 2017), and also considered checklist duration, location, number of observers, distance travelled, day of year the checklist was recorded on, and time of day at which observations began. All continuous variables were implemented with thinplate 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 into predictions, and to incorporate any unmeasured environmental factors that correlate with space. Predictions of probability of occurrence were then made for each species at the plot locations where lizards were surveyed, at a resolution of approximately  $1 \text{ km}^2$  grid cells. To obtain standardized estimates of predation pressure we considered a hypothetical eBird transect conducted by a single observer, lasting for 60 minutes, 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 am and 3 pm, for all days of the year. To summarize per species predation pressure at each plot location we considered the maximum probability of presence 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 non-ideal times of day for sighting the species in question). In addition to using maximum predator occurrence we also considered mean occurrence, but results were qualitatively similar, and so we present only the maximum.

We used three complimentary sets of bird species to analyze predation pressure. First, we considered all potential lizard predators, second all cuckoo species, and third all pigeon species. The two taxonomically restricted sets were chosen to represent specialized lizard predators, and definitive non-predators respectively. Cuckoos in particular are important predators of anoles, and both islands have a specialized species of lizard-cuckoo. This led us to hypothesize that they might represent a group for which predation signals on community structure may be especially clear. In contrast pigeons 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 predatory birds, all cuckoos, and all pigeons [non-predatory control]). These probabilities of predatory bird presence provided us with quantifiable estimates of predation at a comparable spatial and temporal scale as the lizard community data.

To evaluate whether greater predator occurrence is associated with increased or decreased lizard community metrics we ran a linear mixed-effects model for anole species richness and abundance, the latter of which was square-root transformed to fulfill model assumptions of residual normality. Predictor variables included our metric of predator presence, habitat type (*i.e.*, forest or human-modified), and island identity, with site (where 3 to 6 plots were grouped) as a random effect. We included two interaction terms. One was a nuisance term to account 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 a hypothesis-driven interaction effect examining differences in the way predation pressure affected anole communities on the two islands. We also included mean annual temperature and mean annual precipitation to control for climate. We conducted backward model selection, dropping each term until only significant ones remained. All modeling was done in R 1.4.1103.

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image1.emf available at https://authorea.com/users/624538/articles/646839-lizard-speciesevenness-but-not-abundance-tracks-with-avian-predator-occurrence-across-islandcommunities

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image2.emf available at https://authorea.com/users/624538/articles/646839-lizard-speciesevenness-but-not-abundance-tracks-with-avian-predator-occurrence-across-islandcommunities Figure 1: Within-island variation in predatory bird presence on the Dominican Republic (a), and Jamaica (b). 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 predation pressure.

#### **Results:**

Across the surveyed plot locations in Jamaica and Hispaniola the combined probabilities of predatory bird species (essentially the expected species richness of avian predators along a hypothetical 1km transect) ranged from 2.36 to 8.00 (Figure 1). Predatory bird presence in the Dominican Republic had a wider range (2.36 - 8.0) than Jamaica, which showed less variation in predation pressure (3.67 - 6.71). On average, however, predator presence was statistically indistinguishable between islands (5.41 for Jamaica and 5.46 for the Dominican Republic; p-value = 0.83).

Across all plots, abundances of lizards were ~21% higher on average in Jamaica, with mean abundance in 15m radius (706 m<sup>2</sup>) plots of 65.39, compared to 53.95 in the Dominican Republic (p-value<0.001). Both islands were similar when comparing species richness of local communities. The average species richness on both Jamaica and the Dominican Republic was slightly less than 4 species (3.55 and 3.63, respectively, p-value = 0.83).

We first assessed the relationship between climate and the presence of both anoles and bird predators individually. Species richness of anoles was positively correlated with mean annual temperature (Spearman correlation coefficient = 0.70, p-value<0.001, figure 4b) and negatively with precipitation (Spearman correlation coefficient = -0.35, p-value<0.001). Similar patterns existed for anole abundance: a positive relationship with temperature (Spearman correlation coefficient = 0.60, p-value,0.001) and a negative relationship with precipitation (Spearman correlation coefficient = -0.29, p-value<0.001). In contrast, predatory bird occurrence was correlated only with mean annual temperature (Spearman correlation coefficient = 0.64, effect of temperature on abundance = 0.12, p-value<0.001,  $r^2 = 0.50$ ; Figure 2a) while its correlation with mean annual precipitation trended negative, but was non-significant (Spearman correlation coefficient = -0.14, p-value = 0.18,  $r^2 = 0.01$ ). While predation pressure correlated with climate 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.



Figure 2. The correlation between mean annual temperature and predator presence (a), and anole species richness (b). The trendlines are modeled from linear regressions.

To address the hypothesis that predation pressure is a significant driver of diversity, we tested whether anole

abundance, species richness, diversity (Shannon index), or evenness correlated with total avian predator pressure at a site. We first examined whether predator occurrence predicted these variables, while controlling for climate and allowing for differences in relationship between island and between forest and human-modified environments. We found a positive relationship between predation and lizard abundance only when climate was not included in the model (predation effect = 5.85, p-value<0.01, Fig 3a). When mean annual temperature and precipitation were included, this apparent relationship disappeared and more intense predation regimes had no correlation with greater numbers of individual lizards (p-value=0.11). Instead, lizard abundance simply increased with warmer temperatures (figure 3b), regardless of predation.

In contrast to the lack of effect of predation on abundance, areas with greater predator presence were associated with more anole species (predator effect = 1.72,  $r^2 = 0.33$ ; Figure 4a.) even while controlling for climate. While this trend was apparent on both islands, it was more extreme on Jamaica, which experienced a steeper increase in richness with predator presence (predator×Jamaica effect = 2.22, p-value= 0.04). This was also true when assessing diversity as the Shannon Diversity Index, for which predation pressure was generally correlated with more diverse communities, but for which this effect was strongest on Jamaica (predator×Jamaica effect = 0.36, p-value= 0.04). Areas with a higher diversity of predator species also had more even anole communities (predator effect = 0.31, p-value = 0.01; Figure 4b; see table 1 for all model outputs).

Specialized predators may have particularly strong effects on community composition of their prey. To assess this possibility, we repeated the analyses summing occurrence of cuckoos on both islands. Cuckoo presence on Jamaica ranged from 0.05 - 1.83, and was on average higher (mean = 0.81) than the Dominican Republic (mean = 0.41, p-value<0.001), where cuckoo presence ranged from 0.04 - 1.04. In contrast to our findings considering all predator birds, cuckoo presence positively correlated with lizard abundance (cuckoo effect = 2.18, p-value<0.001). We did, however, find that areas with the greatest cuckoo presence had more anole species (cuckoo effect on lizard richness = 0.90, p-value<0.001), higher values of anole diversity (cuckoo effect on h = 0.31, p-value<0.001), and greater anole community evenness (cuckoo effect on evenness = 0.17, p-value<0.001). In fact, cuckoo presence was a better predictor of abundance, evenness, and diversity than was climate, which dropped out of the models (Table 1).

When we repeated these analyses with pigeons (our non-predatory "control" group), we found no relationship with the abundance or species richness of anole communities (p-value=0.99 and 0.79 respectively. However, we found that the correlation with pigeons and anole diversity varied between islands: Jamaican anole communities exhibited a positive relationship with pigeon occurrence (Jamaica effect = 0.16), whereas the correlation was slightly negative in the Dominican Republic (DR effect = -0.03, interaction-term p-value=0.01). Finally, our results showed a significant relationship between pigeon presence and community evenness, however areas with more pigeons tended to have (very slightly) less even communities (effect = -0.04, p-value = 0.04), whereas for the true predators presence positively correlated with more even communities.



Figure 3. Changes in anole abundance has a positive relationship with increasing predator presence (a) when climate is not controlled for in the model. When climate is included in the model, this significant relationship between abundance and predator presence disappears, and anole abundance instead positively

correlates only with mean annual temperature, as illustrated in (b). The solid lines shows an overall higher average abundance in forested plots than in human modified habitats represented by the dashed line which is consistent between models.



Figure 4: Changes in species richness (a), and evenness (b) with increasing predator presence. Closed circles represent forested plots, and open triangles represent human modified plots. Jamaica and the Dominican Republic are shown in green and gold respectively.

Table 1. All model summary outputs for linear mixed effects models, including AIC and marginal  $r^2$  values for each model.

Lizard community trait	Max predator presence	AIC	$\mathbb{R}^2$ marginal	Intercept	Jamaica	Forest	Forest x Jamaie
AB	All pred. birds	450.66	0.47	-0.74		1.87	
$\mathbf{SR}$	All pred. birds	261.18	0.33	-1.63	-3.78	0.38	
$\mathrm{EV}$	All pred. birds	-48.76	0.47	-0.03	-0.16	-0.20	0.25
Н	All pred. birds	13.52	0.61	-0.26	-1.18	-0.18	0.29
AB	Cuckoos	445.31	0.50	7.75		2.08	
SR	Cuckoos	262.05	0.67	2.35	-0.71	0.41	
$\mathrm{EV}$	Cuckoos	-50.12	0.48	0.86	-0.26	-0.18	0.25
Н	Cuckoos	15.07	0.57	1.20	-0.32	-0.16	0.27
AB	Pigeons	373.89	0.29	0.02		2.33	
SR	Pigeons	212.82	0.30	0.78			
$\mathrm{EV}$	Pigeons	-105.69	0.32	0.66	-0.05	-0.18	0.12
H	Pigeons	-1.47	0.36	0.36	-0.42	-0.11	

# Discussion

Our findings suggest that climate plays a major role in dictating anole community diversity, and that bottomup forces predominate, such that both bird and anole richness is strongly correlated with mean annual temperature (a proxy for ecosystem productivity). Further, more lizard-specialized predator occurrence was positively correlated with anole community metrics, even more than climate effects, suggesting that these specialist predators may be exerting a stronger top-down effect. Nevertheless, top-down effects from predators seem to leave some signatures in anole communities. We found that areas with higher predator presence also tended towards higher evenness and greater overall diversity in anoles, whereas in general these relationships were not observed with pigeons, our non-predatory "control" group. Our finding that anole species richness was highest where bird predation pressure was highest could be interpreted either as support for bottom-up forces controlling bird occurrence, or as greater top-down pressure on dominant competitors facilitating higher lizard diversity (although, interestingly, without reducing total lizard abundance). Either way, it demonstrates no evidence that greater predator pressure results in a net loss of species richness, as would be expected in the case of extreme top-down forcing inducing local extirpation of prey species.

Our observation that more lizards and more bird species are present in areas where there is higher resource abundance is consistent with the idea 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 (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 (Siemann 1998, Haddad et al. 2001, Wenninger and Inouye 2008, Bragazza et al. 2015). Lizards rely on vegetation for microhabitat and arthropods for food, and a greater abundance of these would therefore support a greater abundance of lizards in these areas. 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 directly interact with lizards).

Our findings show that there are more avian predators and anole prey species in warmer climates. In these cases, predator presence and anole community richness appear to be dictated by resource availability and environmental suitability. This is especially true for cuckoo occurrence, which even when controlling for climate shows a strong positive correlation with anole community abundance. It is more likely that we could detect a direct bottom-up effect for these more specialized predators, since lizard abundance will be more limiting for them than for other predators that may also be consuming mammals, insects, amphibians, and birds in addition to lizards.

While our findings suggest that diversity is driven by bottom-up forces, some of our results can be interpreted as showing signatures of top-down effects that could be operating in conjunction. On both islands, we saw that areas with more intense predation also had lizard communities with higher evenness (Figure 3b). Interestingly, there did not appear to be any relationship between predation pressure and lizard abundance, despite there being a positive correlation with community evenness. This suggests that while predator presence seems to track with prey presence, there may be some feedback where predators alleviate competition between anole species, potentially by reducing the abundance of the numerically dominant competitor, and thereby granting more resources for other anole species. This would then result in both minimal changes in community wide abundance, while also increasing both anole species richness and community evenness. Prey switching has been noted in birds, and this would especially serve to increase evenness such that any common competitor eliminated can be replaced by another single less common one (Murdoch 1969, Fitzpatrick et al. 2009). The presence of specialist predators seems to have particularly accentuated effects. We found that while cuckoo presence had a positive relationship with lizard abundance and richness, it was also a significant predictor of community evenness – more so than temperature or precipitation. It is thus possible that cuckoos specifically exert some top-down control of island lizard communities.

While our results may be indicative of predators playing some role regulating diversity, we also found some significant relationships when considering our non-predatory guild: pigeons. Higher pigeon presence was weakly associated with less even lizard communities on both islands and alternatively lower and higher diversity on Hispaniola and Jamaica respectively. Because there is no direct causal link by which pigeons (which are not-insectivores, and therefore neither consume nor compete with anoles) we suspect that pigeon presence captures some other aspect of environmental variation that is not completely accounted for by our climate variables. Importantly however, the significant relationship between pigeons and anole evenness was negative (beta = -0.04), suggesting that the positive relationship found with predatory species is not a characteristic found between birds and anoles generally. Similarly, the effect of pigeons on anole community diversity was generally modest and differed in sign and magnitude on the two islands – its effect was weak and negative on Hispaniola (beta = -0.03), and positive of moderate size on Jamaica (beta = 0.16; Table 1). This was in contrast to all other analyses of predator effects, which, even when a significant interaction effect

between island identity and predation pressure existed, was always of the same sign and order of magnitude in strength on both islands. Together, these patterns suggest that the inferred signature of avian predation on these islands is likely real, rather than purely driven by unmeasured features of the environment that affect anoles and birds in tandem.

In addition to birds, snakes, bats, and introduced mammals such as rats and mongoose also prey on lizards, and were not considered in this study. Other potential predators include large spiders, and Solenopsis ants which feed on anole eggs (Reves-Olivares et al. 2020, Andrews and Rand 2022). While lists of mammal and snake occurrence on these islands as a whole exist, our study focused on birds because 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 are lower overall than what lizards likely experience from all predator sources. Hispaniola has more species of predator snakes than Jamaica (4 and 2 respectively), but fine-scale data on local coexistence is limited, so this this does not necessarily guarantee that snake occurrence is greater at individual sites. Regardless, our measurements consequently may have underestimated the effect of total predation in shaping lizard communities, though we have no a priori expectation that these other forms of predation would have different consequences than those of birds. 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 density, 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, likely due to high variance in observed abundance in some checklists (e.g. many hundreds or thousands of individuals, presumably when distant flocks were observed). As such eBird and similar databases at best represent a imperfect substitute for broad-scale time and area-standardized ecological surveys.

Although previous studies generally report negative correlations between anole abundance and predation pressure, thereby implicating predators presence as important drivers of *Anolis* community structure (Waide and Reagan 1983, Buckley and Jetz 2007, Calsbeek and Cox 2010, Pringle et al. 2019), our results show no evidence that predation pressure either reduces overall anole abundance or leads to local extirpation and declines in species richness. The reasons 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, which often found that predation may quickly lead prey to go locally extinct. 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. On the other end of the spectrum, studies comparing lizard abundances versus predator richness across multiple islands account for multiple species of both prey and consumer, but they rarely consider which species on an island actually co-exist with one another on a local scale. Buckley and Jetz (2007), for instance, conclude that sharp reductions of predators are a major driver of increased lizard densities. However, in such cross-island comparisons larger islands will nearly always have more predator species, even if such predator species do not occur everywhere on the islands. As such, actual local predator pressure may be unrelated to total number of predators on the island as a whole. If some other aspect of island size correlates with average lizard density, then a negative relationship between island-wide predator number and locally measured lizard density may be uncovered, even if the mechanisms driving predator number and lizard density are not directly related.

#### Conclusion

Our study utilized a large dataset of bird detections spanning several years, and combined this with local scale *Anolis* community surveys at several locations 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. Despite the large sample size of predator and lizard observations across these islands, our results fail to detect a strong or consistent signal of predators diminishing lizard abundance or diversity. Instead, correlations between predation pressure and lizard community diversity tended to be positive, which could suggest that predators decrease competition in the community and facilitate higher lizard species richness and greater lizard evenness. Ultimately, experimental approaches

that manipulate predator density or access to lizard communities may be needed to tease apart potential mechanisms. Regardless, the patterns in predator and lizard abundance that we document within islands stand in contrast to past assessments of the importance of predators on both small experimental islands, and macroecologically across islands. This finding points to an important knowledge gap related to the way that predation pressure manifests at different scales. Irrespective of predators, suggesting that bottom-up, rather than top-down 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.

#### References:

Andrews, R. 1979. Evolution of life histories: a comparison of Anolis from matched island and mainland habitats. Breviora **454** :1-51.

Andrews, R., and A. S. Rand. 2022. Fifty Years of Observations on Anolis Lizards at Barro Colorado Island, Panama. Herpetologica**78** :145-153.

Báez, S., S. L. Collins, D. Lightfoot, and T. L. Koontz. 2006. Bottom-up Regulation of Plant Community Structure in an Aridland Ecosystem. Ecology 87 :2746-2754.

Bragazza, L., R. D. Bardgett, E. A. D. Mitchell, and A. Buttler. 2015. Linking soil microbial communities to vascular plant abundance along a climate gradient. New Phytol **205** :1175-1182.

Buckley, L. B., and W. Jetz. 2007. Insularity and the determinants of lizard population density. Ecol Lett 10 :481-489.

Calsbeek, R., and R. M. Cox. 2010. Experimentally assessing the relative importance of predation and competition as agents of selection. Nature465 :613-616.

Canter, E. J., C. Cuellar-Gempeler, A. I. Pastore, T. E. Miller, and O. U. Mason. 2018. Predator identity more than predator richness structures aquatic microbial assemblages in Sarracenia purpure leaves. Ecology **99** :652-660.

Denno, R. F., D. Lewis, and C. Gratton. 2005. Spatial variation in the relative strength of top-down and bottom-up forces: causes and consequences for phytophagous insect populations. Annales Zoologici Fennici **42** :295-311.

Doherty, T. S., A. S. Glen, D. G. Nimmo, E. G. Ritchie, and C. R. Dickman. 2016. Invasive predators and global biodiversity loss. Proc Natl Acad Sci U S A 113 :11261-11265.

eBird. 2021. eBird: An online database of bird distribution and abundance. eBird, Cornell Lab of Ornithology, Ithaca, New York.

Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, T. E. Essington, R. D. Holt, J. B. Jackson, R. J. Marquis, L. Oksanen, T. Oksanen, R. T. Paine, E. K. Pikitch, W. J. Ripple, S. A. Sandin, M. Scheffer, T. W. Schoener, J. B. Shurin, A. R. Sinclair, M. E. Soule, R. Virtanen, and D. A. Wardle. 2011. Trophic downgrading of planet Earth. Science **333** :301-306.

Evans, K. L., P. H. Warren, and K. J. Gaston. 2005. Species-energy relationships at the macroecological scale: a review of the mechanisms. Biol Rev Camb Philos Soc 80 :1-25.

Fick, S. E., and R. J. Hijmans. 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. International Journal of Climatology **37**:4302-4315.

Fisher, R. N., A. V. Suarez, and T. J. Case. 2002. Spatial Patterns in the Abundance of the Coastal Horned Lizard. Conserv Biol16 :205-215.

Fitzpatrick, B. M., K. Shook, and R. Izally. 2009. Frequency-dependent selection by wild birds promotes polymorphism in model salamanders. BMC Ecol **9**:12.

Frishkoff, L. O., E. Gabot, G. Sandler, C. Marte, and D. L. Mahler. 2019. Elevation shapes the reassembly of Anthropocene lizard communities. Nat Ecol Evol **3** :638-646.

Frishkoff, L. O., G. Lertzman-Lepofsky, and D. L. Mahler. 2022. Evolutionary opportunity and the limits of community similarity in replicate radiations of island lizards. Ecol Lett **25** :2384-2396.

Gripenberg, S., and T. Roslin. 2007. Up or down in space? Uniting the bottom-up versus top-down paradigm and spatial ecology. Oikos**116** :181-188.

Gurevitch, J., J. A. Morrison, and L. V. Hedges. 2000. The Interaction between Competition and Predation: A Meta-analysis of Field Experiments. Am Nat **155** :435-453.

Guyer, C. 1988. Food Supplementation in a Tropical Mainland Anole, Norops Humilis: Demographic Effects. Ecology **69** :350-361.

Haddad, N. M., D. Tilman, J. Haarstad, M. Ritchie, and J. M. Knops. 2001. Contrasting effects of plant richness and composition on insect communities: a field experiment. Am Nat **158** :17-35.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community Structure, Population Control, and Competition. The American Naturalist94 :421-425.

Hammerschlag, N., A. C. Broderick, J. W. Coker, M. S. Coyne, M. Dodd, M. G. Frick, M. H. Godfrey, B. J. Godley, D. B. Griffin, K. Hartog, S. R. Murphy, T. M. Murphy, E. R. Nelson, K. L. Williams, M. J. Witt, and L. A. Hawkes. 2015. Evaluating the landscape of fear between apex predatory sharks and mobile sea turtles across a large dynamic seascape. Ecology**96** :2117-2126.

Heckel, D. G., and J. Roughgarden. 1979. A Technique For estimating the Size of Lizard Populations. Ecology **60** :966-975.

Hixon, M. A., and B. A. Menge. 1991. Species diversity: Prey refuges modify the interactive effects of predation and competition. Theoretical Population Biology **39**:178-200.

Hunter, M. D., and P. W. Price. 1992. Playing Chutes and Ladders: Heterogeneity and the Relative Roles of Bottom-Up and Top-Down Forces in Natural Communities. Ecology **73** :724-732.

Lapiedra, O., T. W. Schoener, M. Leal, J. B. Losos, and J. J. Kolbe. 2018. Predator-driven natural selection on risk-taking behavior in anole lizards. Science **360** :1017-1020.

Losos, J. B. 2009. Lizards in an evolutionary tree: ecology and adaptive radiation of anoles University of California Press.

Mclaughlin, J. F., and J. Roughgarden. 1989. Avian Predation on Anolis Lizards in the Northeastern Caribbean - an Inter-Island Contrast. Ecology **70** :617-628.

Medina, F. M., E. Bonnaud, E. Vidal, B. R. Tershy, E. S. Zavaleta, C. Josh Donlan, B. S. Keitt, M. Corre, S. V. Horwath, and M. Nogales. 2011. A global review of the impacts of invasive cats on island endangered vertebrates. Global Change Biology **17**:3503-3510.

Meserve, P. L., D. A. Kelt, W. B. Milstead, and J. R. Gutierrez. 2003. Thirteen Years of Shifting Top-Down and Bottom-Up Control. BioScience53 .

Murdoch, W. W. 1969. Switching in General Predators: Experiments on Predator Specificity and Stability of Prey Populations. Ecological Monographs **39** :335-354.

Novosolov, M., G. H. Rodda, A. Feldman, A. E. Kadison, R. Dor, and S. Meiri. 2016. Power in numbers. Drivers of high population density in insular lizards. Global Ecology and Biogeography 25 :87-95.

Paine, R. T. 1966. Food Web Complexity and Species Diversity. The American Naturalist 100 :65-75.

Piovia-Scott, J., L. H. Yang, A. N. Wright, D. A. Spiller, and T. W. Schoener. 2019. Pulsed seaweed subsidies drive sequential shifts in the effects of lizard predators on island food webs. Ecol Lett 22 :1850-1859.

Poulin, B., G. Lefebvre, R. Ibanez, C. Jaramillo, C. Hernandez, and A. Stanley Rand. 2001. Avian predation upon lizards and frogs in a neotropical forest understorey. Journal of Tropical Ecology17 :21-40.

Pringle, R. M., T. R. Kartzinel, T. M. Palmer, T. J. Thurman, K. Fox-Dobbs, C. C. Y. Xu, M. C. Hutchinson, T. C. Coverdale, J. H. Daskin, D. A. Evangelista, K. M. Gotanda, A. M. I. t. V. N, J. E. Wegener, J. J. Kolbe, T. W. Schoener, D. A. Spiller, J. B. Losos, and R. D. H. Barrett. 2019. Predator-induced collapse of niche structure and species coexistence. Nature **570** :58-64.

Reyes-Olivares, C., A. Guajardo-Santibanez, B. Segura, N. Zanartu, M. Penna, and A. Labra. 2020. Lizard predation by spiders: A review from the Neotropical and Andean regions. Ecol Evol **10** :10953-10964.

Ripple, W. J., and R. L. Beschta. 2012. Trophic cascades in Yellowstone: The first 15 years after wolf reintroduction. Biological Conservation 145 :205-213.

S. M. Billerman, B. K. Keeney, P. G. Rodewald, and T. S. Schulenberg. 2022. Birds of the World. Cornell Laboratory of Ornithology, Ithaca, NY, USA.

Schoener, T. W., J. B. Losos, and D. A. Spiller. 2005. Island biogeography of populations: an introduced species transforms survival patterns. Science **310** :1807-1809.

Schoener, T. W., and A. M. Y. Schoener. 1978. Inverse relation of survival of lizards with island size and avifaunal richness. Nature 274 :685-687.

Schoener, T. W., and D. A. Spiller. 1996. Devastation of prey diversity by experimentally introduced predators in the field. Nature**381** :691-694.

Siemann, E. 1998. Experimental Tests of Effects of Plant Productivity and Diversity on Grassland Arthropod Diversity. Ecology **79** :2057-2070.

Team, R. D. C. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Waide, R. B., and D. P. Reagan. 1983. Competition Between West Indian Anoles and Birds. The American Naturalist **121** :133-138.

Wenninger, E. J., and R. S. Inouye. 2008. Insect community response to plant diversity and productivity in a sagebrush–steppe ecosystem. Journal of Arid Environments **72** :24-33.

Wright, A. N., J. Piovia-Scott, D. A. Spiller, G. Takimoto, L. H. Yang, and T. W. Schoener. 2013. Pulses of marine subsidies amplify reproductive potential of lizards by increasing individual growth rate. Oikos:122: 1496–1504.

Wright, A. N., L. H. Yang, J. Piovia-Scott, D. A. Spiller, and T. W. Schoener. 2020. Consumer Responses to Experimental Pulsed Subsidies in Isolated versus Connected Habitats. Am Nat **196** :369-381.

Wright, S. J. 1979. Competition Between Insectivorous Lizards and Birds in Central Panama. American Zoologist 19 :1145-1156.

Wright, S. J. 1981. Extinction-Mediated Competition: The Anolis Lizards and Insectivorous Birds of the West Indies. The American Naturalist117 :181-192.

Wright, S. J., R. Kimsey, and C. J. Campbell. 1984. Mortality Rates of Insular Anolis Lizards: A Systematic Effect of Island Area? The American Naturalist **123** :134-142.

Wunderle Jr., J. M. 1981. Avian Predation upon Anolis Lizards on Grenada, West Indies. Herpetologica **37** :104-108.