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Lizard and frog removal increases spider abundance but does not cascade to increase herbivory

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Abstract

Insectivorous vertebrates, especially on islands, can exert top-down control on herbivorous prey, which can transfer through a food chain to reduce herbivory. However, in many systems insectivorous vertebrates feed on more than one trophic level, especially consuming arthropod predators, and this intraguild predation can diminish trophic cascades. Our goal was to determine, using an exclosure experiment, the relative importance of anole lizards and coqui frogs in controlling spider and arthropod abundances as well as herbivory rates in the understory of the Luquillo Experimental Forest, Puerto Rico. We found that exclosures removing both anoles and coquis doubled spider abundance compared to exclosures with anoles and coquis at natural densities. The effect of coquis on spiders was greater and occurred more quickly than that of anoles, potentially because of the higher natural densities of coquis and removal of both vertebrates produced no interactive effects. We found support for the idea that anoles, but not coquis, reduce foliar arthropod abundances on one of the two studied plant species. However, there was also evidence that anole removal decreased herbivory, the opposite of what we would expect if there was a trophic cascade. Potential explanations include that anoles reduced predatory arthropods on foliage more than they reduced herbivorous arthropods. Results highlight that the food web in tabonuco forest is not simple and that there are complex and dynamic relationships among vertebrate insectivores, predatory arthropods, and herbivorous arthropods that do not consistently result in a trophic cascade.

Abstract in Spanish is available with online material

KEYWORDS
Anolis gundlachi, Eleutherodactylus coqui, food web, functional redundancy, Puerto Rico, top-down effects, trophic cascade

1 | INTRODUCTION

If predators exert top-down control on herbivores, this interaction can indirectly influence damage to tissues of primary producers via a trophic cascade (Halaj & Wise, 2001; Schmitz et al., 2000).

Insectivorous vertebrates, especially on smaller islands with less complicated food webs, generally exert top-down control on arthropod herbivores (Borkhataria et al., 2006; Spiller & Schoener, 2007). However, even in relatively simple systems, interactions among trophic levels exist such that top predators may exhibit intraguild

predation and feed on intermediate predators (Mooney et al., 2010; Polis et al., 1989). Theory predicts that the direct negative effects of predators on herbivores could be offset by the simultaneous suppression of other herbivore predators (Polis & Holt, 1992; Polis & Strong, 1996). Thus, predicting the effect of a top predator on plant damage generally requires understanding the relative effects of top predators on both intermediate predators and herbivores.

Many top predators on islands are insectivores that do not feed exclusively on one trophic level. A well-known example is *Anolis* lizards on small islands that consume both carnivorous and herbivorous arthropods (Schoener, 1988). The top-down effect on plants, therefore, depends on the strength of the interaction with predatory versus herbivorous arthropods (Pacala & Roughgarden, 1984). For example, Spiller and Schoener (1990a) found that lizard removal led to an increase in leaf scaring but a decrease in galling, which they suggest occurred through two distinct trophic pathways. Lizards directly reduced abundances of Homoptera that caused leaf scars but indirectly increased the abundances of tiny, gall-forming Diptera through their effect on spiders (Spiller & Schoener, 1990b). The best test of the importance of intraguild predation removes top and intermediate predators independently, and one such experiment showed weak compensatory predation (Spiller & Schoener, 1994). Although particular case studies differ, a meta-analysis on the topic suggests that intraguild predation by insectivorous vertebrates generally does not weaken trophic cascades (Mooney et al., 2010).

A large body of literature shows that insectivorous vertebrates on islands reduce the abundances of other predators, in particular, that of spiders (Gruner, 2005; Rogers et al., 2012). Especially on tropical islands in the Caribbean, it is well known that lizards exert top-down control on spiders, with Schoener and Toft (1983) first noting the strong, negative relationship between these groups. Pacala and Roughgarden (1984) provided experimental evidence that lizards were causally responsible when they excluded anoles and found that orb-weaving spiders were 20–30 times more abundant after 6 months. Fewer studies have investigated similar effects of terrestrial amphibians (i.e., salamanders) on spiders (typically studied in mainland and temperate systems) (Hickerson et al., 2012; Wyman, 1998), and these studies have found that effects are equivocal and depend on forest conditions (Hocking & Babbitt, 2014; Homyack et al., 2010). Moreover, the relationship between terrestrial frogs and spiders is often complex and has not been investigated experimentally in many systems (von May et al., 2019; Wise & Chen, 1999).

In Puerto Rican forests, anecdotal data suggest that insectivorous vertebrates control herbivorous prey because insectivorous vertebrates have high densities and herbivory rates are low (Angulo-Sandoval & Aide, 2000). However, top-down control effects of lizards and frogs have only been studied separately and in different habitats of the Bisley Experimental Watershed in the Luquillo Experiment Forest. Dial and Roughgarden (1995) removed *Anolis* lizards from tree crowns for 6 months while sampling spiders, and flying and foliar insects, and found that anole exclusion increased abundances of large arthropods and spiders, but not small arthropods or flying

arthropods. They also found that the effects of anoles cascaded to producers and removing the former increased leaf damage. Beard et al. (2003) conducted small (1 m^3) enclosure and plot-level (20 m x 20 m) experiments in the understory that focused on excluding coquis, finding that such exclusion increased the abundances of understory flying insects and also increased leaf damage. However, they did not quantify the abundances of spiders in particular or arthropods on plants.

The objective of this research was to determine the effects of each of two dominant insectivores (anoles and coquis) on abundances of spiders, and of flying and foliar arthropods, as well as on herbivory rates in the understory of tabonuco forest. Based on the results from previous studies (Beard et al., 2003; Dial & Roughgarden, 1995), we hypothesized that removal of anoles and coquis would increase arthropod prey and herbivory rates through trophic cascades. To test this hypothesis, we conducted an exclosure experiment in which we removed anoles only, coquis only, and both anoles and coquis and compared the results to control plots that contained both vertebrate species at natural densities. This replicated, full factorial design facilitated the disentanglement of effects of these insectivorous vertebrates and the determination of their relative importance in structuring food web dynamics.

2 | METHODS

2.1 | Study site

The experiment was conducted in the Luquillo Experimental Forest in the northeastern corner of Puerto Rico (18°19'12" N, 65°49'12" W; 380 m a.s.l.). The forest is classified as subtropical wet (Ewel & Whitmore, 1973). Annual rainfall at the site averages 3,500 mm, with all months receiving > 200 mm of rain, and daily average maximum and minimum temperatures are 25.2°C and 20.5°C, respectively (Thompson et al., 2004).

The experiment was conducted in closed-canopy tabonuco (*Dacryodes excels*) forest. No native mammals (other than bats) inhabit the Luquillo Experimental Forest (Willig & Gannon, 1996). At the time of this study, densities of eleutherodactylid frogs and anoline lizards were high, with each estimated to be over 20,000 individuals ha^{-1} (Reagan, 1996; Stewart & Woolbright, 1996). They are both insectivores but not top predators in that they are consumed by large invertebrates, reptiles, and birds (Reagan & Waide, 1996).

Arachnids are the principal arthropod predators in the food web (Pfeiffer, 1996). Spiders primarily occupy habitat near the forest floor, occurring in the foliage of tree seedlings and herbaceous growth (Pfeiffer, 1996). At the time of this study, 22 species of spider were recorded in the understory, and four species of web-building spiders accounted for 95.7% of their mean density (36,194 individuals per ha^{-1}); the most common species, *Leucauge regnyi* (Tetragnathidae), accounted for 50% of the individuals in understory censuses (Pfeiffer, 1996).

2.2 | Experimental design

In the spring and summer of 1999, 40 plots were arrayed in eight blocks in the forest near the El Verde Field Station. Blocks were between 20 m and 400 m apart and were established to characterize spatial variation within an approximate 49,500 m^2 area of forest. Block elevation ranged from 330 m to 415 m. Each block contained five plots: exclosures for the four removal combinations of coquis (yes or no) and/or anoles (yes or no) and an open control plot the same size as the exclosures but with no netting to evaluate the effect of the physical structure of the exclosure. Exclosures were cubic, 3 m x 3 m x 3 m in size, constructed using 5.1-cm-diameter polyvinyl chloride pipes, and surrounded by 0.64 cm mesh plastic netting. The netting surrounded the plot and was embedded about 20 cm into the ground. In each plot, four seedlings each of *M. bidentata* and *P. glabrescens* were planted in 50-cm long, 10.2-cm-diameter PVC tubes filled with a 50:50 mixture of commercially available topsoil and river sand.

In September 1999 before any plots were closed, one month of pre-treatment measurements were made in all 40 plots. In October 1999, exclosures were closed (except for the open control [OC]) and one of four treatments was randomly assigned and applied to each exclosure. The OC and the closed control (CC) had natural densities of anoles and coquis; the anole exclosure (AE) had no anoles and a natural density of coqui; the coqui exclosure (CE) had no coqui and a natural density of anoles; and the full exclosure (TE) had no coquis and no anoles. Anoles and coquis were stocked at the following levels: 5 *Anolis gundlachi* and 16 *Eleutherodactylus coqui*. *A. gundlachi* were used because they are the most common understory anole, and *E. coqui* were used because they are the most common frog species in the forest (Reagan, 1996; Stewart & Woolbright, 1996).

Post-treatment measurements were taken monthly in all plots for 10 months until July 2000. Each month, enclosures were visually searched and censused for anoles, coquis, and spiders. Arthropods on each potted plant, hereafter foliar insects, were also counted via visual inspection (as in Dial & Roughgarden, 1995). In addition, arthropods were collected on two sticky traps (700 cm^2), hereafter referred to as flying insects, placed about 0.5 m off the forest floor near potted plants in each plot. Sticky traps were collected and replaced each month. Herbivory was measured by estimating the leaf area lost as a percentage of total leaf area (cm^2 cm^{-2}) from recently expanded leaves on each of the potted plants.

2.3 | Statistical methods

To assess the effects of anole or coqui removal, we conducted separate analyses on each of six response variables: spider abundance, flying insect abundance, insect abundance on *M. bidentata* or *P. glabrescens*, and herbivory on *M. bidentata* or *P. glabrescens*. The statistical model was a general linear mixed model (glmm) with anole removal and coqui removal (each as a binary factor), month (a

10-level categorical factor), and their interactions as fixed effects. Blocks and plots within blocks were considered to be random effects; covariance among repeated measurements within plots was modeled using a first-order autoregressive structure or with a compound symmetry structure for those responses with estimation and convergence problems (i.e., flying insect abundance and herbivory on each plant species).

Pre-treatment values of response variables generally differed among plots; consequently, we adjusted for this variability in initial condition by including the pre-treatment response as a covariate in the statistical model, and we allowed the relationship between the post-treatment response and the corresponding pre-treatment response to vary with time by including the interaction of the covariate and time. The effect of the physical exclosure structure on each response variable, as well as on coqui densities and anole densities, was assessed by comparing closed and open control treatments (i.e., CC versus. OC) using a separate but similar statistical model to that described above.

Prior to analysis, we computed the mean abundance of insects on the two sticky traps in each plot, the mean abundance of insects on each plant species, and the mean herbivory on each plant species in each plot; we used these means as response variables in analyses. Although response variables were measured as counts or percentages, we assumed a normal distribution in all analyses; residual analysis indicated that the assumptions of normality and homogeneity of variance, as well as the assumption of linearity with the pre-treatment covariate, were not violated. Because responses were not necessarily static through time, we investigated interactions of treatment factors and month. We also investigated paired contrasts to help in interpretation.

To conduct statistical analysis, we used R software version 3.6.2 (R Core Team, 2019). We used the glmmTMB package for model fitting version 0.2.3 (Brooks et al., 2017), the ANOVA function in the car package to obtain Type III hypothesis tests (version 3.0.6) (Fox & Weisberg, 2019), and the emmeans package (version 1.4.3.1) (Lenth, 2019) for estimation of means and standard errors, and for Tukey-adjusted pairwise comparisons among means. We generally considered relationships to be significant when $p \leq 0.05$, although marginally significant results ($0.05 < p \leq 0.10$) are discussed as well.

3 | RESULTS

3.1 | Exclosure effectiveness

The closed (CC) and open (OC) control plots had statistically indistinguishable numbers of anoles and coquis throughout the experiment ($p = 0.81$, 0.91, respectively, see S1 Table for all treatment effectiveness statistics) suggesting that stocking rates reflected background densities. During the experiment, on average, 4.83 anoles occurred in exclosures with anoles and 4.75 anoles occurred in open control plots. On average, there were 15.9 coquis

in exclosures with coquis and 15.9 coquis in open control plots (Figure 1).

More spiders were observed in the CC plots (mean = 25.7) than in the OC plots (mean = 22.1) (exclosure: p = 0.01). However, CC and OC plots follow the same general pattern of decline in spiders over time, which was notably different than the temporal pattern for each of the three exclusion treatments in which spiders increased in abundance over time (Figure 2a).

There was no evidence of differences between CC and OC plots for flying insects throughout the experiment (exclosure: p = 0.92, Figure 3a), foliar insects on *Manilkara* (exclosure: 0= .51, Figure 4a), or herbivory on *Manilkara* or *Piper* (exclosure: p = 0.58, p = 0.35, Figure 5a,c, respectively). The number of foliar insects on *Piper* increased over time in the OC plots, whereas abundance in the CC plots was stable (exclosure x time: p = 0.03; Figure 4c).

3.2 | Treatment effects

3.2.1 | Spiders

Both anole removal and coqui removal increased spider abundance (anole removal: p = 0.042; coqui removal: p < 0.001; Figure 2b; see Table 1 for all treatment statistics) and did so consistently (i.e., no significant interaction between anole and coqui removal affected spider abundance; p > 0.05). The magnitude of the positive effect of anole removal on spider abundance increased over time, especially after six months and later (anole removal * time: p = 0.023). Similarly, the magnitude of the positive effect of coqui removal increased over time, particularly after four months and later (coqui removal * time: p < 0.001; Figure 2a). The positive effects of vertebrate removal on spider abundance persisted over the timeframe of the study; in
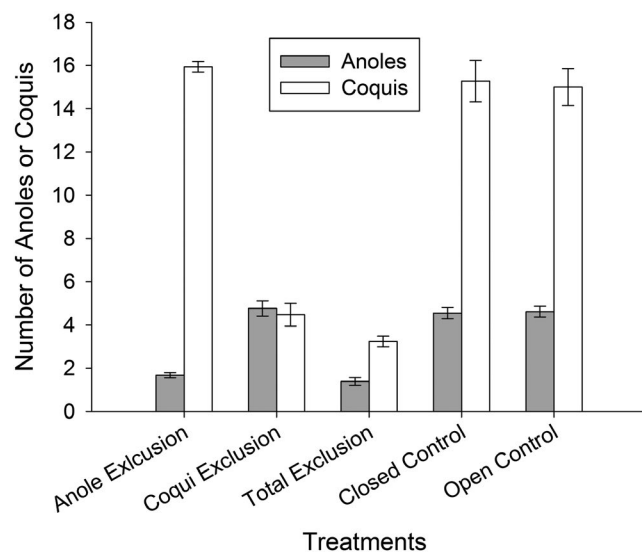
contrast, spider abundance in control plots declined beginning after six months (Figure 2a).

3.2.2 | Flying and foliar insects

We found a marginally significant interaction between coqui and anole removal on the number of flying insects (anole removal * coqui removal: p = 0.070), such that the combined removal of the two insectivores was statistically greater than the sum of their separate removals and resulted in fewer flying insects (Figure 3b).

The number of foliar insects on *Manilkara* increased over time (p < 0.001) and with anole removal (p = 0.007; Figure 4a, b). There was a significant interaction between anole removal and time for the number of insects on *Piper* (p = 0.029), which reflected a shift toward fewer insects on *Piper* with anole removal over time (Figure 4d).
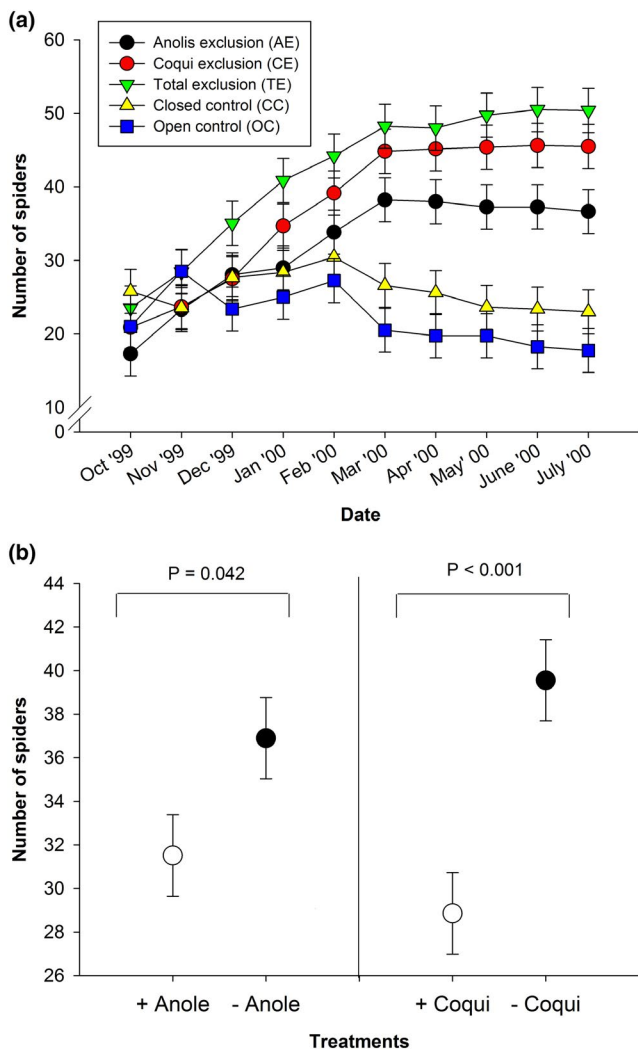
3.2.3 | Herbivory

Herbivory on *Manilkara* and on *Piper* increased with time (p < 0.001, p < 0.001, respectively; Figure 5a). There was less herbivory on *Manilkara* when anoles were removed (p = 0.027; Figure 5b). There was no evidence that herbivory on *Piper* was affected by vertebrate removal (Figure 5c).

4 | DISCUSSION

Using an exclosure experiment, we investigated whether the removal of two dominant insectivorous vertebrates in the understory would increase the abundances of arthropod prey and reduce herbivory rates. The most robust result was that coqui removal, in particular, and to a lesser extent anole removal, increased spider abundance. Moreover, anole removal increased the abundance of foliar insects on one of the two plant species; however, unlike previous studies, this did not cascade through the food web to reduce herbivory rates (Dial & Roughgarden, 1995). Rather, we found evidence that anole removal decreased herbivory rates, which is counter to the expectation from a trophic cascade. Potential explanations include that anole removal increases predatory arthropods more than it increases herbivorous arthropods (Mooney et al., 2010). Because we did not identify foliar insects as predatory or herbivorous, we cannot address this hypothesis further, but future studies could identify mechanisms giving rise to this relationship.

4.1 | Effects on spiders

Similar to other tropical island ecosystems (Gruner, 2005; Rogers et al., 2012), the loss of insectivorous vertebrates resulted in

FIGURE 1 Mean number (± SE) of coqui or anoles censused in each of five treatments. Values were averaged across time (10 months) and blocks (n = 8)

FIGURE 2 Estimated marginal mean number of spiders (± SE) during a 10-month experiment in tabonuco forest, Puerto Rico (a) by treatment, and (b) shown summarized with the main effects of with anoles (CE and CC) and without anoles (AE and TE), and with coquis (AE and CC) and without coquis (CE and TE)

increased abundances of spiders, suggesting that the natural densities of coquis and anoles limit spider abundance in the tabonuco forest of Puerto Rico. Increases in spider abundance in the absence of either coquis or anoles and the lack of any increases in the control plots substantiate this assertion. The effects of vertebrate removal on spiders required at least four months to manifest statistically detectable responses. This suggests that spiders moved into exclosures with vertebrate removals and then these localized abundances stabilized at the higher values. Because a similar increase did not occur in the closed control treatments, this response was not a function of the exclosure structure (Spiller & Schoener, 1988). As in other studies (e.g., Borkhataria et al., 2006), each vertebrate exclusion treatment had unique effects on spider abundance and we did not see any type of interactive effects (compensation or synergies); the exclusion of both coquis and anoles had the greatest effect (i.e., the sum of their separate effects).

The effects of removing coquis on the abundance of spiders were greater than those involving the removal of anoles, in that the response was observed earlier and the increase in spider abundance was greater. Both vertebrate predators consume spiders, so the mechanism for each of these effects is likely a consequence of direct predation (Spiller & Schoener, 1990a). The greater density of coquis compared to anoles may account for the greater experimental effect (around 16 versus 5 per exclosure, respectively). Anoles and coquis do not differ in the number of prey consumed per individual, but spiders may comprise a greater percentage of the diet for coquis than for anoles (Reagan, 1996; Stewart & Woolbright, 1996). Also, most spiders are nocturnal, which might make them more apparent prey for the nocturnal coquis than for diurnal anoles.

Compared to the closed control treatment, removal of both coquis and anoles increased the number of spiders by a factor of 2.2. Removal of only coquis or only anoles resulted in an increase in spiders by a factor of 2.0 and 1.6, respectively. This effect on spider abundance is in the same order of magnitude (1.5–3 times) as that associated with lizard removal in the Bahamas (Schoener & Spiller, 1987; Spiller & Schoener, 1988). When looking at the effect of anoles only, the response of spider abundance was much less than in some studies, where spiders increased by a factor of 10–30 (Pacala & Roughgarden, 1984; Schoener & Toft, 1983; Toft & Schoener, 1983). This may transpire because the food web of the tabonuco forest is larger and more complex compared to those on smaller islands in the Bahamas (Schoener, 1989) or Lesser Antilles (Goldwasser & Roughgarden, 1993).

4.2 | Effects on flying insects

Results from a study conducted at the same time in tabonuco forest understory of Puerto Rico suggest that the arthropods on sticky traps would have included members of the Diptera (75% of counts), Hymenoptera (12%), Coleoptera (4%), and Homoptera (2%), with the large majority between 1 and 2 mm in length (Beard et al., 2003). Corroborating previous research in tabonuco forest (Dial & Roughgarden, 1995), the removal of anoles had no statistical effect on the abundances of flying arthropods. Coqui removal also had no statistical effect, but this was in contrast to previous research in tabonuco forest suggesting that coqui removal can increase flying insects (Beard et al., 2003).

The only interactive effect between anole and coqui removal involved the abundance of flying insects. The interaction was only marginally significant and therefore could be spurious. If the relationship is real, it suggests that the removal of both anoles and coquis reduced the number of flying insects more than did the sum of their separate removals, but it also suggested that fewer flying insects persisted in the presence of both species. It is difficult to explain why flying insects might decrease with both anoles and coquis present and with the removal of both anoles and coquis. The most obvious explanation is that together these insectivores decrease flying insects enough through direct predation for it to be measurable and that when both are removed it increases predators
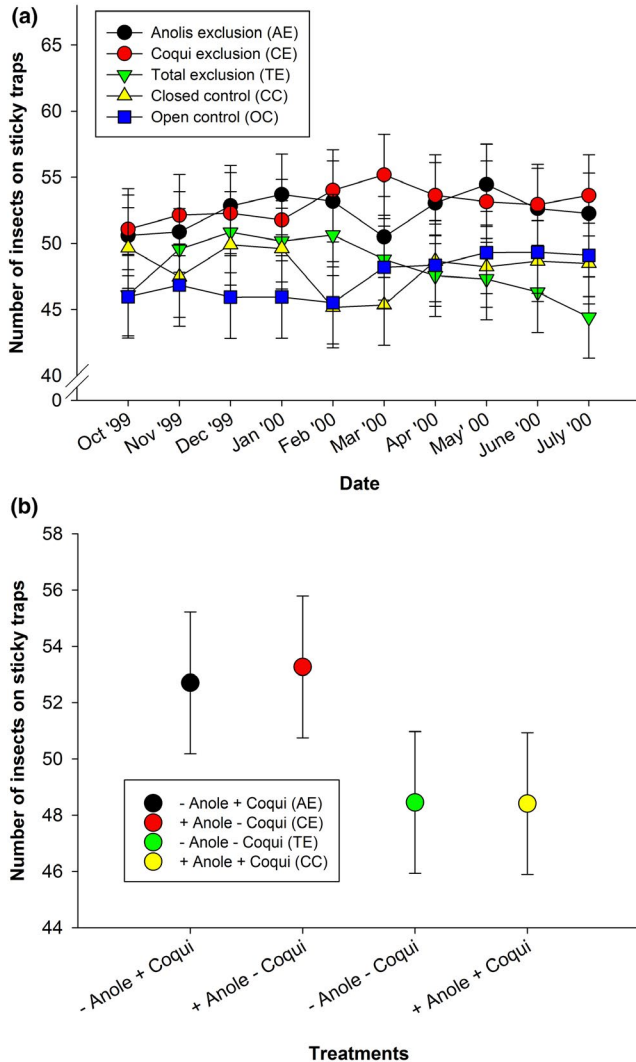
FIGURE 3 Estimated marginal mean number of insects on sticky traps (± SE) during a 10-month experiment in the tabonuco forest, Puerto Rico (a) by treatment, and (b) shown summarized without anoles, with coquis (AE); with anoles, without coquis (CE); without anoles or coquis (TE); and with anoles and coquis (CC) (Anole removal * coqui removal: $p = 0.070$)

of flying insects enough for the effects to be measurable. The latter explanation is similar to the indirect increase in the abundances of Diptera in the presence of anoles through their effect on spiders in the Bahamas (Spiller & Schoener, 1990b). However, these results are more complicated and suggest that the relationships among vertebrates, spiders, and flying insects in the El Verde food web do not resemble a simple food chain.

4.3 | Effects on foliar insects and herbivory

In this study, the effect of insectivorous vertebrates on the abundance of spiders was much greater than that on foliar arthropods. The only significant relationship between vertebrates and foliar insects was associated with anoles (as in Dial & Roughgarden, 1995; Perfecto et al., 2021). This is not that surprising because coquis are known to have an extremely diverse diet and can primarily consume leaf litter insects (Beard, 2007; Choi & Beard, 2012).

We found that anole removal significantly increased the number of foliar insects on *Manilkara*. This suggests that anoles are directly consuming foliar insects on *Manilkara* and supports previous research suggesting that anoles reduce foliar insects on tabonuco (Dial & Roughgarden, 1995). We also found an interaction between anole removal and time on the number of foliar insects on *Piper*, such that there were more insects on *Piper* with anole removal at the beginning of the experiment, but fewer at the end of the experiment (Figure 4d). This interaction may reflect the increasing role of spiders and other predatory insects in reducing foliar insects by the end of the experiment; spider abundance increased with anole removal over time. Because these results suggest that anole removal over the course of the experiment can increase foliar insects on one plant species while simultaneously decreasing foliar insects on another plant species, interactions among trophic levels may depend on the identity of plant species and the use of particular plant species in experiments could influence conclusions about food web interactions.

If anoles control herbivorous insects on *Manilkara*, as suggested by the increase in foliar insects on *Manilkara* with anole removal, herbivory rates should increase on *Manilkara* with anole removal. However, the evidence does not support this. The only significant result from the glmm suggesting that removal of either anoles or coquis influenced herbivory rates suggests that herbivory is reduced on *Manilkara* with anole removal. This is the opposite of what we might expect if anoles were controlling herbivorous insects and suggests that the foliar insects that anole removal increases on *Manilkara* may be predatory of herbivorous insects. Alternatively, anole removal could be increasing the types of herbivorous insects that do not result in leaf area loss while decreasing the types of herbivorous insects that do. This anomalous result contradicts previous research suggesting that anoles (Dial & Roughgarden, 1995) and coquis (Beard et al., 2003) reduce herbivory in tabonuco forest.

In other studies, the effect of vertebrate insectivores on leaf damage is assumed to be based on whether herbivorous arthropods are more prone to be consumed by the vertebrate predator or by spiders (Spiller & Schoener, 1990a, 1990b). Because we saw little change in herbivory on *Piper*, it may be assumed that the increase in spiders may have reduced herbivorous insects to the same level as removal of vertebrates, thus resulting in no change in leaf damage (Pacala & Roughgarden, 1984). There was some support for this in that with anole exclusion the number of foliar insects on *Piper* decreased when spider abundance increased (Figures 2b and 4d) and that the open control (OC) plots that had fewer spiders and more foliar insects over time (Figures 2a and 4c).

We propose that anoles can have greater control of foliar arthropods than do spiders on some plant species, and such effects may cascade to influence leaf damage in some situations (Dial &
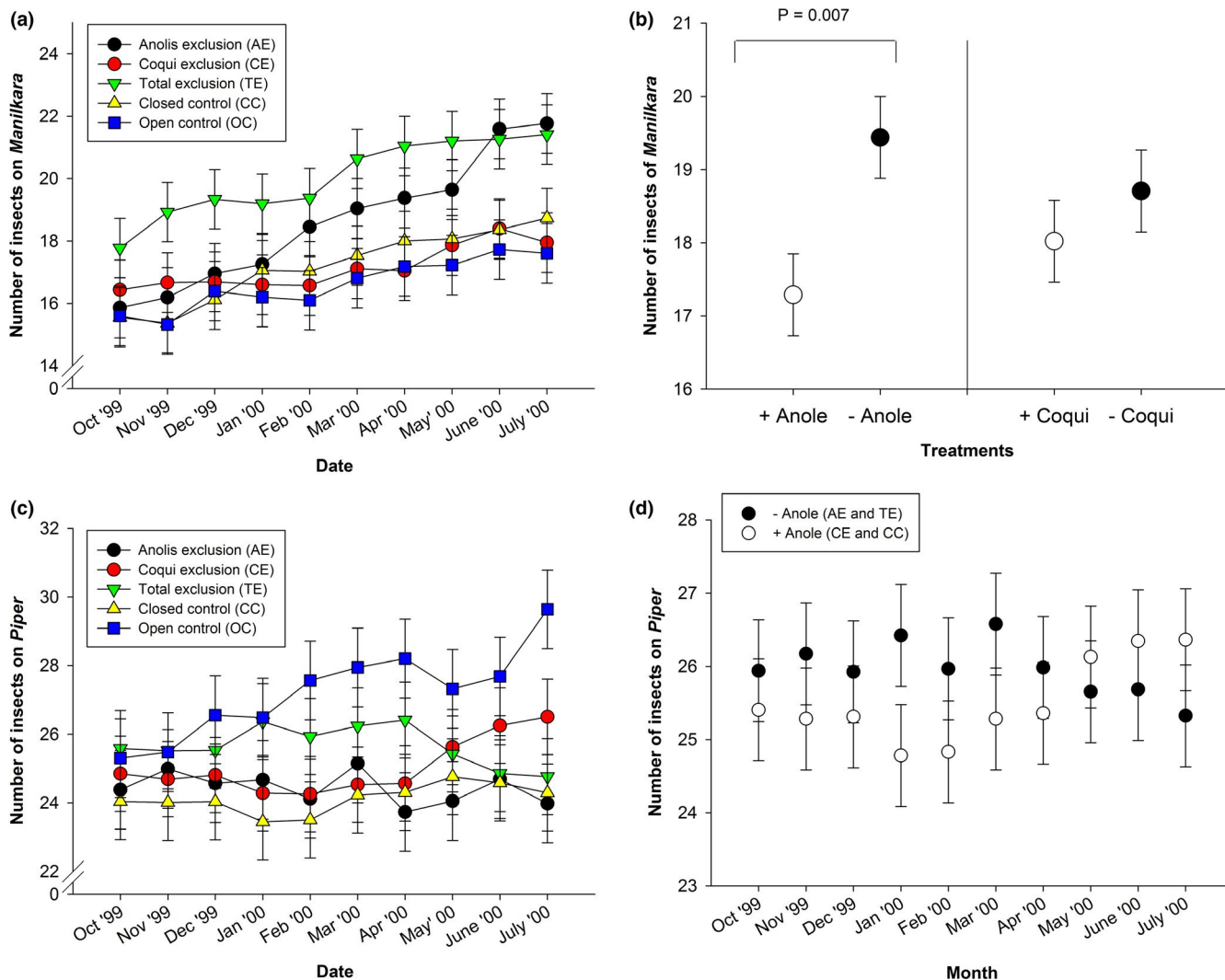
FIGURE 4 Estimated marginal mean number of insects (± SE) during a 10-month experiment in the tabonuco forest, Puerto Rico (a) on *Manilkara* plants by treatment, (b) on *Manilkara* shown summarized with anoles (CE and CC) and without anoles (AE and TE), and with coquis (AE and CC) and without coquis (CE and TE), (c) on *Piper* plants by treatment, and (d) on *Piper* shown summarized with and without anoles by month (Anole removal * time: $p = 0.029$)

Roughgarden, 1995). In other situations (i.e., different plant species or areas of the forest), complex interactions with predatory arthropods may reduce such cascading effects. With our experimental design, we could not explicitly test whether spiders played a compensatory role when vertebrates were removed (Spiller & Schoener, 1994). A clearer test of such compensatory effects would include treatments that involve the removal of spiders and the removal of insectivorous vertebrates.

4.4 | Limitations

This experiment was conducted in the understory of tabonuco forest, but anoles and coquis also occupy the sub-canopy and canopy. Results of this experimental study likely differed from those of Dial and Roughgarden (1995) in which top-down effects of anole removal on leaf damage were evident because that research was conducted

in the canopy, in a different area of the forest, with a different plant species (i.e., tabonuco), and using different anoline species. The results also differed from previous research in the understory suggesting that coquis reduce leaf damage (Beard et al., 2003), potentially because of the different plot sizes, methods used to measure herbivory, and plant and arthropod composition of focal portions of the forest.

The lack of taxonomic resolution in our study may hamper data interpretation. For example, while spiders were counted visually, they were not identified to species, and they were not removed from the plots for later identification to not influence longer-term treatment responses. Consequently, intertaxon or interguild differences might be obscured in our analyses. For example, non-significant results may have arisen when different taxa or different guilds responded in opposite directions, and certain significant differences in the responses of insects or spiders may reflect the most abundant taxa or guilds in those groups, respectively. Furthermore, leaf litter
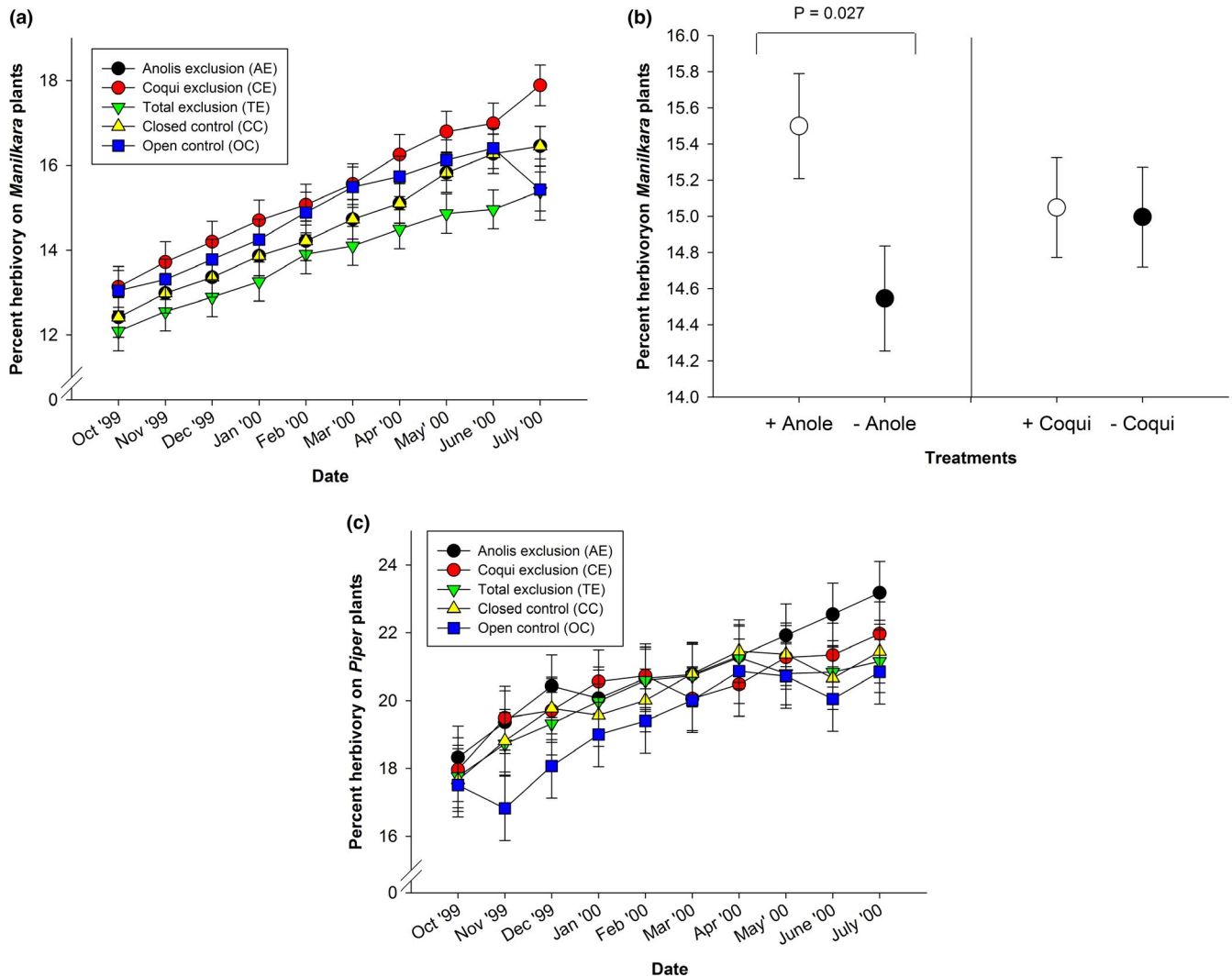
FIGURE 5 Estimated marginal mean percent herbivory (± SE) during a 10-month experiment in the tabonuco forest, Puerto Rico (a) on *Manilkara* for all treatments, (b) on *Manilkara* shown summarized with anoles (CE and CC) and without anoles (AE and TE), and with coquis (AE and CC) and without coquis (CE and TE), and (c) on *Piper* for all treatments

insects could have played an important role in these interactions but were not measured in our study (Beard et al., 2003; Prather & Belovsky, 2019).

As with any study, our results primarily apply to tabonuco forest at the time of data gathering, which was 20 years ago. Importantly, successional dynamics, primarily as a result of the frequent hurricanes and droughts, shape the forest (Beard et al., 2005; Brokaw et al., 2012). In the two decades before our study, two major hurricanes struck the forest: Hugo (category 4) in 1988 and Georges (category 3) in 1998, just one year before this experiment started. These disturbances and subsequent secondary successional processes influence coqui and invertebrate populations (Klawinski et al., 2014; Schowalter et al., 2014; Willig et al., 2014; Woolbright, 1996), and we might expect interactions among these taxa to change at different stages during successional dynamics (Prather & Belovsky, 2019).

As far as long-term changes in abundances, we have no evidence of consistent long-term temporal change in coqui numbers, with

estimates as recent as 2017 being similar to those from the early 1990s (Willig et al., 2019). It is suspected that anole numbers have also remained relatively stable over time, although this has been studied less. Moreover, evidence supporting increases in invertebrate abundances is as common as evidence supporting decreases in invertebrate abundances over the past 30 years (Schowalter et al., 2017; Willig et al., 2019). Without greater taxonomic resolution, it is difficult to view our results in light of how these changes may influence the interactions observed during this experiment. Yet, we have no a priori reason to expect that the uncovered relationships are not general.

Finally, we did not observe many exclosure effects, except a small increase in spiders after about month 6 and a more rapid decrease in the number of foliar insects on *Piper* over time (Figures 2a and 4c). Thus, the main relationships observed were not influenced by the exclosures, but this is something to remain mindful of in future studies (Spiller & Schoener, 1988).

TABLE 1 Analysis of deviance tables (Type III Wald chi-square tests) comparing anole removal and coqui removal on response variables

Variables	Chi-sq	df	p-values	Significance
Spider abundance				
Anole removal	4.15	1	0.042	*
Coqui removal	16.41	1	<0.001	***
Time	129.84	9	<0.001	***
Spiders (pre-conditions)	2.29	1	0.130	
Anole removal * coqui removal	0.07	1	0.794	
Anole removal * time	19.29	9	0.023	*
Coqui removal * time	31.24	9	<0.001	***
Time * spider (pre-conditions)	18.72	9	0.028	*
Anole removal * coqui removal * time	16.76	9	0.053	•
Flying insect abundance				
Anole removal	0.01	1	0.916	
Coqui removal	0.01	1	0.901	
Time	4.76	9	0.855	
Flying insects (pre-conditions)	4.06	1	0.044	*
Anole removal * coqui removal	3.27	1	0.070	•
Anole removal * time	5.67	9	0.772	
Coqui removal * time	9.25	9	0.414	
Time *flying insects (pre-conditions)	6.09	9	0.730	
Anole removal * coqui removal * time	6.23	9	0.717	
Abundance of foliar insects on *Manilkara*				
Anole removal	7.31	1	0.007	**
Coqui removal	0.75	1	0.388	
Time	35.99	9	<0.001	***
Foliar *Manilkara* (pre-conditions)	63.61	1	<0.001	***
Anole removal * Coqui removal	0.85	1	0.356	
Anole removal * time	6.24	9	0.715	
Coqui removal * time	7.90	9	0.545	
Time * foliar *Manilkara* (pre-conditions)	14.12	9	0.118	
Anole removal * Coqui removal * time	5.49	9	0.789	
Abundance of foliar insects on *Piper*				
Anole removal	0.29	1	0.590	
Coqui removal	2.52	1	0.112	
Time	10.40	9	0.319	
Foliar *Piper* (pre-conditions)	195.31	1	<0.001	***
Anole removal * Coqui removal	0.14	1	0.701	
Anole removal * time	18.59	9	0.029	*
Coqui removal * time	6.10	9	0.730	
Time * foliar *Piper* (pre-conditions)	5.03	9	0.832	
Anole removal * Coqui removal * time	13.39	9	0.146	
Herbivory on *Manilkara*				
Anole removal	4.91	1	0.027	*
Coqui removal	0.02	1	0.894	
Time	724.58	9	<0.001	***
Herbivory *Manilkara* (pre-conditions)	117.81	1	<0.001	***

TABLE 1 (Continued)

Variables	Chi-sq	df	*p*-values	Significance
Anole removal * coqui removal	2.54	1	0.111	
Anole removal * time	8.08	9	0.526	
Coqui removal * time	6.46	9	0.693	
Time * Herbivory *Manilkara* (pre-conditions)	92.36	9	<0.001	***
Anole removal *Coqui removal* time	4.39	9	0.884	
Herbivory on *Piper*				
Anole removal	0.14	1	0.704	
Coqui removal	0.17	1	0.677	
Time	149.55	9	<0.001	***
Herbivory *Piper* (pre-conditions)	59.98	1	<0.001	***
Anole removal * coqui removal	0.35	1	0.557	
Anole removal * time	1.92	9	0.993	
Coqui removal * time	5.01	9	0.833	
Time *Herbivory *Piper* (pre-conditions)	1.29	9	0.998	
Anole removal * coqui removal *time	8.07	9	0.527	

Note: Time is over 10 months, and pre-treatment conditions are used to control the test for the conditions measured the month before treatments started. Df = degrees of freedom, P-values are presented and significance codes: ***$p \leq 0.001$, **$0.001 < p \leq 0.01$, *$0.01 < p \leq 0.05$, •$0.05 < p \leq .10$.

4.5 | Conclusions

This study highlights that the food web of tabonuco forest is not simple and that complex interspecific dynamics characterize vertebrate insectivores, predatory arthropods, and herbivorous arthropods. Differences between the results of this study and others suggest that food webs in different areas of the forest (i.e., canopy versus understory) and even on different plant species (i.e., source webs) may not function in the same way (Prather, 2014; Schowalter, 2017). For example, the clear link between anoles, herbivorous insects, and herbivory rates in the canopy (Dial & Roughgarden, 1995) is not as evident in the understory. Furthermore, coquis have a complex relationship with arthropods, like studies on the effects of amphibians on arthropods in temperate areas (Hocking & Babbitt, 2014; Homyack et al., 2010), that may vary greatly in response to forest conditions, such as time since the last hurricane. The role these insectivores play in the leaf litter community should be addressed in future studies.

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