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ASSESSING THE FUNCTIONAL SIMILARITY OF NATIVE AND INVASIVE *ANOLIS* LIZARDS IN THE FOOD WEBS OF STRUCTURALLY-SIMPLE HABITATS IN FLORIDA

Nathan W. Turnbough
University of Tennessee, Knoxville, nturnbou@vols.utk.edu

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To the Graduate Council:

I am submitting herewith a dissertation written by Nathan W. Turnbough entitled "ASSESSING THE FUNCTIONAL SIMILARITY OF NATIVE AND INVASIVE *ANOLIS* LIZARDS IN THE FOOD WEBS OF STRUCTURALLY-SIMPLE HABITATS IN FLORIDA." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology and Evolutionary Biology.

Arthur C. Echternacht, Major Professor

We have read this dissertation and recommend its acceptance:

David A. Buehler, Susan E. Riechert, Daniel Simberloff

Accepted for the Council:

Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

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ASSESSING THE FUNCTIONAL SIMILARITY OF NATIVE AND INVASIVE *ANOLIS* LIZARDS IN THE FOOD WEBS OF STRUCTURALLY-SIMPLE HABITATS IN FLORIDA

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ABSTRACT

Invasive species often displace ecologically-similar native species, but the extent to which invading and displaced species function similarly in the food web processes of invaded communities is largely unknown. I investigated whether populations and individuals of an invasive *Anolis* lizard (the brown anole, *Anolis sagrei*) and the native congener it displaces in Florida (the green anole, *Anolis carolinensis*) are functionally equivalent in the food webs of open and structurally-simple habitats. In a system of invaded and uninvaded dredge-spoils islands, I found that both arthropod communities and winter bird communities covaried with brown anole abundance (and therefore the identity of the dominant anole species operating in island food webs) in ways that were generally well explained as the direct and indirect food web effects of greater *Anolis* predation pressure on arthropods following brown anole invasion. Larger-bodied ground and foliage-dwelling arthropods tended to be negatively associated with brown anole abundance, as was total foliage arthropod abundance; by contrast, smaller-bodied arthropods, which are less likely to serve as brown anole prey, tended to be positively associated with brown anole abundance. The abundances of arthropod-consuming birds were also negatively associated with brown anole abundance, possibly reflecting exploitative competition for prey. Although many of the observed patterns were partly or entirely co-explained by environmental and spatial covariables, both statistical evidence and mechanistic considerations strongly suggested that at least some arthropod response groups were differentially affected by green anole and brown anole populations. To evaluate the potential contribution of anole perching and foraging behavior to differential population-level effects, I compared the per-capita effects of male green and brown anoles for several arthropod prey taxa that were stocked, over a series of experiments, into field enclosures erected over small cabbage palms (*Sabal palmetto*). Despite significant differences in every measured behavioral attribute, male green and brown anoles had statistically indistinguishable effects on six of seven prey taxa, suggesting that individuals of these two species have similar per-capita effects on prey assemblages when they forage in spatially-proximate locations. This dissertation represents one of the few existing comparisons of the relative food web effects of terrestrial vertebrate predators.

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CHAPTER 1:

INTRODUCTION

Biological invasions constitute one of the greatest threats to the conservation of biodiversity (Vitousek et al. 1996, Wilcove et al. 1998, Clavero and García-Berthou 2005). Contributing to this threat are invasive species that displace their ecologically-similar native counterparts, leading in some cases to the local extirpation of those native species (e.g., Hrabik et al. 1998, Ricciardi et al. 1998, Byers 1999). Although native species displacement may be the greatest and most obvious negative impact in such invasions, little attention has been given to the further impacts that may follow, including those mediated by trophic interactions. To the degree that invaders *displace* a native species, they also *replace* that species in the food web of the invaded community (e.g., Suarez et al. 2000, MacDonald et al. 2002, Wu et al. 2009). Are invaders functionally equivalent to the native species they replace in food webs, or do they modify food web dynamics? If invaders alter the flow of energy and matter through the system, they may affect the composition and abundances of species in the community (e.g. Beisner et al. 2003). Assessing these further impacts and identifying the factors that modulate their occurrence and strength are important for understanding, managing, and predicting the effects of invasion (Parker et al. 1999, Olden et al. 2004, Ricciardi et al. 2013). Moreover, because the effects of species displacements directly relate to issues concerning the importance of species identity and trait values in ecological systems, their study can inform the broad range of ecological models and applications that explicitly or implicitly involve functional equivalence or redundancy among species (e.g., Hairston et al. 1960, Walker 1992, Hubbell 2006, Parker et al. 2010).

The functional similarity of invading and displaced species in food web processes can be considered at two levels: the population and the individual. At the population level, functional similarity simply measures the degree to which the compared species differ in their net effects on other members of the food web. Population-level similarity is therefore a pattern, and it can be influenced both by differences in species abundances (or biomasses) and differences in per-capita effects (Parker 1999; see also Chapter 2, Figure 2.1). Although differences in net effects are likely to be the level of functional similarity most useful for documenting invasion impacts and setting conservation or management priorities, they cannot be predicted or mechanistically modeled without knowledge of (or assumptions about) the relative per-capita effects of the invading and displaced species on other food web members—that is, their individual-level functional similarity. Because differences in per-capita food web effects reflect differences in the rates or occurrence of underlying trophic interactions, studies that assess these differences and the factors that cause them can improve mechanistic understanding of ecological systems, and thus have import beyond their usefulness for understanding and predicting invasion impacts. It is important to note that nonconsumptive processes—for example trait-mediated effects or habitat modifications—can also affect the functional similarity of native and invading species (e.g., Wikström and Kautsky 2004, James et al. 2011). However, for consumers and especially predators, trophic interactions may be, on average, the most important driver of impacts.

In general, the available evidence suggests that predators occupying similar trophic positions are unlikely to be functionally equivalent across all ecologically relevant responses, but data are scarce for comparisons of native versus introduced species, closely-related species, and terrestrial species—especially terrestrial vertebrates. Additional research is needed in these areas, as generalities concerning functional similarity in one class of comparison might not apply to others. For instance, meta-analyses suggest that introduced predators have, on average, greater impacts on prey populations than do native predators (Salo et al. 2007, Paolucci et al. 2013), but these analyses compare the effects of predators that operate in different systems and vary widely in phylogenetic affinity. By contrast, invader–native species displacements often involve closely-related species (e.g., Porter et al. 1988, Kiesecker et al. 2001, Santulli et al. 2014), and the question of functional similarity among invading and displaced species applies, quite obviously, to their effects in the same system. Most within-system assessments of the functional similarity of predator species have been in aquatic environments (e.g., Menge 1983, Van Buskirk 1988, Morin 1995, Chalcraft and Resetarits 2003b, Resetarits and Chalcraft 2007), but because food web structure and dynamics differ between aquatic and terrestrial systems (Strong 1992, Polis and Strong 1996, Shurin et al. 2006), the results of these studies may have limited applicability to the functional similarity of terrestrial predators. Functional similarity studies in terrestrial systems are dominated by comparisons of syntopic native arthropod species (e.g., Riechert and Lawrence 1997, Schmitz and Suttle 2001, Finke and Denno 2005, Otto et al. 2008, Philpott et al. 2008, Sanders and van Veen 2011). However, as per the theory of limiting similarity, coexisting native species may be expected to differ more in their ecology (and thus trophic interactions) than would similarly-related invading and displaced native species. Moreover, these arthropod studies may have limited applicability to terrestrial vertebrates, as great differences in size and phylogenetically-linked biological traits likely cause arthropods and vertebrates to function differently in food webs (Woodward et al. 2005, Brose et al. 2006, Bersier and Kehrli 2008). As the above limitations in the available data reveal, the degree to which closely-related native and invading predators are functionally similar in food web processes is very much an open question, particularly for terrestrial vertebrates.

Introductions of *Anolis* (Polychrotidae) lizards provide many opportunities to further our understanding of the relative food web effects of ecologically-similar and, in many cases, closely-related vertebrate predators. Members of this New World genus have been introduced to dozens of locations around the world in the past century (Kraus 2009), and since many anole species thrive in human-disturbed environments and frequently stowaway in cargo or nursery stock shipments (Powell et al. 2011), further introductions are likely to continue well into the foreseeable future. Introduced anoles are presently known or suspected to have displaced a single anole species on the U.S. mainland (Campbell 2000), several anole species in the Caribbean (Powell et al. 2011), and a scincid lizard in Japan's Ogasawara Islands (Hasegawa et al. 1988, Suzuki and Nagoshi 1999). Competitive displacement and niche partitioning are hallmarks of anole–anole interactions in the Caribbean (reviewed in Losos 2009), and in this region, at least, additional examples of native or resident anole displacements are likely to multiply in the future. Whether anoles will displace more distantly-related lizard taxa in the far-flung and expanding reaches of their invaded range remains to be determined.

Anoles have been extensively studied for decades, both in their natural history and as model organisms for a variety of behavioral, ecological, and evolutionary phenomena (Losos 2009), and the literature accumulated from these studies forms a rich backdrop for informing and interpreting studies of anole displacement effects, particularly when the displaced species is also an anole. For instance, studies of interspecific competition, niche partitioning, and natural history have yielded vast amounts of data on the habitat use and diets of many anole species. Further, the concept of ecomorphs—groups of species that utilize similar microhabitats and have independently evolved similarities in morphology and behavior—emerged from the study of Caribbean *Anolis* (Williams 1972, Williams 1983), and for the scores of *Anolis* species with ecomorph associations, multiple morphological and behavioral traits (e.g., toepad size and foraging movement rates) may be surmised from ecomorph class if they have not already been characterized (Moermond 1979, Glossip and Losos 1997, Johnson et al. 2008; reviewed in Losos 2009). Knowledge of similarities and differences in the diets and ecological, morphological, and behavioral traits of invading anoles and displaced lizard species can facilitate both the prediction of displacement impacts and the mapping of differential effects to particular trait value differences (see Chalcraft and Resetarits 2003a).

Reciprocally, knowledge of the functional similarity between invading anoles and displaced lizard species (particularly anoles) can improve our understanding of anole ecology and the ecological and evolutionary processes for which anoles serve as a model system. For instance, much research has been focused on how morphological adaptations corresponding to habitat use affect anole locomotor performance for various aspects of the habitat (e.g., Losos and Sinervo 1989, Elstrott and Irschick 2004, Irschick et al. 2005), but how those morphological adaptations (or behavioral adaptations, for that matter) affect trophic interactions with other species remains almost entirely unstudied. If, for example, toepad size affects foraging success in leafy microhabitats, then functional equivalence studies may reveal greater per-capita effects on foliage-dwelling arthropods for anoles with larger toepads, and these studies may in turn provide insight into the selective forces driving the evolution of larger toepads in anoles perching higher in the vegetation (Macrini et al. 2003, Stuart et al. 2014).

The brown anole, *Anolis sagrei*, is one of the most widely introduced and best studied species of *Anolis*. Native to Cuba and the Bahamas, this highly invasive “trunk–ground” anole has been introduced around the world to locations as disparate as islands in the Caribbean (Minton and Minton 1984, Powell et al. 2011 and references therein), Mexico (Calderon et al. 2003, Zamora-Abrego et al. 2006), the U.S. mainland (Oliver 1950), the Hawaiian Islands (Kishinami and Kishinami 1996, McKeown 1996), Taiwan (Norval et al. 2002), Singapore (Tan and Lim 2012), and, most recently, Bermuda (Stroud and Giery, in prep.). Since their introduction onto mainland Florida in the 1940s (Lee 1985, Kolbe et al. 2004), brown anoles have spread throughout much of Florida and into several surrounding states, as far north as South Carolina and as far west as Texas (King et al. 1987, Thomas et al. 1990, Echternacht et al. 1995, Campbell 2003, Turnbough 2006, 2012); disjunct populations also occur in California (Mahrdt et al. 2014). In Florida, brown anoles invade nearly all terrestrial habitat types, from dense forests to urban environments (Turnbough, pers. obs.), but they reach their highest abundances in open and disturbed habitats (Meshaka et al. 2004).

As brown anoles invade open and disturbed habitats in Florida, they quickly displace a less abundant native congener, the green anole (*Anolis carolinensis*). Green anoles are the only anole species native to North America, to which they dispersed from Cuba no later than the Pleistocene (Buth et al. 1980, Holman 1995, Glor et al. 2005). Although green anoles are "trunk–crown" ecomorphs (Williams 1983, Losos 2009), they inhabit a wide variety of habitat types and generally utilize the full range of available vertical space within them (i.e., from ground to treetops; Collette 1961, Jenssen et al. 1995). This spectrum of habitat use represents a niche expansion from their ancestral stock in Cuba (*A. porcatus*) that undoubtedly resulted from the absence of other *Anolis* (see Schoener 1975, Lister 1976). In densely vegetated or structurally complex habitats, brown anole invasion leads to an upwards shift of green anole perch height distributions and a possible decline in their densities (Vincent 2002), with a resulting pattern of coexistence seems to mimic the niche partitioning observed between brown anoles and green anole analogs in Cuba and the Bahamas (Schoener 1968, Lister 1976, Rodríguez-Schettino et al. 2010). In open or structurally-simple habitats, however, the upwards shift in green anole perch height is accompanied by the rapid crash of their populations (Campbell 2000, Stuart et al. 2014), which effectively changes the identity of the anole operating in the food webs of these systems. The mechanisms responsible for the vertical displacement of green anoles are incompletely understood, at least for males (see Edwards and Lailvaux 2013), but the reduction of their densities likely results from a combination of intraguild predation by adult brown anoles on juvenile green anoles (Gerber and Echternacht 2000), reduced green anole fecundity (Vincent 2002), and fewer territory options in the higher vegetation (Echternacht 1999).

Although broad ecological similarities between green and brown anoles imply that they share nearly identical sets of predator and prey species (i.e., they occupy the same food web node), differences in their abundance and ecomorph-associated behavioral patterns likely cause them to differ in both their net and per-capita effects on other food web members. Both species are small, diurnal, territorial, sexually-dimorphic, generalist insectivores that utilize a similar range of perch heights in the vegetation (when the other species is rare or absent; Edwards and Lailvaux 2012, Stuart et al. 2014) and consume similar types of prey (at least at the ordinal level; Campbell 2000). Their nearly identical size, as measured by snout–vent length, probably ensures that they share the same suite of lizard predators (see Campbell and Echternacht 2003, Meshaka et al. 2004 and references therein). Despite these similarities, brown anoles attain higher population densities in relatively open or simple habitats, such that their displacement of green anoles from these habitats results in at least a three-fold increase in total *Anolis* density (Campbell 2000). Moreover, because brown anoles have heavier build than the more gracile green anoles, total *Anolis* biomass is likely to be 4–5 times greater in these habitats following brown anole invasion (see Campbell 2000). Such increases in anole density and biomass are likely to alter the flow of energy and matter through the anole food web node and affect the abundances of at least some arthropod prey species. In addition, patterns of per-capita interaction strengths with prey species likely differ between green and brown anoles due to differences in their perch and foraging behavior. For instance, trunk–ground brown anoles are more likely to perch near or on the ground than are trunk–crown green anoles, which are more likely than brown anoles to perch on the leaves and outer branches of vegetation (Schoener 1975, Stuart et al. 2014, Turnbough unpubl. data). Thus, per-capita effects on ground-dwelling arthropods may be greater for brown anoles than green anoles, and per-capita effects on foliage-dwelling arthropods may be greater for green anoles than brown anoles. As another example, the more active foraging mode of green anoles may allow them to more frequently detect and capture hidden or cryptic prey (Huey and Pianka 1981).

Data to evaluate the functional similarity of green and brown anoles in food webs are not available in the current literature, nor have the relative food web effects of any two *Anolis* in the same system been rigorously assessed. This lack of data is not due to a want of brown anole studies: the direct and indirect food web effects of brown anoles have been intensively studied in the Bahamas since the 1980s, and their impacts in Taiwan have more recently been investigated. In their native Bahamian range, brown anoles have strong negative impacts on web spiders and weak negative impacts on large, aerially-active arthropods (Spiller and Schoener 1988, 1998; Schoener and Spiller 1996, 1999), and indirect evidence from altered herbivory levels suggests that brown anoles also negatively impact folivorous arthropods (Spiller and Schoener 1990, 1994). Moreover, small aerially-active arthropods and parasitoids are frequently positively affected by brown anoles, probably through the negative brown anole effect on web spiders (Spiller and Schoener 1994, Schoener and Spiller 1999, Schoener et al. 2002; note that studies in this system technically address the effects of all lizards and not just brown anoles, but brown anoles comprise the vast majority of such lizards). In Taiwan, invading brown anoles have been found to negatively impact salticid spiders and alter the composition of ant assemblages (Huang et al. 2008a, b). Although the main features of documented brown anole food web effects generally correspond well to those observed for other species of *Anolis* (Pacala and Roughgarden 1984, Dial and Roughgarden 1995), similar types of quantitative data are lacking for green anoles or their Caribbean analogs. Convincing—but circumstantial—evidence links green anole invasion of the Ogasawara Islands to declining or extirpated populations of diurnally-active longicorn beetles, jewel beetles, bees, and odonates (Makihara et al. 2004, Abe et al. 2008, Karube 2009, Yoshimura and Okochi 2010). Whether brown anoles would likely have similar impacts in the Ogasawara Islands, or whether green anole effects on arthropods in the Bahamas or Taiwan would likely be similar to those of brown anoles, cannot be assessed from the currently available data.

Data concerning the relative food web effects of different anole species in the same system have been reported in only three studies, each of which yielded inconclusive results. Dial (1992) presented differences in the prey suppression patterns of two trunk–crown anoles in Puerto Rican rainforest canopies, but because these patterns derived from small sample sizes ($n = 2$) and were not analyzed statistically, the likelihood that they could have arisen by chance is unknown. In Florida, Campbell (2000) statistically evaluated sticky-trapped arthropods on islands dominated by green versus brown anoles, but the comparison was unreplicated ($n = 1$) and thus the patterns he observed cannot be differentiated from sampling error. Losin (2012) found little evidence that experimental reduction of male brown anole or male crested anole (*A. cristatellus*, another trunk–ground invader) densities affected sticky-trapped or pitfall-trapped arthropods in South Florida, but this outcome probably resulted from a combination of small reductions in total *Anolis* densities (apparently averaging around 12%, assuming 1:1 population sex ratios) and relatively short timeframe (arthropods were sampled eight weeks after density manipulations). The lack of robust data concerning the relative food web effects of different lizard species in the same environment is not limited to anoles; with the exception of Petren and Case's (1996) comparison of prey depletion levels for two gecko species in unenclosed aircraft hangars in Hawaii, I have been unable to find comparative food web effect data for any non-anoline lizard species (though prey niche overlap studies abound).

In this dissertation I assess both the population-level and individual-level functional similarity of green anoles and brown anoles in the food webs of open and structurally-simple habitats in central Florida. Characteristics of the habitats utilized for this effort are, to varying degrees, similar to those of the wide range of natural, semi-natural, and human-modified habitats in which brown anoles appear, anectodotally, to largely displace green anole populations. Such habitats are a common element of many landscapes in Florida and other southeastern states, and the population dynamics of native species that make use of them may be affected by changes wrought by invasive species. If the food web effects of green anoles and brown anoles vary greatly in these habitats, the total landscape-level impacts of brown anole invasion could be substantial, particularly in landscapes greatly modified by humans.

In Chapter 2, I use a series of invaded and uninvaded spoils islands to assess whether brown anole abundance (a proxy for the extent of green anole displacement) is associated with variation in the composition of three different arthropod communities sampled from two habitat types. These islands belong to the system of spoils islands used by Campbell (2000) to experimentally demonstrate a crash in green anole population densities following brown anole invasion, and thus Chapter 2 addresses the population-level functional similarity of green anoles and brown anoles in island food webs.

In Chapter 3, I use experimental cabbage palm (*Sabal palmetto*) enclosures to compare the per-capita effects of individual green anole and brown anole males on various arthropod prey taxa. Cabbage palms are a common and often dominant vegetational component of habitats in which brown anoles displace green anole populations, including those sampled in the Chapter 2 study. Chapter 3 thus addresses the individual-level functional similarity of green anoles and brown anoles in food webs, and serves as a test for one of the mechanisms (namely, differential per-capita effects) potentially responsible for patterns observed in Chapter 2.

In Chapter 4, I investigate whether a negative association between the abundances of brown anoles and foliage-dwelling arthropods affects the habitat use patterns, and thus local abundance, of insectivorous (mostly foliage-gleaning) birds, again using the system of invaded and uninvaded spoils islands. This chapter extends the study of population-level functional similarity beyond downstream effects on arthropod communities (Chapter 2) to effects that may reverberate back up food chains to potential anole competitors.

In addition to investigating the community-level impacts of a particular instance of invasion for a widely-introduced invasive lizard, this dissertation generates data regarding the functional similarity of closely-related vertebrate predators in food web processes, a subject for which few data exist.

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CHAPTER 2:

ARTHROPOD COMMUNITY DIFFERENCES ON ISLANDS DOMINATED BY NATIVE VERSUS INVASIVE *ANOLIS* LIZARDS

ABSTRACT

When invasive species displace ecologically similar resident species, the total impacts of invasion will depend upon the degree to which the invading and displaced species are functionally equivalent in ecological processes, including food web interactions. Though studies suggest that ecologically similar species are unlikely to have functionally equivalent effects on all relevant responses, closely related species have rarely been compared, especially among terrestrial vertebrates. I sampled arthropod communities on a series of 33 similar islands in Florida to assess whether invading *Anolis* lizards (brown anoles, *Anolis sagrei*) differ in their food web effects from the native congener they displace (green anoles, *A. carolinensis*). Brown anole abundance, a proxy for the extent of green anole displacement, significantly explained community composition patterns for ground-active and foliage-dwelling arthropods, but not aerially-active arthropods. Within ground and foliage arthropod communities, significant associations between brown anole abundance and response group abundances were always negative for responses comprised primarily of large (adult length > 2 mm) arthropod species and positive for responses composed primarily of small (adult length ≤ 2 mm) arthropod species. Brown anole abundance was negatively associated with the total abundance and biomass of foliage arthropods, but not ground arthropods. In general, significant associations between brown anole abundance and arthropod responses were well explained as the direct and indirect food web effects of greater anole predation pressure on arthropods following brown anole invasion. Although the contingencies of invasion in this system of islands caused the explanatory power of brown anole abundance to overlap substantially with that of both environmental and spatial covariables, in most cases the competing explanations offered by these

covariables did not match patterns expected from relevant ecological mechanisms. This study represents the first statistically-validated, population-level assessment of the relative food web effects of two different anole species, and it is one of few existing investigations into the functional equivalence of vertebrate predator species in natural systems.

INTRODUCTION

Invasive species frequently displace ecologically similar resident species (e.g., Case et al. 1994, Lodge et al. 2000, Reitz and Trumble 2002). Understanding how these displacements further impact invaded ecosystems is important not only for identifying, managing, and predicting the effects of invasions (Parker et al. 1999, Olden et al. 2004, Ricciardi et al. 2013), but also for generating insight into the importance of species identity and trait values in ecological systems (Finke and Snyder 2010). Because the potential for displacements to affect community composition or ecosystem functioning depends upon the degree to which invading and displaced species are functionally equivalent, or redundant, in ecological processes, studies of their effects can inform the broader range of ecological models and applications that explicitly or implicitly revolve around equivalence or redundancy among species. Examples of these include models and analyses in which species are aggregated into guilds, functional groups, or trophic levels (e.g., McQueen et al. 1986, Leibold 1989, Sugihara 1997, Hubbell 2006), the use of redundancy-influenced species valuations to set conservation priorities or determine expendability (Walker 1992), and restoration activities that replace lost species with nonnative ones (Lazell 2002, Parker et al. 2010). For displacements involving consumers, particularly predators, further impacts are probably most frequently governed by similarity in the species' trophic interactions with other food web members, though nonconsumptive processes can also be important (e.g., James et al. 2011).

In general, studies indicate that the effects of consumers occupying similar trophic positions are unlikely to be functionally equivalent across all ecologically relevant responses, but closely related species have only rarely been investigated. Many studies have demonstrated differential food web effects among consumers belonging to different families, orders, classes, or even phyla (e.g., Morin 1995, Murakami and Nakano 2000, Snyder and Wise 2001, Chalcraft and Resetarits 2003b, Finke and Denno 2005, Grabowski et al. 2008). Such studies are valuable, but invader–resident displacements often involve species that are more closely related (e.g., Gurnell et al. 2004, Larson and Magoulick 2009, Short and Petren 2012). Since species traits ultimately drive patterns of effects, and trait similarities are likely to correlate with phylogenetic affinity (at least within families and genera), it is reasonable to expect that displacements of closely related species will result in lesser impacts, on average, than those involving more distantly related taxa. However, even morphologically and ecologically similar congeners can differ in their effects and responses to prey in ways that might be difficult to predict *a priori* (Resetarits and Chalcraft 2007), or have drastically different community-level effects (Porter et al. 1988, Porter and Savignano 1990). Since natural systems are complex and there are myriad opportunities for species idiosyncrasies and context dependencies to influence species displacement impacts (see Mack et al. 2000, Ricciardi and Simberloff 2009), near-term progress in predicting these impacts may hinge on our ability to distill patterns or mechanistic insights from an accumulation of case studies. Additional case studies will be needed for such efforts, and data for terrestrial vertebrates are currently particularly scarce.

In Florida and probably elsewhere in the southeastern U.S., invasive brown anole lizards (*Anolis sagrei*) displace their native counterpart, the green anole (*A. carolinensis*). Brown anoles are native to Cuba and the Bahamas, but they have been introduced around the world to locations that include several Caribbean islands, the U.S. mainland, the Hawaiian Islands, Taiwan, and Singapore (Oliver 1950, McKeown 1996, Norval et al. 2002, Powell et al. 2011 and references therein, Tan and Lim 2012). In the U.S., brown anoles have spread from their initial introduction onto mainland Florida in the 1940s as far north as South Carolina and as far west as Texas, with disjunct populations occurring in California (Lee 1985, King et al. 1987, Turnbough 2006, Mahrdt et al. 2014). Brown anoles are known both anecdotally and experimentally to displace green anoles in Florida (Christman 1980, Campbell 2000), and observational evidence suggests this effect also occurs in at least Louisiana (Edwards and Lailvaux 2012). In densely vegetated or structurally complex habitats, brown anole invasion leads to an upward shift in green anole perch height distributions and a possible reduction in green anole densities (Echternacht 1999, Vincent 2002), a pattern of coexistence that seems to mimic niche partitioning between brown anoles and green anole analogs in Cuba and the Bahamas (Schoener 1968, Rodriguez-Schettino et al. 2010). In open or structurally simple habitats, however, brown anoles can displace green anoles entirely, or nearly so, which effectively changes the identity of the anole operating in the food webs of these systems (Campbell 2000). Disturbed and naturally open environments comprise a large and ever-increasing portion of the Florida landscape, and they are the focus of this study. Because these environments provide habitat for a variety of wildlife, if green and brown anoles have differential food web effects within them, the cumulative, landscape-level effects of brown anole invasion could be substantial.

Green and brown anoles are ecologically similar and likely share nearly identical sets of predator and prey species. Both species are small, diurnal, territorial, sexually dimorphic, generalist insectivores that perch at a similar range of heights in the vegetation (when the other species is absent or rare; Edwards and Lailvaux 2012, Stuart et al. 2014) and consume similar types of arthropod prey. Syntopic populations of the two anoles in Florida have a high degree of overlap in both the kinds and proportional composition of arthropod prey consumed, at least at a coarse (predominantly ordinal level) taxonomic scale (Campbell 2000). Given their nearly identical sizes (as measured by snout–vent length, SVL), they probably also share the same suite of lizard predators, and several known green anole predators have been observed to consume brown anoles (Campbell and Echternacht 2003, Meshaka et al. 2004 and references therein). These similarities in predators and prey imply that green and brown anoles occupy the same node in food webs.

Despite their identical positions in food webs, green and brown anoles are likely to differentially affect other food web members through two mechanisms that are probably common among invader–resident displacements (Figure 2.1; all tables and figures are in Appendix 2). First, invaders often maintain higher densities or standing biomass than do the species they displace (Byers et al. 2002, Snyder and Evans 2006); unless greater conversion efficiencies are responsible for the difference (e.g., Byers 2000), greater invader densities or biomass will likely result, at minimum, in negative impacts on frequently consumed prey species. Brown anole densities in both their native and introduced range rank among the highest reported for lizards (Schoener and Schoener 1980, Campbell and Echternacht 2003)—up to 1.2 adult anoles per square meter in Florida. Although such extreme densities are probably rarely attained or subsequently maintained, population data from experimental introductions in Florida suggest that brown anole densities are typically at least three times greater than those of displaced green anoles (Campbell 2000). Further, brown anoles are more robust and weigh about 1.5 times more (for a given SVL) than the more slender green anoles, at least in central Florida (Campbell 2000). Thus, brown anole invasion probably increases total anole biomass in open habitats in Florida by a factor of 4–5x, and the deduction that at least some arthropod prey must be affected by this increase seems inescapable. Second, invading and displaced species may have differing patterns of per-capita trophic interaction rates with other species due to differences in their foraging behavior, prey preferences or handling abilities, or other morphological or behavioral differences; in the absence of greater invader abundance or biomass, these differential per-capita interactions are likely to negatively impact some food web members and positively affect others. The relative per-capita effect patterns of green and brown anoles are likely to be influenced in several ways by their membership in different ecomorph classes—groups of species that utilize microhabitats in similar ways and exhibit correlated morphological and behavioral attributes (Williams 1983, Losos 2009). As trunk–ground anoles, brown anoles are more likely to perch closer to or on the ground than are trunk–crown green anoles, which are more likely to perch on the leaves and outer branches of the vegetation (Schoener 1975, Stuart et al. 2014, Chapter 3). Thus, relative to green anoles, brown anoles may have greater per-capita effects on ground-active prey and weaker per-capita effects on foliage-active prey. Trunk–ground anoles are also better characterized as sit-and-wait foragers than are trunk–crown anoles, which spend more time actively moving through their environment; as a result, brown anoles may be less likely than green anoles to detect hidden or cryptic prey. Of course, both greater densities and differential per-capita interactions may act in concert to generate impacts from brown anole–green anole and other invader–resident displacements, and given the complexities of natural food webs and the variety of direct and indirect effects that may occur, the net impacts of species displacement may differ from predictions derived from differences in species densities, traits, or ecologies.

I sampled arthropod communities on a series of invaded and uninvaded islands in Florida to assess how these communities may be impacted by the identity of the anole operating within the food web. Brown anoles displace and essentially replace green anoles in some habitat types on these islands, with consequent increases in total *Anolis* density (Campbell 2000), and I predicted that arthropod community composition would be altered in these habitats on invaded islands. Based on anole density patterns, behavioral differences, dietary data, and food web effects in other systems, I made several additional predictions (Table 2.1) concerning the relative strengths of invasion impacts on arthropods in differing habitats, community types, and size classes. To my knowledge, this study represents the first statistically-validated, population-level assessment of the relative food web effects of different lizard species, anoline or otherwise.

METHODS

Study system

This study was conducted on dredge-spoils islands in Mosquito Lagoon, an estuary in Volusia and Brevard Counties, Florida. In the 1950's, a regularly-spaced, nearly linear array of more than 60 spoils islands was created along the western edge of Mosquito Lagoon as a byproduct of dredging operations for the Intracoastal Waterway (ICW), a large shipping channel (Campbell 2000). From this array I selected the 34 large (0.6–3.6 ha), dome-shaped islands west of the ICW between Oak Hill and Haulover Canal that contained an open interior (xeric habitat) fully or partially encircled by an inner band of forest habitat and an outer band of brackish marsh habitat (Figure 2.2). Study islands were roughly equidistant from the mainland (mean distance = 240 m, SD = 76 m), and several were connected to one or two other "islands" by marsh habitat. I considered marsh-connected islands to be independent sampling units under the rationale that compared to similar islands with closely-approaching but disjunct marshes, such connections were unlikely to appreciably affect the xeric and forest arthropod communities under study; this assumption was supported *a posteriori* by a lack of significant difference in the relative similarity of arthropod communities on marsh-connected versus unconnected neighbors (one-way Wilcoxon signed-rank tests, $n = 11$, all P values ≥ 0.29; see Appendix S1 for greater detail). All study islands and adjacent mainland areas were protected within the combined boundaries of Canaveral National Seashore and Merritt Island National Wildlife Refuge.

Xeric and forest habitat features were broadly similar across study islands. Xeric habitats were open expanses of sand and shell fragments that contained scattered clumps of scrubby vegetation and little to no intervening ground cover; small coquina sandstone rocks were also present on many islands. Fully or partly surrounding xeric habitats were bands of forest that ranged approximately 7–36 m in mean width and varied in structure from dense, scrubby thickets to mature forests with relatively open understories. Vegetation in both habitats was dominated by southern redcedar (*Juniperus virginiana var. silicicola*) and cabbage palms (*Sabal palmetto*); other vegetation was comprised mostly of *Serenoa repens*, *Schinus terebinthifolia*, *Morella cerifera*, and *Myrcianthes fragrans*. Differences in xeric and forest vegetation among islands were primarily related to the relative abundances of these species, their stature, and the total extent of their cover. Some variation in habitat structure was correlated with island position: the ten northernmost study islands were situated in relatively deep surrounding waters and tended to have steeper elevation profiles with less extensive, scrubbier forests and marshes (see Appendix S1 for habitat structure data).

Spoils islands in Mosquito Lagoon serve as a model system for brown anole displacement of green anoles in open or disturbed Florida habitats (Campbell 2000). Green anoles were well-established in this system when the islands were first utilized for anole studies in 1995 (Stuart et al. 2014), and I assumed that green anoles had attained typical population densities on all study islands prior to the arrival of brown anoles (with a single exception discussed below). Brown anole colonization of the islands probably began in the late 1980s, when their presence was first reported in Brevard and Volusia counties (Cochran 1990, Campbell 1996). Although anoles can naturally colonize islands (e.g., Schoener et al. 2001, Calsbeek and Smith 2003) and overwater dispersal of green anoles has been observed in this system (Campbell 2000), in most cases brown anoles were probably accidentally transported to islands by the recreational boaters, anglers, and campers that frequently visit them. Three study islands were previously used in a brown anole introduction experiment that demonstrated a rapid decline in green anole densities concurrent with brown anole population expansion (Campbell 2000). In that experiment, decimated green anole populations were largely displaced from xeric and forest habitats and remained primarily in marshes and adjacent forest–marsh edges. Thus, in this study I inferred the presence of dense brown anole populations to indicate that brown anoles had effectively replaced green anoles in the food webs of xeric and forest habitats, and I assumed that this transition was in progress on islands where brown anoles were present but relatively rare.

Anole abundance estimates and arthropod sampling

I assessed relative brown anole abundance and sampled arthropod communities on study islands in June 2006. The logistics of travel between islands prevented a randomized order of island visitation; instead, I divided the islands into blocks of four adjacent islands, with a remaining block of two islands, and randomized the visitation of island blocks. Some modifications to the planned visitation order were made as necessitated by adverse weather and other factors (Appendix S1). All sampling activities were completed for islands within a block over a period of two consecutive days.

To estimate brown anole abundance, I summed the counts obtained in four 10-minute visual searches conducted along different sections of the xeric–forest edge. Searches were conducted between 0800 and 1030 h in sunny or partly sunny conditions. In each search, forest edge vegetation was methodically scanned over a route approximately 15 m long, and the species and sex of all adult anoles observed within 4 m of the forest edge were recorded. Search routes were haphazardly divided among three observers, and I made minor adjustments to brown anole count totals to correct for differences in observer detection probabilities (Appendix S1). Repeated counts taken over multiple dates on three islands showed that individual counts and island totals were repeatable to within a few anoles, and mark-resight density estimates (Heckel and Roughgarden 1979) made for two of those islands demonstrated that brown anoles were rare where count totals were low (total count = 2, density [95% CI] = 167–618 lizards/ha) and abundant where totals were high (total count = 55, density = 4,630–5,790 lizards/ha). Although green anoles were also counted, total green anole counts were too low (maximum = 7) for this count method to provide meaningful relative abundance estimates. On one island, neither anole species was observed during this study or subsequent fieldwork; I considered this island to lack anoles and excluded it from all analyses. Additional details concerning search route locations, count adjustments, repeated counts, and density estimates are provided in Appendix S1.

In order to model the predicted effects of green anole replacement in island food webs, I classified islands into two groups according to the presumed identity of their dominant anole species—"green anole islands" and "brown anole islands." The available evidence from Campbell's (2000) introduction experiment indicates that green anoles were almost completely displaced from xeric and forest habitats (except forest–marsh edges) when brown anole densities reached approximately 1500–2500 lizards/ha, which likely corresponded to total brown anole counts around 3–9 in this study (Appendix S1). I used a gap in the ranked order of brown anole count totals as the delimiter between green anole and brown anole islands (total count ≤ 2 and ≥ 8, respectively). For descriptive purposes in figures, uninvaded green anole islands are distinguished from those on which brown anoles were present, but rare.

Prior to statistical analyses, brown anole abundance estimates were $\log_{10}$(total count + 1) transformed (hereafter, BA_{Abund}) to reduce the leveraging power of the highest abundances and eliminate the positive relationship between abundance estimates and their variance.

Foliage-dwelling arthropod communities (FOL) were sampled by sweep netting the forest edge along the same routes used for anole counts. Four samples, each consisting of 20 sweeps (net diameter = 38 cm) taken between one and two meters in height, were collected per island between 0700 and 1600 h on the day before or the day after the anole counts. Sweep samples were placed on ice in the field and later frozen to facilitate arthropod retrieval. Plant species composition was estimated to the nearest 10% for the vegetation swept in each sample.

Ground and aerially-active arthropod communities (GND, AER) were sampled at two locations in both the xeric and forest habitats (subscripts $_{Xer}$ and $_{For}$). At each sampling station

(Appendix S1), a linear array of three pitfall traps (spaced 4 m apart) and one sticky trap was set up and left open for 24 hours; pitfall trap locations were shifted as necessary in xeric habitats so that each trap was sited on open ground 1 m away from the nearest vegetation. Pitfall traps were clear plastic cups (diameter 11.5 cm, height 7.2 cm) partly filled with Sierra™ brand propylene glycol antifreeze (diluted to 50% in water) and covered with a raised, plastic plate rain guard. Sticky traps were the same plastic cups coated with Tanglefoot adhesive (Contech Enterprises Inc.) on their outer walls and mounted upside down 1 m above the ground on an upright PVC pipe. All vegetation within 0.5 m of sticky traps was trimmed away in forest habitats. Mineral spirits were used to clear adhesive from sticky-trapped arthropods prior to preservation.

All collected arthropods at least 1 mm in length were preserved in 70% ethanol and sorted to morphospecies. Morphospecies were identified at least to order, and usually to family, using published keys (e.g., Kaston 1978, Borror et al. 1989, Ubick et al. 2005, Marshall 2006); genus and species identifications were made in some cases, particularly among ants and spiders. The lengths of all collected arthropods were measured to the nearest 0.1 mm with digital calipers for biomass estimation. In cases where more than five individuals of the same morphospecies were captured in a single trap and were similar in size, the lengths of five haphazardly chosen representatives were measured and their mean estimated biomass was applied to the unmeasured individuals. Biomass was estimated using several published sets of arthropod length–biomass power models. For each morphospecies, I selected the model offering the finest taxonomic resolution (see Hodar 1996, Gruner 2003); when such resolution was available from multiple publications, I gave priority first to similarity in the community type used to construct the model (ground vs. foliage) and second to a combination of geographic proximity and habitat similarity (prioritized Sample et al. 1993 > Hodar 1996 > Gruner 2003).

Environmental and spatial explanatory covariables

I assembled sets of environmental and spatial covariables to assess, as well as statistically control for, the explanatory power of environmental variation for arthropod community variation. Environmental covariables included factors likely to affect arthropod community structure as well as those that can affect arthropod representation in samples (Table 2.2). Spatial covariables modeled distance relationships among islands and primarily served as proxies for spatially-structured environmental factors that may not have been captured by environmental covariables. I assembled different covariable sets for xeric, forest, and xeric–forest edge habitats.

Environmental covariables potentially affecting arthropod community structure were derived using principal component analyses (PCAs) of habitat structure and vegetational composition variables. Structural features (Table 2.3) were characterized using both visual assessments in the field and measurements taken from freely available aerial imagery (Florida Land Boundary Information System, http://data.labins.org/2003/). Xeric and forest vegetational compositions were evaluated by visually estimating, for four non-overlapping regions, the proportion of visible vegetated area covered by each of the common plant species. For analysis of foliage arthropods collected at the xeric–forest edge, plant species representation in the swept vegetation was used for PCA instead of proportional cover estimates. Environmental covariable sets also included measures of vegetational diversity, calculated as Simpson’s diversity index ($1 - D$; Magurran 2004) using plant cover or swept vegetation estimates as abundances. Principle component interpretations and further details regarding data collection for habitat structure and vegetational composition variables are supplied in Appendix S1.

Environmental covariables potentially affecting the relationship of arthropod samples to sampled communities were based on sampling date and conditions. Sampling date (day in June) was used to capture seasonal variation in arthropod communities and broad changes in weather patterns. For 24-hour pitfall and sticky trap sampling in the xeric and forest habitats, finer-scale variation in the prevailing weather conditions was modeled using a PCA of weather data (maximum and minimum temperatures, five-day weighted rainfall totals; Appendix S1) from the nearby Titusville NOAA weather station (15 km from the nearest study island). For forest edge sweep samples, conditions present during sampling were more relevant and were modeled with a PCA of the time (minutes past 0700 h, square-root transformed) and temperature (1 m above ground in xeric habitat shade) at the start of sweep sampling. Because the sweep net interacted differently with wet foliage than dry foliage, observation of whether rain fell the previous afternoon or evening was also incorporated into the forest edge covariable set.

Spatial covariables were generated using Moran's eigenvector maps (MEM) and selected to optimize explained arthropod community variation. The MEM framework is a generalized form of the principle coordinates of neighbor matrices (PCNM) approach (Dray et al. 2006); PCNM uses the eigenvalue decomposition of a truncated matrix of geographic distances among sampling units to generate spatial variables (eigenvectors) that model spatial variation at a range of scales (Borcard and Legendre 2002). Greater flexibility in modeling spatial variation is provided by MEM through the incorporation of a spatial weighting matrix, which allows different connectivity/neighborhood algorithms to be used and various relationships between geographic distance and similarity to be defined. Since choice of the spatial weighting matrix is the most critical MEM step, unless the appropriate weighting matrix (i.e., the nature of response variable spatial interactions) is known or expected, Dray et al. (2006) recommend a data-driven approach that selects the best fitting spatial weighting matrix using (for small samples) the bias-corrected Akaike's information criterion (AIC_C; Hurvitch and Tsai 1989). Following this recommendation, I generated 126 unique spatial weighting matrices using two different neighborhood algorithms and a two-parameter distance–similarity function, and selected from among them the best-fitting MEM set for each analyzed arthropod community (Appendix S1). Significant MEM within best-fitting sets were retained for spatial covariable sets (number retained: $\text{GND}_{\text{Xer}} = 4$, $\text{GND}_{\text{For}} = 3$, FOL = 3, $\text{AER}_{\text{Xer}} = 6$, $\text{AER}_{\text{For}} = 2$). Island position along the ICW (range 0–14.2 km) was also included in spatial covariable sets.

Statistical analysis strategies

Brown anole invasions were not distributed independently of island location at the time of this study, resulting in multicollinearity among BA_{Abund} and both environmental and spatial covariables. The proximity of invasions to boat ramps, general habitat similarity across islands, and experimental introductions onto uninvaded islands in this system (Campbell 2000, Campbell and Echternacht 2003) suggest that these associations were simply artifacts of invasion contingencies (see Discussion), but because explanatory overlap between BA_{Abund} and other covariables affected inferential power in this study, I explicitly characterized its extent. I used analysis techniques that partitioned the response variation explained by BA_{Abund} and explanatory covariable sets into fractions that were jointly explained and fractions that were uniquely explained (Legendre and Legendre 1998, Økland 2003). Because initial community-level dissimilarity analyses revealed that most of the variation jointly explained by BA_{Abund} and spatial covariables was also jointly explained by environmental covariables, for detailed analyses of community differences I partitioned variation only between BA_{Abund} and environmental covariables.

To characterize the strength of $\mathrm{BA}_{\mathrm{Abund}}$ explanatory power and its overlap with explanatory covariables, for each response I determined the proportion of variation that was uniquely explained by $\mathrm{BA}_{\mathrm{Abund}}$ ($R^{2,\,\mathrm{BA[...]}}$) in each of three models. In the "anole model", $\mathrm{BA}_{\mathrm{Abund}}$ was the only explanatory variable and thus it uniquely accounted for all explained variation ($R^{2,\,\mathrm{BA}}$). Excepting cases in which the addition of one or more suppressor covariables increased the variation explained by $\mathrm{BA}_{\mathrm{Abund}}$ (see Legendre and Legendre 1998 pp. 532–534, Maassen and Bakker 2001), the anole model yielded the maximum proportion of variation attributable to brown anoles. Next, I selected a "best model" using either the $\mathrm{AIC}_{\mathrm{C}}$ scores of all possible models (univariate responses) or a manual stepwise procedure (multivariate responses). Variation uniquely explained by $\mathrm{BA}_{\mathrm{Abund}}$ in the best model ($R^{2,\,\mathrm{BA-Best}}$) conservatively estimated the variation attributable to brown anoles within the most parsimonious framework, and was defined as zero for best models not containing $\mathrm{BA}_{\mathrm{Abund}}$. Lastly, the "full model" contained $\mathrm{BA}_{\mathrm{Abund}}$ and all explanatory covariables in the relevant set(s); excluding suppressor covariable effects, variation uniquely explained by $\mathrm{BA}_{\mathrm{Abund}}$ in this model ($R^{2,\,\mathrm{BA-Full}}$) represented the minimum attributable to brown anoles. Because the full model approach consigned all jointly explained variation to environmental covariables, it afforded the strongest and most conservative statistical evidence for anole effects available in this study. Spatial covariables were used only in community-level dissimilarity analyses; their use is denoted by a superscripted "+S" in explained variation fractions (e.g., $R^{2,\,\mathrm{BA-Full+S}}$).

Together, the anole, best, and full model approaches permitted a fuller assessment of the evidence for anole effects and expanded the range of possible inferences. Because this was an observational study and causal relationships could not be established, jointly explained variation was statistically confounded and there was no way to accurately determine, for any given response, how much of this variation should be attributed to BA_{Abund}. As a solution to this uncertainty, the three-model strategy outlined above bracketed the range of variation attributable to BA_{Abund} and generated a parsimony-based best estimate. This strategy offered several advantages over a more typical reliance on parsimony alone. In effect, it created a strength-of-evidence hierarchy in which significance in the anole, best, or full models provided, respectively, weak, moderate, or strong statistical support for anole effects. It also supplied information about why BA_{Abund} was present or absent in the best model. For instance, BA_{Abund} may have been in the best model because it explained response variation better—perhaps only slightly so—than a correlated covariable or more efficiently than a combination of covariables, or because it explained variation that other covariables could not. Inclusion of the full model results allowed the novelty of BA_{Abund}'s contribution to the best model ($R^{2,\,\text{BA-Best}}$) to be assessed: the smaller the difference between $R^{2,\,\text{BA-Best}}$ and $R^{2,\,\text{BA-Full}}$, the greater the novelty. Conversely, BA_{Abund} may have been absent from the best model because it explained little variation or because the variation it explained was better captured by one or more covariables; which of these possibilities occurred was revealed by the anole model results. Inclusion of the anole model also made it possible to recognize the presence of suppressor covariables in the best model, as indicated by substantially greater $R^{2,\,\text{BA-Best}}$ than $R^{2,\,\text{BA}}$. Such recognition is important because BA_{Abund}–response associations that emerged only after one or more covariables entered the model (i.e., significant $R^{2,\,\text{BA-Best}}$ but nonsignificant $R^{2,\,\text{BA}}$) could represent statistical artifacts;

consequently, they constituted weaker evidence for anole effects than associations that remained significant in the absence of other variables (i.e., both $R^{2,\,\mathrm{BA-Best}}$ and $R^{2,\,\mathrm{BA}}$ significant).

Since sample sizes were small given the number of explanatory variables modeled, I used adjusted *R*-squared measures for all measures of explained variation. The bias of unadjusted R^2 is well-studied and increases both with smaller sample sizes and greater numbers of explanatory variables (Kromrey and Hines 1995, Cohen et al. 2002). Adjusted R^2 (R^2_{adj}) measures correct for this bias and are greater than zero only when the amount of explained variation is greater than that expected from an equal number of unrelated random variables (e.g., Mittlböck and Waldhör 2000). Small, negative values are sometimes produced by bias-correcting R^2 adjustments; these were reported as zero, a logical standard practice (Mittlböck and Waldhör 2000, Cohen et al. 2002). A related issue occurs when the R^2_{adj} of combined variable sets is less than the R^2_{adj} of one of the individual sets being combined; following the same logic used for negative R^2_{adj} values, in variation partitioning the R^2_{adj} of combined variable sets was constrained to be greater or equal to the maximum R^2_{adj} among the individual, pre-combined variable sets.

I used permutation tests with 9999 permutations to determine statistical significance ($\alpha = 0.05$) and obtain *P*-values in all variation partitioning analyses. To facilitate the communication and discussion of results, I considered $\mathrm{BA}_{\mathrm{Abund}}$ to be significantly associated with a response if it significantly explained unique variation in any one of the anole, best, or full models.

Multivariate community composition analyses

Arthropod community data sets were created for each sampled community in each habitat. For FOL and AER, within-island subsamples were pooled and data sets were the total number of individuals captured for each morphospecies; for GND data sets, mean number of individuals per trap was used instead because raccoons destroyed some pitfall traps on some islands. Species captured on only one or two islands (i.e., $\leq 6\%$ of islands) were considered poorly sampled and were excluded from community data sets (McCune and Grace 2002). Alate ants were also excluded from AER data sets because large numbers were captured on a single sampling date midway through the study, potentially obscuring AER patterns of greater interest. Total and per-trap abundances were square-root transformed to reduce the influence of numerically dominant species in measures of community dissimilarity. Bray-Curtis (Sørensen) distances/dissimilarities were used for all analyses requiring distance matrices due to their performance with, and relevancy to, ecological data (Faith et al. 1987, McCune and Grace 2002).

To test whether arthropod communities differed on green versus brown anole islands, I used the function “adonis” in the R package ‘vegan’ (Oksanen et al. 2010, R Development Core Team 2010) to perform permutational multivariate analysis of variance using distance matrices (PERMANOVA; Anderson 2001), with BA_{Abund} as the explanatory variable. PERMANOVA tests for differences in multivariate location and does not require multivariate normality, but it can be affected by differences in multivariate dispersion; similarity in multivariate dispersion among green anole and brown anole islands was verified for each community using permutation tests in the vegan function “betadisper” (all $P \geq 0.17$). To visualize arthropod community relationships among islands, I plotted the best two-dimensional nonmetric multidimensional scaling (NMDS) solution derived from Bray-Curtis distances, obtained using the vegan function “metaMDS” with three sets of 50 runs (successive sets retained the previous set’s best solution).

I also used distance-based redundancy analysis (db-RDA; Legendre and Anderson 1999) to partition the dissimilarity in arthropod communities explained by $\mathrm{BA}_{\mathrm{Abund}}$, environmental covariables, and spatial covariables into jointly explained and uniquely explained variation fractions. This technique uses principle coordinate analysis (PCoA) to extract eigenvectors from a multivariate response distance matrix and redundancy analysis (RDA; van den Wollenberg 1977), a form of constrained ordination, to determine the maximum amount of eigenvector variation explained by explanatory variables (see Appendix S1 for more detail). Bias-correcting adjustments were applied to db-RDA R^2 values following Peres-Neto et al. (2006). Separate db-RDAs were performed for each explanatory variable set and all combinations thereof, and the resulting R^2_{adj} values served as inputs in a variation partitioning algorithm that divided the total variation explained across all three sets into seven fractions of uniquely or jointly explained variation (Borcard et al. 1992, Økland 2003). Note that negative jointly explained fractions occurred when the variation explained by combined explanatory variable sets was greater than the sum of the variation individually explained by the component sets (Legendre and Legendre 1998, pp. 532–534).

Arthropod community dissimilarity uniquely explained by $\mathrm{BA}_{\mathrm{Abund}}$ in the anole and full models ($R^{2,\,\mathrm{BA}}_{\mathrm{adj}}$, $R^{2,\,\mathrm{BA-Full+S}}_{\mathrm{adj}}$) was determined in the course of db-RDA variation partitioning; to determine $R^{2,\,\mathrm{BA-Best+S}}_{\mathrm{adj}}$, I selected a best community dissimilarity model by performing stepwise variable selection in the RDA step of db-RDA. For best model selection I used only positive eigenvectors (to simplify the analyses), $\alpha = 0.05$ for both variable entry and retention in the model, and a maximum R^2_{adj} stopping rule set by the full model R^2_{adj} (Blanchet et al. 2008). Significance levels for explanatory variable contributions in db-RDA were determined by permuting residuals under the reduced model (ter Braak and Šmilauer 2002).

Further analyses were conducted only for arthropod communities that differed between green and brown anole islands, as evidenced by significance in PERMANOVA (i.e., the anole model). I used PERMANOVA as a global test of significant difference; additional analyses were used to characterize the nature of differences and were not adjusted for multiple comparisons. The results of all analyses are presented, precluding concern over "data-dredging" or "cherry-picking" in the use of multiple unadjusted tests (see also Moran 2003). As discussed above, spatial covariables were excluded from further analyses.

Significant PERMANOVAs could have resulted from differences in total arthropod abundance, relative arthropod abundances, or a combination of both. To investigate the role of relative abundances, I converted arthropod abundances on each island to relative abundances prior to square-root transformation and conducted db-RDA variation partitioning and best model selection as described above. I also conducted separate relative abundance analyses for arthropod taxa with relatively large numbers of species in the sampled communities ("species-rich taxa": Coleoptera, Diptera, Formicidae, and Araneae). Species abundances within taxon data sets were relativized by total abundances for that taxon on each island, then square-root transformed. Islands lacking individuals in a given taxon data set were excluded from its analysis, and analyses were conducted only for data sets retaining a representative mix (invaded and uninvaded) of at least half (≥ 16) the islands.

Arthropod abundance, biomass, and diversity analyses

Univariate arthropod community attributes—abundance, biomass, richness, and evenness—were analyzed using generalized linear models (GLMs; McCullagh and Nelder 1989). For each response variable, I determined the fraction of adjusted *R*-squared deviance ($R^2_{\mathrm{D,\,adj}}$; Ricci 2010) uniquely explained by $\mathrm{BA_{Abund}}$ in the anole, best, and full models (i.e., $R^{2,\,\mathrm{BA}}_{\mathrm{D,\,adj}}$, $R^{2,\,\mathrm{BA-Best}}_{\mathrm{D,\,adj}}$, and $R^{2,\,\mathrm{BA-Full}}_{\mathrm{D,\,adj}}$). These fractions were obtained from the difference in $R^2_{\mathrm{D,\,adj}}$ for a given model with and without $\mathrm{BA_{Abund}}$ (see Legendre and Legendre 1998, pp. 528–532), and their significance was assessed with permutation tests in the R package 'glmperm' (Werft and Potter 2010, Werft and Benner 2010). When $R^{2,\,\mathrm{BA-Best}}_{\mathrm{D,\,adj}}$ or $R^{2,\,\mathrm{BA-Full}}_{\mathrm{D,\,adj}}$ fractions were greater than additive for the combination of $\mathrm{BA_{Abund}}$ and covariables (i.e., when jointly explained variation fractions were negative), I awarded half the synergistic increase in explained variation to $\mathrm{BA_{Abund}}$. Best models were selected using the criterion of lowest $\mathrm{AIC_C}$ score among all possible $\mathrm{BA_{Abund}}$ and environmental covariable models. All arthropod species, including those captured on fewer than three islands, were used in construction of univariate response variables.

Arthropod abundances were estimated by summing the total number of individuals captured and modeled using Poisson or negative binomial GLMs with a natural log link (O'Hare and Kotze 2010). For GND models, ln(number of traps) was included as an offset because the number of recovered pitfall traps differed among islands. Separate analyses were conducted for total arthropod abundance, small and large species abundances (both overall and within the species-rich taxa), and ordinal-level abundances (orders captured on fewer than 8 islands were not analyzed). To make the results more interpretable and comparable to previous anole food web studies, Hymenoptera was split into Formicidae and non-ant hymenopterans (hereafter "Hymenoptera"), and Hemiptera was split into Heteroptera ("Hemiptera") and Auchenorryncha plus Sternorryncha ("Homoptera"); these divisions were present in all "ordinal-level" analyses. In contrast to other anole food web studies (e.g., Dial and Roughgarden 1995, Schoener and Spiller 1999), arthropods were assigned to size categories based on measured or estimated adult body lengths for the species, not measured individual lengths. This distinction tightens the link between the response patterns and the differential effects of anole predation on arthropod species of different size (Appendix S1); for this study, the distinction was important primarily for crickets and some spiders. I selected 2 mm as the cutoff between size classes (small ≤ 2.0 mm, large > 2.0 mm) because the majority of arthropods in the gut contents of adult brown anoles are at least 2 mm in length (Schoener 1968, Spiller and Schoener 1990a, Wright 2009).

As a first step in arthropod abundance modeling, I used quasi-Poisson GLMs in R to assess (with Pearson residuals) the dispersion present in the full model (Venables and Ripley 2002). If the full model was not overdispersed (dispersion < 1.5, corresponding approximately to $p > 0.05$ in a X^2 goodness-of-fit test with df = 23 [FOL] or 24 [GND, AER]; McCullagh and Nelder 1989), I used Poisson regression to partition $R^2_{\mathrm{D,\,adj}}$ fractions (Cameron and Windmeijer 1996, Mittlböck and Waldhör 2000).

When overdispersion was present in the full model, abundances were analyzed with negative binomial (NB) regression (Hilbe 2008; see Appendix S1 for parameter estimation details). To my knowledge, $R^2_{\mathrm{D,\,adj}}$ measures have not previously been applied to NB regression models. I used simulated data sets in R to evaluate the bias-correcting properties of two potential $R^2_{\mathrm{D,\,adj}}$ measures that differed in their estimation of model dispersion (Appendix S1). Although both measures performed reasonably well, in this study I used the measure derived by Ricci (2010) for exponential dispersion models because it was the better performer under modeling scenarios most representative of abundance modeling in this study.

Arthropod biomass estimates were pooled within islands and cube-root transformed prior to analysis with Gaussian GLMs (i.e., ordinary least squares, OLS). For GND biomass analyses, pooled biomass estimates were divided by the number of contributing traps before the cube-root transformation was applied. Assumptions of homoscedasticity and normality of residuals were verified for all full and best Gaussian GLMs. Note that Gaussian GLM $R^2_{\mathrm{D,\ adj}}$ is equivalent to OLS R^2_{adj} (Cameron and Windmeijer 1997, Ricci and Martínez 2008).

I also used Gaussian GLMs to separately analyze the richness and evenness components of arthropod community diversity (but see Jost 2010). Islands with extremely low arthropod counts relative to the data set were excluded from these diversity analyses (number of excluded islands: $\mathrm{GND_{Xer}} = 2$, $\mathrm{GND_{For}} = 1$). Richness was estimated using sample-based rarefaction in EstimateS v8.2 (Gotelli and Colwell 2001, Colwell 2009). Sample-based rarefaction curves for each island were scaled by the mean number of individuals per trap, and the richness corresponding to the minimum number of captured individuals in the data set was estimated, when necessary, by linearly interpolating between points on the curves. Evenness was measured with Pielou's J' (Pielou 1969, Magurran 2004); for $\mathrm{GND_{Xer}}$, J' was transformed by squaring prior to $R^2_{\mathrm{D,\ adj}}$ partitioning in order to meet OLS model assumptions.

For each univariate response, I used a model averaging approach (Burnham and Anderson 2002) to estimate the effect of brown anole replacement of green anoles in island food webs (hereafter "replacement effect", "RE"). In this information-theoretic approach, the likelihoods (given the observed data) of all possible BA_{Abund} and environmental covariable models were used to weight respective BA_{Abund} regression coefficients, and the weighted average of this coefficient across all models was used to calculate the proportional change in the response, relative to green anole-dominant conditions, expected to occur with an increase BA_{Abund} typical of invasion in this system (RE_{Avg}; Appendix S1). For example, RE_{Avg} values of −0.4, 0, and 2.0 indicate, respectively, that the response would be expected to decrease by 40%, remain unchanged, or increase by 200% following brown anole invasion and typical population buildup on (previously) green anole islands. Confidence intervals for the model-averaged BA_{Abund} coefficient were similarly used to generate RE_{Avg} confidence intervals. For each response I also calculated the most parsimonious RE (RE_{Best}) using the BA_{Abund} regression coefficient from the best model.

Several aspects of the RE calculations are worth noting. First, positive REs were unbounded, but negative REs were bounded by −1 (= 100% reduction following invasion) in Poisson and NB models and were unlikely to substantially exceed −1 in Gaussian models. Second, RE_{Avg} (but not RE_{Best}) magnitudes were necessarily lessened by explanatory overlap between BA_{Abund} and environmental covariables. Finally, REs were not evaluated for statistical significance (although RE_{Avgs} with confidence intervals excluding zero could perhaps be considered the equivalent of statistically significant; see Burnham and Anderson [2002] for arguments against the use of significance terminology in information-theoretic approaches), and they did not serve, as did partitioned $R^{2,\,BA[...]}_{D,\,adj}$ fractions, as a measure of statistical evidence for anole effects. Rather, REs provided a measure of modeled effect size that either (1) accounted for multicollinearity among explanatory variables and consequent model selection uncertainty (RE_{Avgs}), or (2) reflected maximized parsimony (RE_{Best}).

Green anole terminology

To simplify the discussion of results, literature references for "green anoles" will include studies on both *A. carolinensis* and its Bahamian analog, *A. smaragdinus*. These two anoles belong to the same species subgroup, and until recent molecular work demonstrated otherwise (Glor et al. 2005), many workers considered *A. smaragdinus* to be a subspecies of *A. carolinensis*. This lumping should not be construed to imply that *A. carolinensis* and *A. smaragdinus* are functionally equivalent across the traits being considered (though they may be), but rather that the two species are sufficiently similar for the lumping to be useful for comparisons against brown anoles.

RESULTS

Brown anoles were observed on 19 (58%) of the 33 study islands and were assumed (on the basis of count totals; Appendix S1) to have displaced green anoles from food webs on 13 islands (39%). However, invasion status was not independent of island location or habitat profiles—invasions were concentrated around boat launches, and the heaviest invasions occurred predominantly on islands with relatively scrubby habitats (Figure 2.3).

Arthropod community dissimilarities were significantly associated with BA_{Abund} in the anole model (PERMANOVA) for ground and foliage arthropods, but not aerial arthropods (Figures 2.4, 2.5). Among the significant associations, explained variation was greatest in GND_{Xer} (17.9%), followed by GND_{For} (9.6%) and FOL (9.4%).

Patterns of explained dissimilarity were similar under the best and full model approaches. As with the anole model, BA_{Abund} significantly explained about twice as much unique variation in the best GND_{Xer} model as in the best GND_{For} and FOL models (GND_{Xer}: $R^{2,\,BA-Best+S}_{adj} = 0.134$, *pseudo-F* [$F^*$] = 5.62, $P = 0.0001$; GND_{For}: $R^{2,\,BA-Best+S}_{adj} = 0.054$, $F^* = 2.88$, $P = 0.0003$; FOL: $R^{2,\,BA-Best+S}_{adj} = 0.062$, $F^* = 2.90$, $P = 0.0001$). In full models containing all environmental and spatial covariables, BA_{Abund} still significantly and uniquely explained dissimilarity in ground arthropod communities—twice as much in GND_{Xer} (8.2%) as GND_{For} (4.0%)—, but $R^{2,\,BA-Full+S}_{adj}$ was not significant for foliage arthropods (Figure 2.4). BA_{Abund} did not enter the best AER_{Xer} or AER_{For} models, nor were $R^{2,\,BA-Full+S}_{adj}$ fractions significant for aerial communities (Figure 2.5).

Ground arthropods

BA_{Abund} significantly explained dissimilarity patterns in GND_{Xer} and GND_{For} relative abundances, but except for a positive association with small arthropod abundance in GND_{Xer}, BA_{Abund} did not significantly explain community-level variation in arthropod abundance (total, small, or large), biomass, richness, or evenness in either habitat (Figure 2.6a, b). Relative abundance dissimilarity $R^{2,\,BA[...]}_{adj}$ fractions were about two times greater in GND_{Xer} than GND_{For} and similar in magnitude to those obtained for community dissimilarities derived from observed abundances. These community-level patterns were greatly influenced by ant assemblages, which comprised the majority of captured ground arthropods (Table 2.4).

In GND_{Xer}, BA_{Abund} significantly explained variation in the abundance and composition of several arthropod orders (Figure 2.6c, e). BA_{Abund} was negatively associated with the abundances of Orthoptera and Coleoptera, all of which were large species (Appendix S2). Positive associations were observed for Collembola and Diptera abundances, which were completely (Collembola) or mostly (Diptera, mean 89%) comprised of small species. Although $R^{2,\text{ BA[...]}}_{\text{D, adj}}$ fractions for total ant and spider abundances were not significant in any model, BA_{Abund} was positively associated with small ant abundance and negatively associated with large spider abundance. Sufficient sample sizes for species-rich taxa relative abundance analyses existed only for ant and spider assemblages, and BA_{Abund} significantly explained dissimilarity patterns in both.

Less abundance and composition variation was explained by BA_{Abund} for arthropod orders in GND_{For} (Figure 2.6d, f). BA_{Abund} was positively associated with Collembola abundance and negatively associated with ant abundance, but it did not significantly explain total abundance variation in the other eight analyzed orders. Most ants were large species (mean = 90%), and $R^{2,\text{ BA[...]}}_{\text{D, adj}}$ patterns obtained for total ant abundance reflected those of large ant abundance. Although BA_{Abund} was not significantly associated with total beetle or spider abundances, it was negatively associated with large species abundances for these orders and positively associated with small spider abundance. Among the species-rich taxa, BA_{Abund} significantly explained relative abundance dissimilarity in ant and spider assemblages, but not beetle or dipteran assemblages.

Most of the ground arthropod responses significantly associated with BA_{Abund} in at least one modeling approach were significantly associated in the parsimony-maximizing best model, but $R^{2,\text{ BA}-\text{Full}}_{\text{D, adj}}$ was significant only for the relative abundance dissimilarities of ground arthropod communities and the ant assemblages that dominated them, and GND_{Xer} Orthoptera abundance.

Among negatively associated responses, $\mathrm{RE}_{\mathrm{Avg}}$-estimated abundance declines ranged from −59% (large $\mathrm{GND}_{\mathrm{For}}$ spiders) to −72% (large $\mathrm{GND}_{\mathrm{Xer}}$ spiders); expected abundances increases among positively associated responses ranged from 155% (small $\mathrm{GND}_{\mathrm{Xer}}$ arthropods) to 2,280% ($\mathrm{GND}_{\mathrm{For}}$ collembolans). Forest collembolans were relatively poorly sampled, and the extreme $\mathrm{RE}_{\mathrm{Avg}}$ and confidence interval values estimated for this order reflected uncertainty in the $\mathrm{BA}_{\mathrm{Abund}}$ regression coefficient resulting from the capture of only a single $\mathrm{GND}_{\mathrm{For}}$ collembolan among all uninvaded islands (the remaining 94% of captures occurred on invaded islands). $\mathrm{RE}_{\mathrm{Avg}}$ confidence intervals overlapped zero for most (71%) of the significantly associated GND abundance responses (Figure 2.6).

Foliage arthropods

In contrast to ground arthropods, several FOL community-level responses were significantly associated with $\mathrm{BA}_{\mathrm{Abund}}$ (Figure 2.7a). Total arthropod abundance and biomass were negatively associated with $\mathrm{BA}_{\mathrm{Abund}}$, reflecting the negative association between $\mathrm{BA}_{\mathrm{Abund}}$ and the abundance of large arthropods, which comprised the majority (mean 83.3%) of FOL arthropods. The association with biomass was stronger than the associations with large and total arthropod abundance due, at least in part, to a negative association between $\mathrm{BA}_{\mathrm{Abund}}$ and the mean length of captured large arthropods, both for all islands and brown anole islands (Appendix S2). Relative abundance dissimilarity patterns were also significantly associated with $\mathrm{BA}_{\mathrm{Abund}}$, with $R_{\mathrm{adj}}^{2,\,\mathrm{BA}[...]}$ fractions similar in magnitude to those derived from the observed abundance dissimilarities (Figure 2.4c, ignoring spatial covariables). Richness, evenness, and small species abundance were not significantly associated with $\mathrm{BA}_{\mathrm{Abund}}$.

At the ordinal level (Figure 2.7b), $\mathrm{BA}_{\mathrm{Abund}}$ was negatively associated with the abundances of FOL Orthoptera, Hemiptera, Coleoptera, Diptera, and Formicidae. $\mathrm{RE}_{\mathrm{Avg}}$-estimated abundance declines for these orders ranged from −57% (dipterans) to −84% (beetles), but in most cases the corresponding confidence interval overlapped zero. Most of the individuals in negatively associated taxa were large species, ranging from 63% (beetles) to 100% (Orthoptera, Hemiptera), and the $\mathrm{BA}_{\mathrm{Abund}}$ association patterns of large beetle, large dipteran, and large ant abundances (Figure 2.7c) were similar to those observed for the total abundances of the corresponding taxa. Although $\mathrm{BA}_{\mathrm{Abund}}$ was not associated with total or large spider abundances, it did significantly explain dissimilarity patterns in the relative abundances of FOL spider assemblages (Figure 2.7c). Dipteran and ant assemblage relative abundance dissimilarities were not significantly explained by $\mathrm{BA}_{\mathrm{Abund}}$.

$\mathrm{BA}_{\mathrm{Abund}}$ significantly explained unique variation in the best model for every associated FOL response, but $R_{\mathrm{adj}}^{2,\,\mathrm{BA-Full}}$ fractions were significant only for FOL and spider assemblage relative abundance dissimilarities, total and large ant abundances, and total arthropod biomass.

Model details, $R_{\mathrm{D,\,adj}}^{2,\,\mathrm{BA[...]}}$ magnitudes, P values, and RE magnitudes for models in Figures 2.6–2.7 are tabulated in Appendix S2.

DISCUSSION

Arthropod communities on spoils islands dominated by green anoles differed from those on islands dominated by brown anoles, and log-transformed brown anole abundance ($\mathrm{BA}_{\mathrm{Abund}}$)—a proxy for the extent of green anole displacement—parsimoniously explained much of this variation. At the community level, $\mathrm{BA}_{\mathrm{Abund}}$ explained 9–18% of the dissimilarity patterns in island ground and foliage arthropod community compositions, nearly the amount explained by entire sets of 4–8 environmental or spatial covariables. Within these communities, BA_{Abund} parsimoniously explained significant variation in the abundances or composition of 33% (GND_{For}) to 67% (GND_{Xer}) of the analyzed arthropod orders, which together comprised 69–93% of total arthropod abundance.

Overall patterns of explained variation corresponded well to the predictions I derived from anole density patterns, resource use, and food web effects (Table 2.1). Matching my prediction of greater invasion impacts in more open habitats, BA_{Abund} explained more dissimilarity in xeric habitat communities than forest habitat communities for both ground and aerial arthropods (Figures 2.4, 2.5). As expected from the more ground-directed foraging of brown anoles (compared to green anoles), dissimilarities in the community compositions of ground arthropods were better explained by BA_{Abund} than were those of foliage arthropods (but see *Foliage arthropods* below for an alternative view of relative impact strengths). Aerial arthropod dissimilarity patterns were not significantly explained by BA_{Abund}, fulfilling my prediction that aerial arthropods would be less affected by invasion than ground and foliage arthropods. And finally, significant associations between BA_{Abund} size-classed arthropod abundance responses were always negative for large arthropods and positive for small arthropods (Figures 2.6, 2.7; see also *Evidence for anole effects*), corresponding to my expectation that larger arthropods would be more negatively affected by invasion than smaller arthropods.

Despite the explanatory power of BA_{Abund} and its general agreement with expected patterns, the ability to infer probable anole effects from BA_{Abund}-explained variation in arthropod communities was complicated and constrained by invasion patterns. Greater brown anole incidence and abundance on relatively scrubby islands, coupled with the nonrandom spatial configuration of those islands, caused the explanatory power of BA_{Abund} to overlap substantially with that of both environmental and spatial covariables. Since the capacity for all study islands to support healthy populations of either anole species was implicitly assumed in this study, it is helpful to examine the probable cause(s) of the invasion patterns before reviewing the evidence for anole effects.

Invasion patterns

Brown anoles were, with a single exception, abundant only on islands with relatively short, scrubby vegetation and shallow, gappy forests (i.e., those with FEhab_1 < 0 in Figure 2.3). Their incidence was also higher on these islands than on those more heavily forested (77% versus 33%).

Several lines of evidence suggest that the mechanism underlying both of the above patterns is rooted in contingency: scrubbier islands were subjected to greater human recreational use, resulting in earlier and more frequent brown anole introductions. Scrubby islands in this system attract recreational use because their open habitats facilitate easy access to most parts of the island; heavily forested islands, on the other hand, are typically ringed by dense, nearly impenetrable mangrove marshes and forest edges that reduce the recreational value of island margins and impede access to more open island interiors. In addition, most of the scrubbier islands—including all the invaded ones—are highly accessible to boaters due to their location in relatively deep waters (Islands 1–10) or proximity to a boat launch (Figure 2.3), whereas all the heavily forested islands lie in shallow waters, and most are farther from boat launches than their scrubbier counterparts. Recreational boaters and campers regularly transport brown anoles to spoils islands (Campbell 2000), most likely because brown anoles are nearly ubiquitous around human habitations in nearby mainland areas, where they occupy trailered (and even docked) boats, recreational equipment, firewood piles, and most anything else stored outdoors. Boaters may also unwittingly transport brown anoles from one island to another, as brown anoles on invaded islands may jump from vegetation onto beached boats (Turnbough, unpubl. obs.). Thus, greater recreational use of scrubbier islands almost certainly increased the likelihood that brown anoles were introduced onto them (1) at some point prior to this study (increasing incidence), (2) at an earlier date (increasing the probability that their populations had built up to high densities), and (3) multiple times (possibly facilitating population survival and growth by overcoming environmental or demographic stochasticity, Allee effects, or limited genetic diversity; see Kolbe et al. 2004, Taylor and Hastings 2005, Simberloff 2009).

Support for the contingency hypothesis is abundant and varied (Appendix S2). Evidence linking recreational use to introductions includes the absence of brown anoles on scrubby islands furthest from boat launches (Figure 2.3) and the close proximity of Island 13—the only heavily forested study island with abundant brown anoles— to a boat launch. Island 13 also supplies evidence against the unlikely possibility that heavily forested islands lacked suitable habitat for brown anoles. Indeed, in reviewing the 100% success rate of ten purposeful introductions of brown anoles onto spoils islands of differing size, age, and habitat characteristics, Stuart et al. (2014) remark that such success "suggests that *A. sagrei* can colonize any spoil island and that ecological sorting is not responsible for the [presence/absence] patterns observed" among 30 spoils islands in this system (18 of which were used in the current study). Further supporting this assertion was their finding that the invasion status of five uninvaded and six invaded focal study islands (all of which were used in the current study) was not predicted by island area, vegetated area, available tree heights, or tree and shrub species diversity.

Although brown anole abundance patterns appear to have been driven primarily by contingency, they may have been influenced to a lesser extent by island structural and habitat features. For example, habitat openness may have allowed invading anoles to more quickly reach island interiors (where surveys were conducted) or more greatly benefit from allochthonous resource inputs (sea grass and carrion) on island shorelines (Appendix S2).

Evidence for anole effects

Two types of evidence, statistical and mechanistic, together suggest that differential food web effects of green and brown anoles were likely to be largely responsible for the observed associations between BA_{Abund} and spoils island arthropods. Because variation jointly explained by explanatory variables is statistically confounded in an observational study, unequivocal statistical evidence for anole effects was provided only by the full model approach ($R_{adj}^{2,\, BA-Full}$), in which all jointly explained variation was partitioned out. However, given that environmental covariables alone explained 47% (AER_{For}) to 59% (FOL) of the variation (R^2) in BA_{Abund} (and 51% [AER_{For}] to 80% [AER_{Xer}] together with spatial covariables), $R_{adj}^{2,\, BA-Full}$ fractions were likely to be small and—especially for univariate responses—nonsignificant. Statistical evidence for anole effects generated by the best model approach was weaker to the extent that $R_{adj}^{2,\, BA-Best}$ and $R_{adj}^{2,\, BA-Full}$ differed: the smaller the difference between these two fractions, the more likely that a lack of significance in $R_{adj}^{2,\, BA-Full}$ occurred due to the forcing of unimportant variables into the model. Evaluation of BA_{Abund}–response associations against patterns expected from potentially causal ecological processes can lend additional weight to, or detract from, the statistical evidence for anole effects. Such "mechanistic" evidence is particularly valuable when opposing patterns are expected from $\mathrm{BA}_{\mathrm{Abund}}$ and its correlated covariables. Although an evaluation of competing mechanistic explanations for each analyzed response is beyond the scope of this paper, general features of $\mathrm{BA}_{\mathrm{Abund}}$–response association patterns appear to be best explained by anole food web effect mechanisms.

In general, the statistical evidence for anole effects was strongest in community composition analyses, particularly for ground arthropods. In both $\mathrm{GND}_{\mathrm{Xer}}$ and $\mathrm{GND}_{\mathrm{For}}$, community dissimilarity was significantly explained by $\mathrm{BA}_{\mathrm{Abund}}$ independently of all environmental and spatial covariables. Moreover, if spatial covariables are excluded, $R_{\mathrm{adj}}^{2,\,\mathrm{BA-Full}}$ fractions also become significant for FOL and $\mathrm{AER}_{\mathrm{Xer}}$ dissimilarities (FOL: $F^* = 2.01$, $P = 0.011$; $\mathrm{AER}_{\mathrm{Xer}}$: $F^* = 2.02$, $P = 0.032$). Spatial covariables represented only the *potential* for spatially-structured environmental variables or ecological processes to explain arthropod community variation; since their explanatory overlap with $\mathrm{BA}_{\mathrm{Abund}}$ for community dissimilarities was mostly shared by environmental covariables, it is unlikely that any unmodeled, spatially-structured variable was broadly responsible for the $R_{\mathrm{D,\,adj}}^{2,\,\mathrm{BA-Full}}$ fractions obtained in further analyses, in which only environmental covariables were partialled out (though such a possibility exists for individual responses, especially those comprising a minor fraction of the community dataset). In these further analyses, full model statistical evidence for anole effects was mostly restricted to the relative abundance patterns of the communities and their dominant assemblages (ants in GND and spiders in FOL). For most orders within communities, statistical support for anole effects was predominantly at the weaker, best-model level. The greater frequency of significant $R_{\mathrm{D,\,adj}}^{2,\,\mathrm{BA-Full}}$ fractions among community and assemblage dissimilarity analyses was due primarily to the greater power of the multivariate analyses to detect small effects, rather than greater $R^{2,\ \mathrm{BA-Full}}_{\mathrm{D,\ adj}}$ magnitudes.

Two general features of the observed $\mathrm{BA}_{\mathrm{Abund}}$–response association patterns appear to be best explained as direct and indirect effects of increased anole predation pressure on arthropod communities. First and foremost, the direction of significant taxon abundance associations always corresponded to the predominant size class of the taxon: positive for orders mostly (> 80%) or wholly comprised of small species (i.e., adult body length ≤ 2 mm), and negative for orders comprised of larger species (Figure 2.8). Negative associations with larger arthropods are consistent with direct predation effects of greater densities of anoles following brown anole invasion. Indeed, I selected a 2 mm size criterion based on the size distribution of brown anole prey, and furthermore the taxa negatively associated with $\mathrm{BA}_{\mathrm{Abund}}$ are regularly consumed by brown anoles (e.g., Lister 1976, Norval et al. 2007, 2010, Giery et al. 2013). Anole-driven declines in large arthropods may, in turn, indirectly benefit smaller arthropods by reducing the strengths of their interactions with larger predators and competitors, producing positive associations between brown anole and small arthropod abundances. Similar dichotomies in the strength or direction of anole effects have been found for arthropod groups that likely differ in their susceptibility to anole predation due to differences in size or ecology (Pacala and Roughgarden 1984, Dial and Roughgarden 1995, Schoener and Spiller 1999, Schoener et al. 2002). The second pattern feature that appears to best fit a mechanism of anole food web effects is the greater explanatory power of $\mathrm{BA}_{\mathrm{Abund}}$ for xeric arthropods than for forest arthropods. Brown anoles reach higher densities in more open and insolated habitats than in more strongly-shaded, closed-canopy forests (Schoener and Schoener 1980, Schoener and Schoener 1982), and thus it follows that their impacts are likely to be stronger in the open interiors of spoils islands than in the midst of island forests. For both ground and aerial arthropods, community dissimilarities were explained by $\mathrm{BA}_{\mathrm{Abund}}$ to a greater degree in xeric habitats than in forest habitats. In further GND analyses, $R^{2,\,\mathrm{BA[...]}}_{\mathrm{D,\,adj}}$ magnitudes (significant or not) were, with few exceptions (e.g., collembolan and spider abundances), greater for $\mathrm{GND}_{\mathrm{Xer}}$ than $\mathrm{GND}_{\mathrm{For}}$ across all comparable community-level and taxon-level responses. The taxonomic breadth of significant associations was also greater in $\mathrm{GND}_{\mathrm{Xer}}$: all six (100%) of the analyzed orders in $\mathrm{GND}_{\mathrm{Xer}}$ were in some way significantly associated with $\mathrm{BA}_{\mathrm{Abund}}$, compared to four of nine (44%) orders in $\mathrm{GND}_{\mathrm{For}}$.

Environmental covariables significantly correlated with $\mathrm{BA}_{\mathrm{Abund}}$ do not appear to provide alternative mechanistic explanations for the above pattern features. $\mathrm{BA}_{\mathrm{Abund}}$ was significantly correlated with composite PCA covariables representing overall habitat scrubbiness (Xhab_1, Fhab_1, and FEhab_1 in Appendix S1) and greater palm and palmetto cover in xeric–forest edge vegetation (Fveg_2 and FEveg_1). In contrast to expected negative associations between $\mathrm{BA}_{\mathrm{Abund}}$ and large arthropods, palms and palmettos likely facilitate higher densities of large ground and foliage-dwelling arthropods because (1) they generate deeper and more structured litter layers than other plant species on the islands, (2) pleats on their leaves (particularly the palms) provide unique retreat sites for a variety of larger-bodied arthropod species (Turnbough, unpubl. obs.), and (3) their “trunks” host an abundance of deep (at least in palms), humus-rich crevices that provide habitat or retreat sites for many additional large arthropod species (Turnbough, unpubl. obs.). Although the stiffness and pleats of palm and palmetto leaves could potentially interfere with the collection of arthropods by sweep net, leading to a negative relationship between palm and palmetto representation in sweep samples and arthropod abundance, such a possibility was not supported by the sample-level data: within-island regressions of FOL large arthropod abundance against palm and palmetto representation yielded regression coefficients centered around zero, and the same held true for small arthropod abundance (Turnbough, unpubl. analyses). Island scrubbiness also fails to explain important aspects of the observed patterns. Though arthropod abundance may generally be expected to decrease with increasing island scrubbiness for a variety of reasons (e.g., less plant biomass likely supports fewer herbivorous and detritivorous arthropods, and consequently fewer predatory arthropods), such an effect should be stronger for smaller arthropods—opposite the observed pattern—because they have larger surface area-to-volume ratios and thus face a higher risk of desiccation in drier, scrubbier habitats. The smallest size classes of arthropods are frequently those most reduced with increasing dryness within or across habitats (e.g., Whittaker 1952, Janzen and Schoener 1968, Janzen 1973a, Levings and Windsor 1984). Nor does island scrubbiness appear to explain the greater explanatory power of BA_{Abund} for xeric arthropods. Differences in xeric habitats, which were more or less scrubby on all islands, were less dramatic than differences in forest habitats, which ranged from scrubby thickets to tall, closed-canopy forests. Assuming that habitat effects on arthropod communities mirror the apparent extent of habitat differences, BA_{Abund} should have better explained variation in forest arthropod communities rather than xeric arthropod communities were it merely an efficient discriminator of island scrubbiness.

Evidence for anole effects should be considered with the limitations of the study in view. In order to simplify the analyses and enable comparisons across explanatory variable sets, response categories, and modeling approaches, I did not test for interactions among explanatory variables, though the existence of important interactions is certainly plausible. It is thus possible that some response variation attributed to BA_{Abund} could be explained by a combination of environmental covariables and their interactions, or that the true effects of anole replacement were misestimated because mitigating interactions with environmental covariables were ignored. The possibility also exists that unmodeled causal variables could account for variation explained by BA_{Abund}. Levels of human disturbance, for example, likely affected arthropod communities and were probably associated with BA_{Abund}, but were only indirectly (and probably incompletely) captured by environmental covariable sets. Co-occurring invasions of the red imported fire ant, *Solenopsis invicta*, might also explain response variation uniquely attributed to BA_{Abund}, though additional db-RDA analyses using fire ant abundance as an explanatory variable indicated that this potential to confound was limited to best model evidence for anole effects on non-ant ground arthropods (Appendix S2). Finally, it should be noted that arthropod community subsample sizes (i.e., the number samples collected per island) were relatively small, and consequently the effects of sampling error on island-level arthropod abundance estimates may have been relatively large. However, jackknife and bootstrap resampling analyses of the subsample-level data (Appendix S2) suggested that ground arthropod communities were subsampled adequately, at least for community-level composition analyses (i.e., db-RDAs), and further that the effects of moderate undersampling of foliage arthropods were likely to be conservative with respect to BA_{Abund} explanatory power for FOL variation (i.e., BA_{Abund} explained more FOL variation as subsample sizes increased).

Ground arthropods

Community dissimilarity patterns explained by BA_{Abund} were greatest for ground arthropods, matching impact strength predictions derived from differences in green and brown anole densities and perch use. Brown anoles are trunk-ground ecomorphs that typically perch on or near the ground (Schoener 1968, Lister 1976, Wright 2009) and therefore likely encounter a greater proportion of ground-active prey than foliage-active or aerial prey. Indeed, of the prey consumed by brown anoles in a structurally-simple Florida system (isolated *Ficus aurea* "tree islands") that were classified by Giery et al. (2013) as either terrestrial or arboreal (total classified: 65% of individuals, 88% of volume), 54% of the individuals and 68% of the prey volume were terrestrial. Since green anoles typically perch higher in the vegetation, even in the absence of brown anoles (Edwards and Lailvaux 2012, Kamath et al. 2013, Stuart et al. 2014), they probably interact with ground-active prey less frequently than do brown anoles. Any differential effects on arthropod communities driven by perch use differences are likely exacerbated by the greater densities of brown anoles. However, it is easy to envision scenarios that could cause brown anole invasions to have greater impacts on foliage arthropods than ground arthropods (e.g., domination of ground arthropod communities, but not foliage communities, by unpalatable or diurnally-hidden arthropods).

Two other studies permit comparison of the relative effects of anoles on ground arthropods versus other community types, and in both, ground arthropods were more strongly affected, though in different ways than observed in the current study. In Pacala and Roughgarden's (1984) enclosure study of the joint food web effects of *A. schwartzi* and *A. bimaculatus* in xeric forest habitat on St. Eustatius in the Lesser Antilles, sticky traps placed on the forest floor revealed a negative effect on total arthropod abundance that that was about 50%

greater (in terms of effect ratios) than the positive effect anoles had on the abundance of aerial arthropods captured on sticky traps hung within the forest understory. In Schoener et al.'s (2002) comparison of arthropod communities on small Bahamian islands with and without natural populations of brown anoles, the negative association of anoles with large arthropods (length > 4 mm) was over three times stronger for pitfall-trapped ground arthropods than for sticky-trapped aerial arthropods. By contrast, neither total nor large ground arthropod abundances were negatively associated with BA_{Abund} in the current study—a surprising result that occurred because the signals from negative associations with some arthropod groups were offset by positively-associated groups or diluted by noise from unassociated groups. For example, BA_{Abund} associations with two of the most abundant large ant species in xeric habitats were opposing in direction (see Figures S2.2 and S2.5 in Appendix S2), and as a result, BA_{Abund} was unassociated both with the abundances of large xeric ants and with the abundances of large xeric arthropods, which were comprised in large part by ants (see below). The discrepancy in findings between this study and the two others cited above probably stemmed from differences among the studies in trapping technique, anole resource use, and habitat setting (Appendix S2).

Ants were the dominant component of ground arthropod communities, and thus patterns of explained GND dissimilarities were driven largely by variation in ant assemblages. Although ants are usually the numerically dominant component of brown anole diets (Schoener 1968, Lister 1976, Wright 2009) and they comprised the near majority (mean 49.1%) of prey individuals found in the stomach contents of brown anoles inhabiting Florida spoils islands (Campbell 2000), the existence of strong BA_{Abund}–ant assemblage associations was surprising. Predation—especially vertebrate predation—is seldom considered to play an important role in structuring ant communities (Hölldobler and Wilson 1990, Cerda et al. 2013; but see Rao 2000, Wanger et al. 2011). Detailed analyses of ant assemblages will be published elsewhere, but their prominence in GND patterns warrants some discussion here of the most prominent BA_{Abund}–ant composition trend.

Much of the BA_{Abund}-explained variation in ant assemblages was due to a negative association between BA_{Abund} and the abundances of large *Pheidole* species (*P. morrisi* and *P. dentata*), and brown anole predation appears to best explain the pattern. Among ant genera, *Pheidole* ants are probably highly palatable to generalist, insectivorous lizards, including anoles (e.g., Vogel and von Brockhusen-Holzer 1984), because they lack both functional stings and chemical defenses (with at least one exception in the Neotropics; Kugler 1979). *Pheidole* rely instead on physical force for defense, particularly from their soldier caste, which possess enlarged heads and mandibles (Wilson 2003), but even the soldiers of most *Pheidole* species are probably too small for their mandibles to provide an effective defense against anoles (maximum *Pheidole* length in this study was 4.8 mm). In the only two studies reporting ant genera in brown anole diets, *Pheidole* comprised 94% of consumed ants in Taiwan (Norval et al. 2011) and 75% of consumed ants in South Florida (Giery et al. 2013); further, indirect evidence from syntopic *Anolis distichus* diets in Giery et al.'s (2013) study suggests that brown anoles *preferentially* consumed *Pheidole* ants (Appendix S2). Huang et al. (2008a) found that brown anoles reduced the abundance of the dominant *Pheidole* species by 45% in a Taiwanese palm plantation, and reasonable assumptions applied to the available data suggest that brown anole predation could cause even greater *Pheidole* declines on Florida spoils islands (Appendix S2). Given the important roles ants play in ecological systems (Hölldobler and Wilson 1990, Folgarait 1998) and their frequency in the diets of many Caribbean *Anolis* (Losos 2009), the possibility that anoles alter ant assemblages by preying on more palatable species deserves further study.

Among non-ant arthropod orders, BA_{Abund} was negatively associated with the abundances of Orthoptera, large Coleoptera, and large Araneae, a pattern consistent with the mechanism of brown anole predation. All of these taxa are regularly present in brown anole diets, and both Coleoptera and Araneae usually rank among the four most-consumed orders (e.g., Lister 1976, Campbell 2000, Wright 2009, Giery et al. 2013). Moreover, per-capita consumption of orthopterans, beetles, and spiders tends to be higher for brown anoles than syntopic green anoles (Schoener 1968, Campbell 2000), though this tendency may be influenced by vertical partitioning in perch use between the two species. Although most brown anole diet studies do not specify prey community type affinities (e.g., terrestrial vs. arboreal), nor resolve prey taxa so finely that such affinities can be surmised, those that do demonstrate that at least some orthopteran, beetle, and spider prey are ground-dwelling (Spiller and Schoener 1990a, Norval et al. 2007, Giery et al. 2013). Thus, observed negative associations between these taxa and BA_{Abund} are at least consistent with the available dietary data. The number and strengths of these associations were greater in GND_{Xer} than GND_{For}, likely due to higher brown anole densities in edge-rich xeric habitats, as discussed above, but possibly also because the more developed ground litter layers of forest habitats provided prey with more or better refugia. Interestingly, many of the morphospecies comprising the negatively associated orders belonged to genera or families that normally remain hidden and inactive (at least on the surface) during the day; interactions between these arthropods and diurnally-foraging anoles may be facilitated by (1) overlapping activity patterns during certain parts of the day or year, or (2) biotic disturbances, for example flushing by predatory ants (Appendix S2).

The abundances of Collembola, Diptera, small Formicidae, and small Araneae were positively associated with BA_{Abund}. With the possible exception of Diptera, these groups have not been observed to associate positively with anole presence or abundance, nor has any group of ground arthropods. To date, positive effects of anoles on arthropods have been demonstrated only for aerially-active arthropods (Pacala and Roughgarden 1984, Schoener and Spiller 1999) and a few subsets of insects inhabiting coffee tree foliage (a lepidopteran leafminer, chrysopid lacewings, hymenopterans, and insects 2–5 mm in length; Borkhataria 2001, Borkhataria et al. 2006); positive associations have also been observed for aerially-active hymenopteran parasitoids, but it is still unclear whether anoles causally contribute to the pattern (Schoener et al. 1995, Schoener and Spiller 1999, Spiller and Schoener 2007). Since dipterans frequently comprise many or most of the aerially-trapped arthropods in these systems, there is a strong chance that positive effects of anoles on dipterans, particularly small species, have gone unreported in the past. When analyzed, however, total and small (< 2 mm) dipteran abundances or biomass have not been positively affected by anoles (Pacala and Roughgarden 1984, Spiller and Schoener 1994, Dial and Roughgarden 1995, Schoener and Spiller 1999, Borkhataria 2001), possibly due to trap location (e.g., ground vs. aerially suspended), less extreme anole effects on proposed intermediate predators (i.e., spiders), or inclusion into the response of large dipterans, which can be negatively impacted by anoles (Dial and Roughgarden 1995). Potential anole effects on collembolans, small (< 2 mm) leaf-dwelling spiders, and small (1–3 mm) arboreal ants have also been assessed and not detected (Dial and Roughgarden 1995, Huang 2007).

If anoles are indirectly responsible for the observed positive associations, the effects are likely mediated by predation on ants or spiders. These two taxa comprised the vast majority of arthropod predators in ground arthropod communities, and differences in their assemblages on green anole and brown anole islands likely impact their competitors and prey. Both ants and spiders are known to impact ground arthropod community structure and to affect the taxa positively associated with BA_{Abund} in this study (Porter and Savignano 1990, Riechert and Lawrence 1997, Lawrence and Wise 2004, Miyashita and Niwa 2006, Sanders and Platner 2007, Moya-Laraño and Wise 2007, Sanders et al. 2011).

To assess the relative support of ant- versus spider-mediated pathways for indirect anole effects on positively associated taxa, I partitioned explained response variation among BA_{Abund} and the dominant features (principle components) of ant and spider ground assemblages (Appendix S2). I gleaned further mechanistic insight by considering the identity and directional association of ant or spider species loading heavily on principle components of explanatory importance. These analyses provided relatively strong support for a spider-mediated effect on Collembola and moderate support for either ant- or spider-mediated effects on small GND_{For} spiders; no support for either pathway existed for small ants and dipterans, however (Appendix S2). In the absence of mechanistic evidence for indirect anole effects on small ants, it is safest to assume that the association was probably driven by environmental differences between green anole and brown anole islands. By contrast, the positive association between BA_{Abund} and dipteran abundances was most likely an artifact driven by an outlying data point; removal of this outlier eliminates the significance of the association in the Diptera and small Diptera best models.

Foliage arthropods

Although foliage community dissimilarities were not as well explained by BA_{Abund} as were ground communities, the inference that anole effects were less important for foliage arthropods may not be warranted. The most prominent anole-associated features of ground arthropod communities were shifts in the relative composition of predatory or omnivorous taxa (ants and spiders) without correspondingly large changes in the total abundances of those taxa. For example, both small and large spider abundances in GND_{For} were relatively well explained by BA_{Abund}, but due to the opposing directions of the associations, BA_{Abund} explained essentially zero variation in total spider abundance (Figure 2.6d, f). Though anole effects of this nature would certainly be important for affected species within ant and spider assemblages, the relatively unchanged total abundances of these assemblages combined with the generalist feeding tendencies of their members may result in limited impacts to lower and higher trophic levels. In contrast, offsetting associations within taxa were not as prominent for foliage arthropods, and negative associations of BA_{Abund} with the abundances of several taxa resulted in negative associations with total arthropod abundance and biomass. Reduced foliage arthropod abundance and standing biomass are arguably greater overall invasion impacts than shifts in the relative compositions of ground ant and spider assemblages.

Magnitudes of the estimated impacts of brown anole invasion on foliage arthropod abundance and biomass were consistent with experimentally-determined anole effects in another system, and were of sufficient strength to suggest the likelihood of further impacts to both downstream and upstream food web components. Dial and Roughgarden (1995) found that rainforest tree canopies with intact anole faunas had 30% fewer large arthropods (length > 2 mm) and 38% less arthropod biomass in their foliage than did trees where anoles were removed, effects that are reasonably similar to the reductions in these responses expected from brown anole invasion of spoils islands—18% in large arthropod abundance and 49% in total arthropod biomass (RE_{Avgs}); note that differences in anole densities achieved between Dial and Roughgarden's treatments were similar to those occurring between green anole and brown anole spoils islands. Anole effects on foliage arthropods in Dial and Roughgarden's study were strong enough to indirectly benefit plants by reducing herbivore damage to leaves, and it is likely that plants on spoils islands experience similar benefits from brown anole invasion. Indeed, insectivorous vertebrates in general and anoles in particular frequently have positive, indirect effects on plants (Spiller and Schoener 1990b, 1994, Schoener and Spiller 1999, Mooney et al. 2010). Upstream food web components are also likely to be impacted by reductions in foliage arthropod abundance and biomass. For example, habitat quality may be degraded for the migrant, foliage-gleaning, insectivorous birds that are common on spoils islands during the winter months (Chapter 4). On spruce trees in Sweden, ant-caused reductions in foliage arthropod biomass averaging only 34%—less than the 49% expected from brown anole invasion—were associated with lower visitation frequency and duration by foraging birds (Haemig 1994). Negative effects of exploitative competition with anoles have been implicated, but not experimentally demonstrated, for insectivorous birds on neotropical and Caribbean islands (Wright 1979, Wright 1981, Wright et al. 1984), and the potential for brown anole invasion to negatively impact insectivorous birds in Florida and elsewhere is a subject worthy of concern and study.

Support for the causal role of anole predation in generating the negative associations with arthropod abundance and biomass was provided by the negative relationship between BA_{Abund} and the mean length of large arthropods. The energetic rewards of larger prey prompt at least one anole species to take greater risks (i.e., potential exposure to predators) in pursuing them (Shafir and Roughgarden 1998), and it is reasonable to expect that greater capture effort by anoles, possibly in combination with greater prey visibility or exposure, would lead to a higher risk of predation for larger arthropods. Some support for this hypothesis is provided by the responses of leaf arthropod size classes in Dial and Roughgarden’s (1995) study: the negative effects of anoles on large arthropods, as measured by proportional differences in abundance, grew stronger with each incremental step in arthropod size class. Also possibly supporting this hypothesis is Spiller and Schoener's (1990a) finding that arthropods consumed by brown anoles were larger, on average, than those passively captured in aerial sticky traps, but this finding could simply reflect anole consumption of non-flying arthropods that happened to be larger, on average, than flying arthropods. Even if predation risk is independent of arthropod size beyond some threshold, reduced survival to maturity may decrease mean sizes in arthropods with immature stages that are exposed to anole predation (e.g., spiders and orthopterans). In the Bahamas, brown anoles can reduce the size distributions of the spider species they negatively impact (Spiller and Schoener 1998), with females of the most heavily impacted common species (*Argiope argentata*) not surviving long enough to reach maturity in enclosures with anoles.

In general, the identities of the taxa negatively associated with BA_{Abund} also support the mechanism of increased anole predation. Orthoptera, Hemiptera, Coleoptera, Diptera, and Formicidae are all common in brown anole diets (e.g., Campbell 2000, Norval et al. 2010), and anoles have previously been found to negatively affect orthopteran, large beetle, large dipteran, and total dipteran abundances (Pacala and Roughgarden 1984, Dial and Roughgarden 1995). Although negative impacts on hemipterans have not been detected in the few studies assessing their response to anoles (Borkhataria 2001, Borkhataria et al. 2006, Murakami and Hirao 2010), most of the hemipterans captured in the current study were lygaeids, which have featured prominently in brown anole diets elsewhere in Florida (Giery et al. 2013). Among the negatively associated taxa, ants seem least likely to have been affected by anole predation. Most of the captured ants were defended with chemical compounds (e.g., *Camponotus floridanus*, *Crematogaster spp.*) or powerful stings (*Pseudomyrmex gracilis*), and comparison of the diets of syntopic anoles elsewhere in Florida suggests that brown anoles do not regularly consume such ants (Giery et al. 2013). It may be possible, however, for brown anoles to negatively affect population densities of these ants by consuming their alate queens. Brown anoles appear to selectively prey on the queens of *Solenopsis geminata* in Taiwan (Norval et al. 2011), and they have been observed to prey on alate queens of the similarly noxious RIFA in Florida (M. Deyrup, pers. comm.). It may also be possible for brown anoles to affect the foraging behavior or population densities of foliage-foraging ants by reducing the availability of arthropod prey in the foliage. Competition between anoles (or other lizards) and ants has not been explored, but brown anoles have been shown to negatively impact web spiders through exploitative competition for shared prey (Spiller and Schoener 1990a).

The lack of significant associations between BA_{Abund} and FOL spider abundances was surprising, given the near ubiquity of negative anole effects on web spiders in food web studies (e.g., Schoener and Toft 1983, Pacala and Roughgarden 1984, Dial and Roughgarden 1995, Spiller and Schoener 1988, Schoener and Spiller 1996). This finding did not result from contrasting associations with different spider families or foraging guilds, nor was it likely to have been caused by a lack of interaction between anoles and the spider species involved (Appendix S2). Interestingly, the best explanation for the pattern appears to be that green anoles are more efficient predators of foliage spiders than are brown anoles, such that the effects of increased anole density following brown anole invasion are offset by weaker per-capita interaction strengths, relative to green anoles, between brown anoles and foliage spiders (see Appendix S2 for evidence supporting this hypothesis).

In contrast to ground arthropod communities, no significant positive associations were observed between BA_{Abund} and foliage arthropod responses, though a positive association with

Lepidoptera abundance approached significance (P = 0.078). Unlike ground communities, anole-associated differences in foliage arthropod communities were primarily driven by taxa comprised partly (Diptera) or mostly (Orthoptera, Hemiptera, and Coleoptera) of herbivorous or detritivorous species. Unless these species have relatively strong competitive interactions with other foliage arthropods, which seems particularly unlikely for the herbivores, reductions in their abundances are unlikely to positively affect other arthropods. The marginal association between $\mathrm{BA}_{\mathrm{Abund}}$ and lepidopteran abundance could represent an indirect food web effect mediated by reduction in large ant abundances. Lepidopterans often respond positively to the exclusion of ants from plant foliage (e.g., Haemig 1994, Philpott et al. 2008, Nahas et al. 2012), and large ant abundance in FOL was able to significantly explain variation in Lepidoptera abundance ($R^2_{\mathrm{D,\ adj}}$ = 0.118, P = 0.023), with which it was negatively associated (Turnbough, unpubl. analyses). With greater sampling effort, the significance of the $\mathrm{BA}_{\mathrm{Abund}}$–Lepidoptera association might be established, and greater light shed on the possible ant-mediated link.

Aerial arthropods

Dissimilarity patterns among aerial arthropod communities were not significantly explained by $\mathrm{BA}_{\mathrm{Abund}}$ for either xeric or forest habitats. This result is at odds with most relevant food web studies, in which anoles usually affect the abundances, biomass, or composition of aerially-captured arthropods (e.g., Pacala and Roughgarden 1984, Dial and Roughgarden 1995, Schoener and Spiller 1999, Schoener et al. 2002). Inadequate sampling is probably to blame for the discrepancy. Manually removing sticky-trapped arthropods and dissolving the adhesive off of them was a time-intensive process, and due to time limitations, only two sticky traps were placed in each habitat. The signal-to-noise ratio was thus probably lower for AER than it was for GND and FOL (which were subsampled six and four times per island, respectively), and may have been too low to detect weak anole effects on aerial arthropods. In particular, the fact that neither BA_{Abund} nor environmental covariables explained any dissimilarity in AER_{For} suggests that sampling levels were too low for at least forest aerial arthropods.

The ability of BA_{Abund} to predict AER_{Xer} dissimilarities was improved by incorporation of environmental covariables into the model, but remained nonsignificant in the full model that included both environmental and spatial covariables (i.e., $R_{\mathrm{adj}}^{2,\,\mathrm{BA-Full+S}}$). With the exclusion of spatial covariables, however, BA_{Abund} significantly explained unique variation in the full model (i.e., $R_{\mathrm{D,\,adj}}^{2,\,\mathrm{BA-Full}}$), even though the amount of dissimilarity jointly explained only by BA_{Abund} and spatial covariables was relatively small (0.5%; Figure 2.5). Because spatial covariables were essentially placeholders for spatially-structured causal factors that may or may not actually exist, it seemed unwise to ignore possibly useful data on account of them; I therefore repeated for AER_{Xer} the set of within-community analyses performed for ground and foliage arthropods (Appendix S2). The results of these analyses supported the general trends observed among ground and foliage arthropods, in that significant associations were negative for large arthropods and positive for small arthropods, and they also revealed that all $R_{\mathrm{adj}}^{2,\,\mathrm{BA[...]}}$ fractions were significant (though small) for community dissimilarities based on relative abundances (see Appendix S2 for further discussion of these and other findings).

Summary and conclusions

This study demonstrated that arthropod communities on islands dominated by native versus invading *Anolis* lizards differ in ways that are generally well explained as direct and indirect effects of increased predation pressure following brown anole invasion. Although evidential strength for these differences as food web effects was constrained by explanatory overlap among brown anole abundance and sets of environmental and spatial covariables, most anole-associated patterns were significantly supported under a parsimony-based best model approach, and some were supported even under the most conservative, full model approach. Furthermore, overall generalities in the association patterns, for example negative associations with large arthropods and positive associations with small arthropods, better fit anole-based mechanistic explanations than covariable-based expectations. If apparent invasion impacts observed in this study extend to other open or disturbed habitats in Florida, brown anoles may have important landscape-level effects on arthropod communities and the organisms that depend on them, for example foliage-gleaning insectivorous birds.

Resident lizard displacement by invading anoles is likely to be an increasingly common phenomenon, and to the extent that observed patterns represented differential anole food web effects, this study provides an assessment of the further impacts that may be generated by such displacements. Introduced anoles are known or suspected to have displaced several anole species in the Caribbean (Powell et al. 2011) and a scincid lizard in Japan’s Ogasawara Islands (Hasegawa et al. 1988, Suzuki and Nagoshi 1999), and given the rapid pace of new anole introductions in the Caribbean and elsewhere (Kraus 2009, Powell et al. 2011, Krysko et al. 2011), additional displacements are likely to be a frequent occurrence in the foreseeable future. Prior to the current study, the relative population-level food web effects of different anole species—or any lizard species, to my knowledge—in the same system had not been robustly assessed (see Chapter 1).

Application of the results presented here to other systems would be greatly aided by knowledge of how differences in anole densities and per-capita effects each contribute to the pattern of net impacts. Significant associations observed between brown anole abundance and arthropod response abundances were all consistent with a simple increase in anole density following invasion, and the extent to which differential per-capita effects might have modulated the magnitudes of these apparent impacts remains unknown. The importance of differential per-capita effects was clearly evident only in the lack of an apparent impact on foliage web spiders, as web spiders have been consistently, strongly, and negatively impacted by increased anole densities in other food web studies. Future research should focus on identifying the nature and relative importance of potential differences in per-capita effects; were these known, better predictions could be made for the impacts of brown anole invasion into habitats where green anole displacement is only partial. Further, if differential per-capita effects can be linked to the trait differences that cause them (see Chalcraft and Resetarits 2003a), the prospects of using differential green and brown anole food web effects to understand or predict the relative food web effects of other anole or lizard species will be greatly improved.

As one of the few case studies of functional equivalence among terrestrial vertebrates, this study provides additional evidence that even closely-related, ecologically similar species may have very different effects within community food webs. In combination with other case studies, past and future, the results presented here may be useful for empirically addressing a variety of interesting questions of practical importance. For example, how rapidly does functional similarity change with decreasing phylogenetic relatedness or autecological similarity, both overall and for particular responses, and which trait types or factors (e.g., body size, activity patterns, aggressiveness) tend to be the most important drivers of such relationships? Or, for a given level of phylogenetic relatedness or trophic similarity, does functional similarity between species systematically differ among different taxa (e.g., lizards vs. birds) or habitats (e.g., aquatic vs. terrestrial)? Although the complexities of ecological communities may render it impossible to accurately predict all the impacts generated by species displacements, it should be possible, with enough accrued data, to at least estimate the relative likelihoods and strengths of different kinds of potential impacts, much as the way a recent meta-analysis (Mooney et al. 2010) allows similar types of predictions to be made for the food web effects of vertebrate insectivores. Such a prospect should be welcomed by ecologists in general and invasion biologists in particular.

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APPENDIX 2:

TABLES AND FIGURES

Table 2.1 Predicted impact patterns for brown anole invasion and displacement of green anoles.

Impact prediction	Rationale	References
Greater in more open habitats	Brown anole densities tend to increase with habitat openness	Schoener and Schoener 1980 Schoener and Schoener 1982b
Greater for ground arthropods than foliage arthropods	Brown anoles are more ground-directed in perching and foraging; green anoles are more foliage-directed	Schoener 1968 Schoener 1975 Stuart et al. 2014
Least for aerial arthropods	Brown anole effects on aerial arthropods tend to be weak, frequently indirect	Schoener and Spiller 1999 Spiller and Schoener 2001 Schoener et al. 2002
More frequently or strongly negative for larger arthropods	Larger arthropods tend to be more common in brown anole diets than smaller arthropods	Schoener 1968 Spiller and Schoener 1990 Wright 2009

Table 2.2 Variables included in environmental covariable sets.

Variable (% PCA Var.)[1]	Covariable set[2]			Description
DATE	X	F	FE	Sampling date (day in June)
WTHR_1 (60)	X	F		First principle component describing variation in sampling date temperature extremes and rainfall variables
SWcond_1 (91)			FE	First principle component describing variation in sweep netting time and temperature
RAINprev			FE	Observation of whether rain fell on an island the day prior to sweep netting
Xveg_DIV	X			Simpson's diversity index of plant cover (xeric and forest habitats) or swept vegetation (forest edge)
Fveg_DIV		F		
FEveg_DIV			FE	
Xveg_1, Xveg_2 (58, 17)	X			First two principle components describing variation in plant community composition (xeric and forest habitats) or swept vegetation composition (forest edge)
Fveg_1, Fveg_2 (54, 20)		F		
FEveg_1, FEveg_2 (53, 31)			FE	
Xhab_1, Xhab_2 (48, 26)	X			First two principle components describing variation in habitat structure variables
Fhab_1, Fhab_2 (64, 21)		F		
FEhab_1, FEhab_2 (56, 21)			FE	

[1] Percent of total variance captured in PCA by listed principle components

[2] X = xeric, F = forest, FE = xeric–forest edge

Table 2.3 Variables used in habitat structure PCAs.

Variable	PCA[1]			Description[2]
SQRT_XER	X		FE	total xeric habitat area (m^2), square-root transformed
XER_Pveg	X		FE	vegetated proportion of xeric habitat area
XER_HT	X		FE	visual estimate of relative xeric vegetation height, classed 1 (short) or 2 (tall)
XER_Pperim	X	F	FE	proportion of xeric habitat perimeter open to marsh or water (not bordered by forest)
FOR_DEP	X	F	FE	depth (or width) of forest; mean of six subsamples
SQRT_FOR		F	FE	total forest habitat area (m^2), square-root transformed
FOR_TYPE		F	FE	visual estimate of forest type, classed 1 (scrubby), 2 (intermediate), or 3 (mature)
FOR_DENS		F		visual estimate of forest understory density; mean of four subsamples

[1] X = xeric, F = forest, FE = xeric–forest edge

[2] Unless described as visual estimates, collected using digital imagery

Table 2.4 Mean percent abundance and species richness of arthropod orders in sampled communities.

	Mean percent abundance[1]					Species richness					
Order	GND_{Xer}	GND_{For}	FOL	AER_{Xer}	AER_{For}	GND_{Xer}	GND_{For}	FOL	AER_{Xer}	AER_{For}	All
Collembola	1.2	1.1				2	2				2
Blattodea	0.1	1.1	0.1			2	5	1			5
Dermaptera	0.1	0.2				2	1				2
Orthoptera	5.3	2.1	12.0	0.4	0.5	2	2	4	1	1	6
Homoptera	0.1	0.1	8.2	1.1	2.2	1	2	15	4	7	21
Hemiptera	0.5	0.1	1.6	1.6	0.6	3	2	6	7	2	15
Thysanoptera			0.9	1.6	1.2			2	5	4	7
Psocoptera		0.6	7.3	2.9	11.6		4	7	5	8	15
Lepidoptera	0.0	0.6	4.3	0.3	1.6	1	3	16	3	4	24
Coleoptera	1.6	2.6	4.7	14.4	12.3	19	24	18	31	26	79
Diptera	1.7	6.5	14.3	71.4	56.6	15	34	46	50	40	122
Hymenoptera:											
Non-ant	0.4	0.2	5.1	2.4	8.5	4	2	24	11	23	56
Formicidae	82.5	60.8	9.0	–[3]	–[3]	17	18	11	–[3]	–[3]	24
Araneae	3.2	7.3	31.7	3.2	3.7	18	39	35	11	8	86
Isopoda	0.6	15.1				3	6				6
Other	2.5	1.5	0.8	0.5	1.2	3	7	4	3	1	14
Total A, R[2]	3,264	2,777	740	641	340	92	151	189	131	124	484

[1] Means of individual island percentages

[2] Total number of individuals (A) and species (R) pooled across islands

[3] Aerially-captured alate ants were excluded from analyses

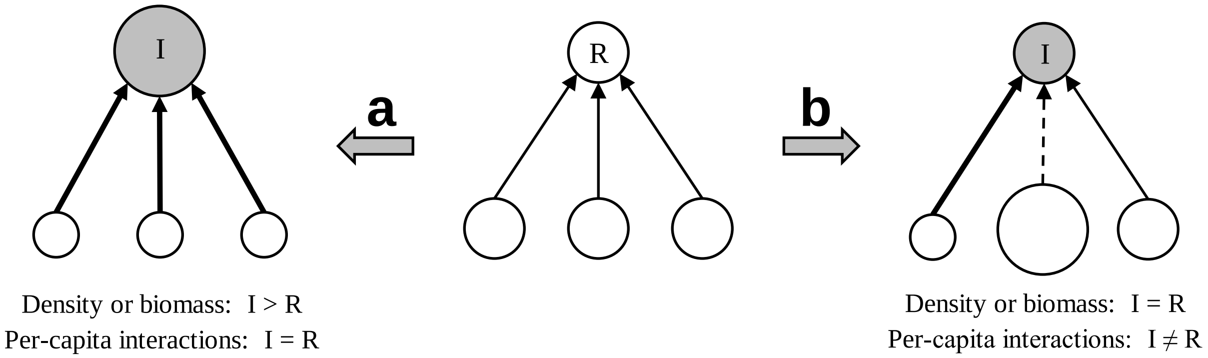


Figure 2.1 Potential food web effects resulting from differences in the (a) density or biomass or (b) per-capita interactions of invading (I, shaded) and displaced resident (R) species. Arrows indicate the direction and magnitude of energy flow; changes in node size represent changes in density and/or biomass.

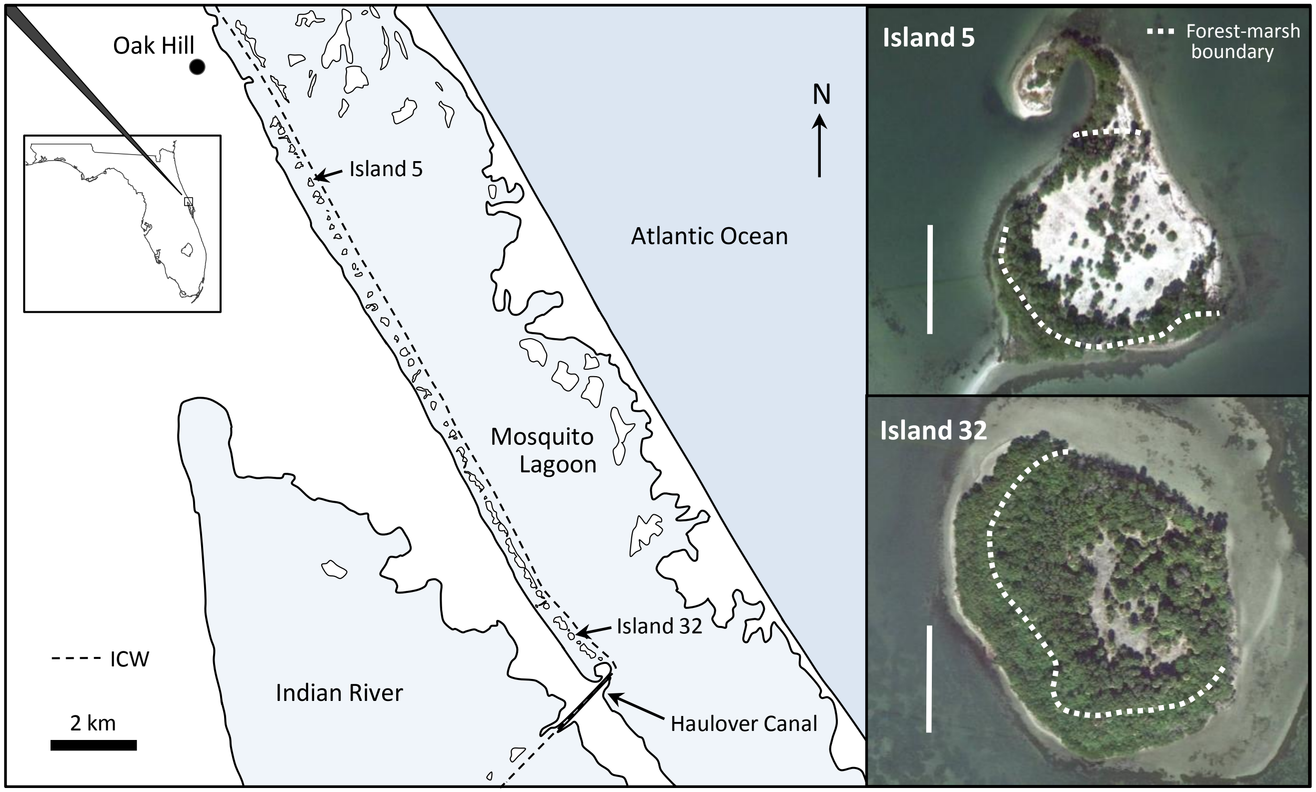


Figure 2.2 Location of study islands and examples showing extremes in island structural features. Island 5 is situated in deep water and is relatively scrubby with an extensive xeric habitat and shallow, fragmented, somewhat stunted forest and marsh habitats. By contrast, Island 32 is situated in shallow water and is heavily vegetated with a diminutive xeric habitat and deep, unfragmented, well-developed forest and marsh habitats. ICW = Intracoastal Waterway. White bars in inset island images represent 50 m. Island images courtesy of Google Earth (GeoEye, U.S. Geological Survey, 2011).

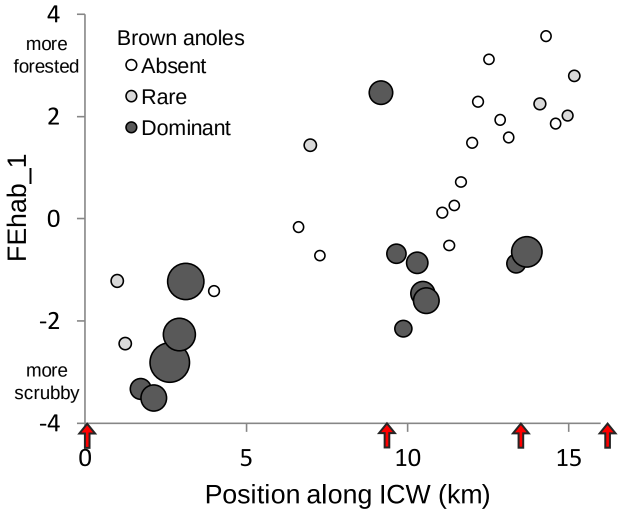


Figure 2.3 Habitat structure and invasion status of study islands. Plot symbol areas are proportional to total brown anole counts plus a constant of 5. Principle component scores (FEhab_1) reflect the extent and stature of xeric and forest vegetation. Arrows mark the locations of boat launches adjacent to the ICW; island and boat launch positions are offset by 1 km to aid visual presentation.

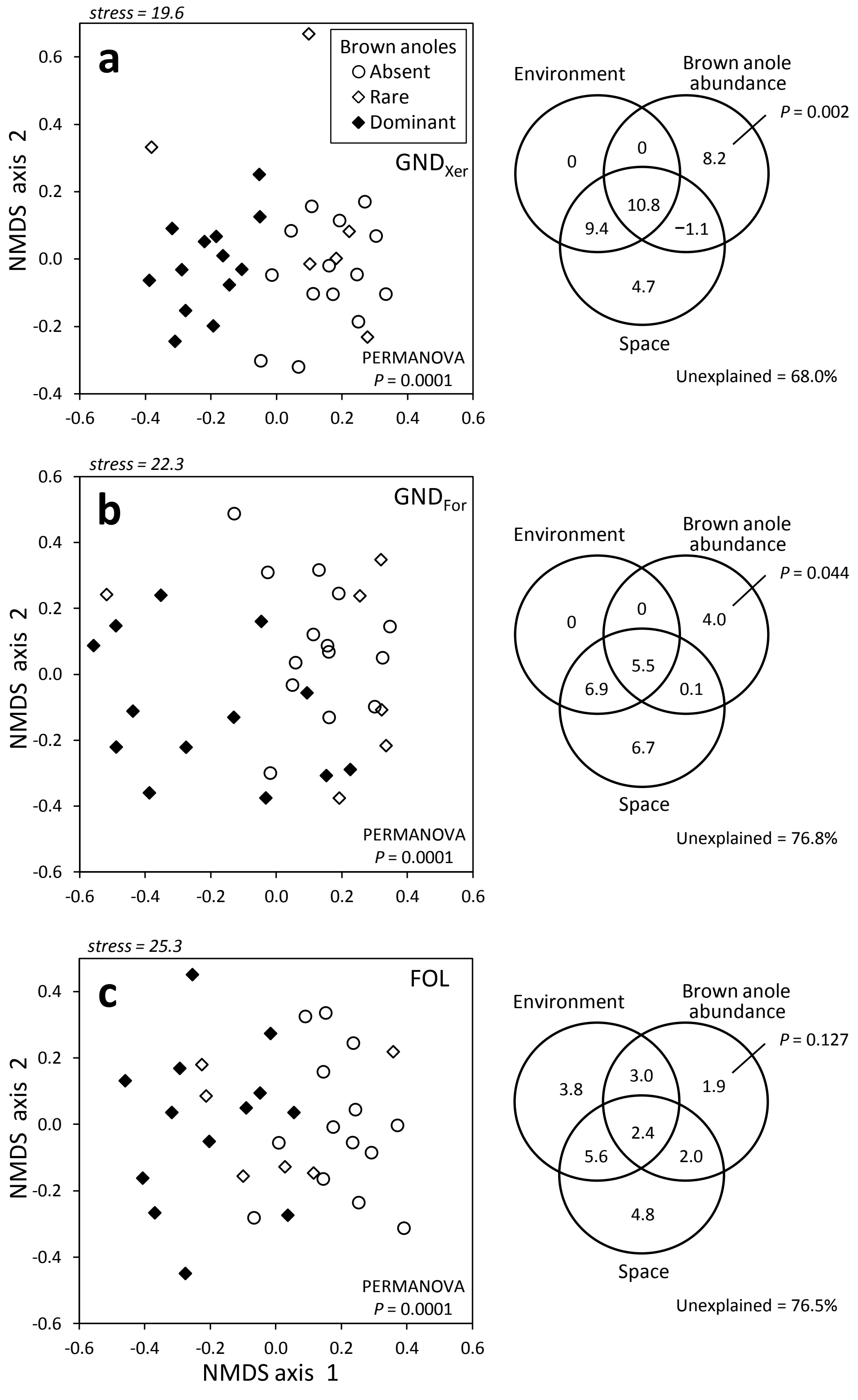


Figure 2.4 Community dissimilarity NMDS plots and partitioned variation fractions (% explained) for (a) GND_{Xer}, (b) GND_{For}, and (c) FOL.

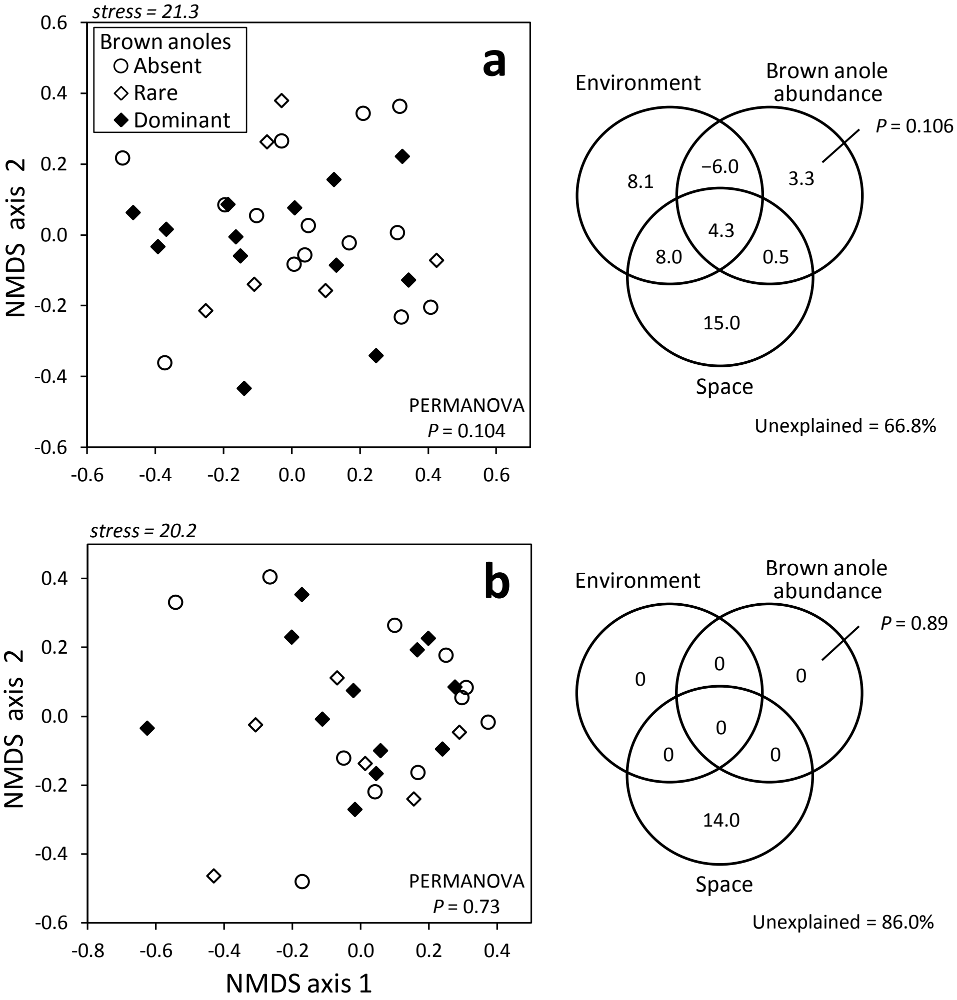
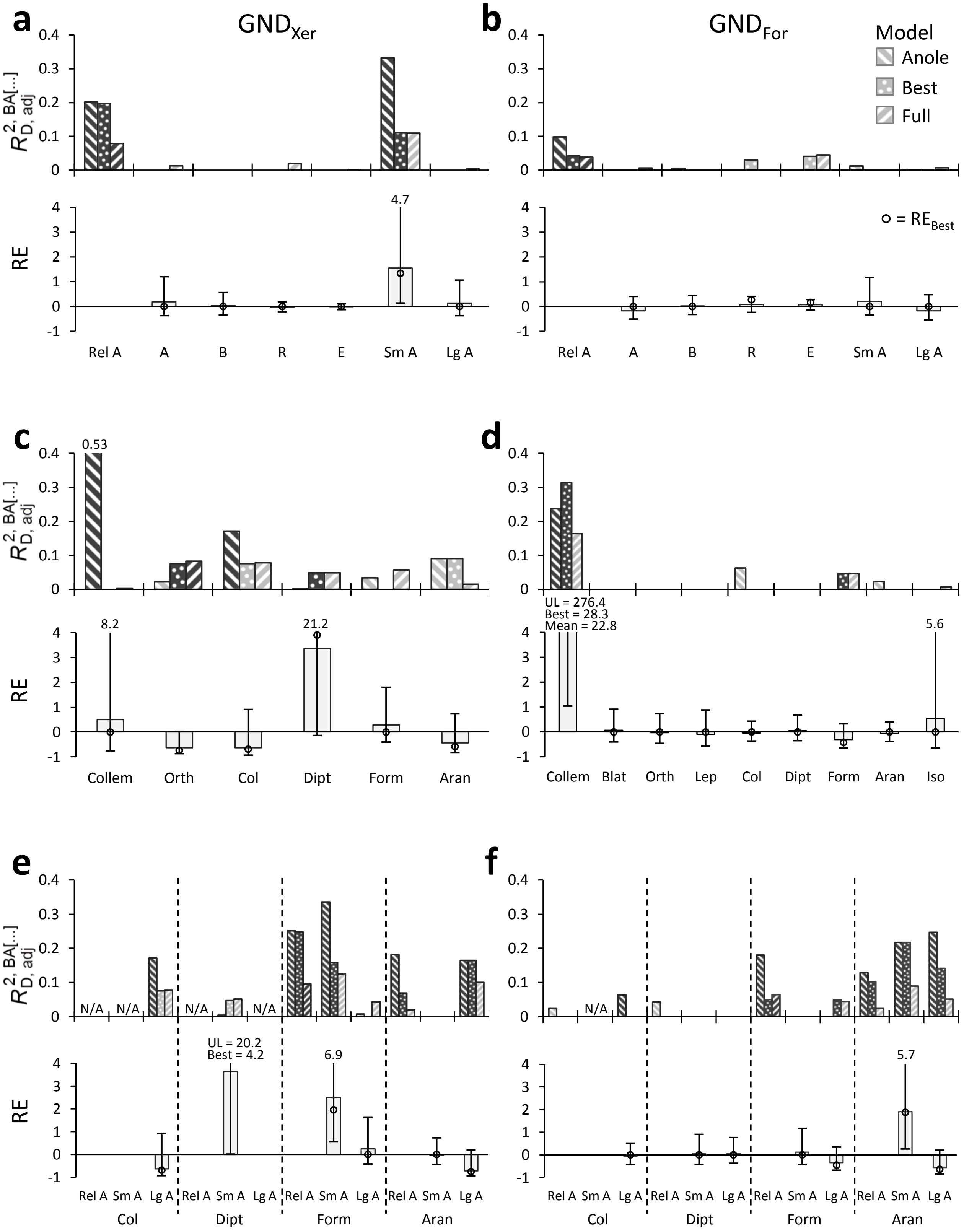


Figure 2.5 Community dissimilarity NMDS plots and partitioned variation fractions (% explained) for (a) AER_{Xer} and (b) AER_{For}.

Figure 2.6 Uniquely explained variation fractions and modeled replacement effects (RE) for GND_{Xer} and GND_{For} (a, b) community-level attributes, (c, d) order abundances, and (e, f) assemblage-level attributes. Error bars denote 95% confidence intervals around RE_{Avg}; RE_{Best} are also shown. Values exceeding figure scales are displayed. Significant variation fractions ($p < 0.05$) are indicated by darker shading. Rel A = relative abundance, A = abundance, B = biomass, R = richness, E = evenness, Sm A = small species abundance, Lg A = large species abundance; Aran = Araneae, Blat = Blattodea, Col = Coleoptera, Collem = Collembola, Dipt = Diptera, Form = Formicidae, Iso = Isopoda, Lep = Lepidoptera, Orth = Orthoptera; N/A = not analyzed.


a
GND$_{Xer}$
b
GND$_{For}$
Model
Anole
Best
Full
$R^{2,\ BA[...]}_{D,\ adj}$
0.4
0.3
0.2
0.1
0
RE
4
3
2
1
0
-1
4.7
○ = RE$_{Best}$
Rel A
A
B
R
E
Sm A
Lg A
c
d
0.53
8.2
21.2
UL = 276.4
Best = 28.3
Mean = 22.8
5.6
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UL = 20.2
Best = 4.2
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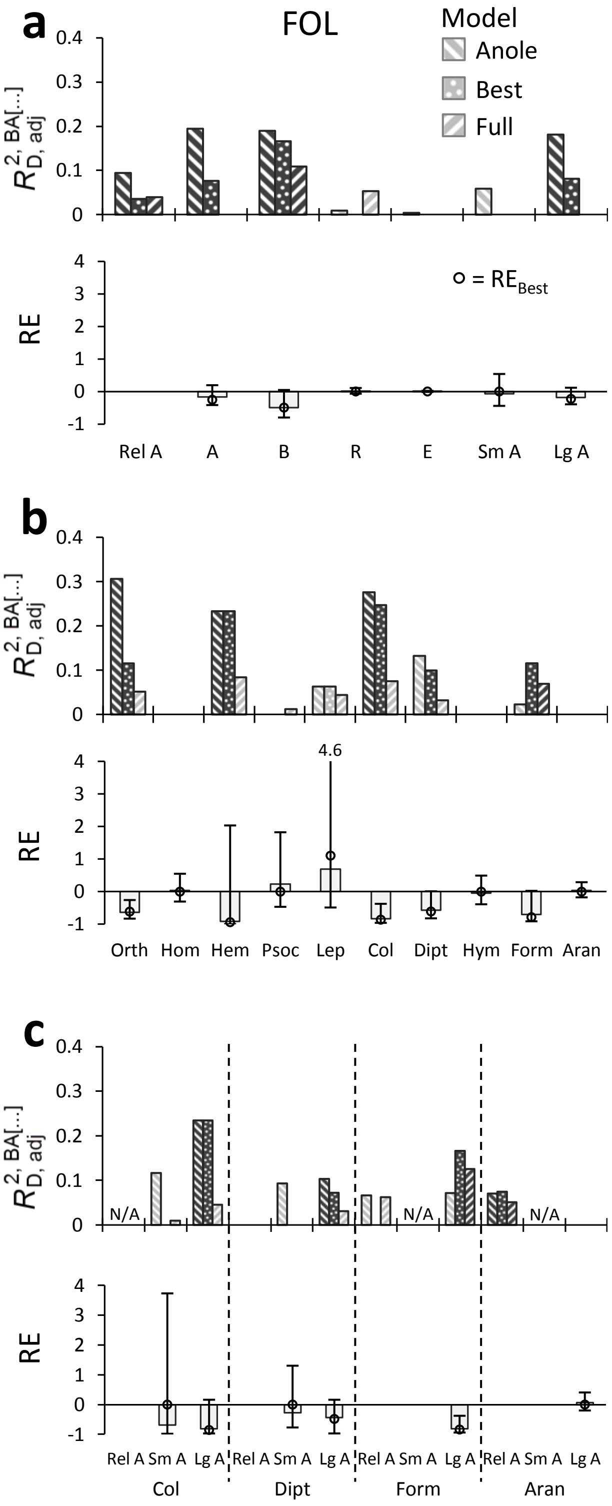

Figure 2.7 Uniquely explained variation fractions and modeled replacement effects (RE) for FOL (a) community-level attributes, (b) taxon abundances, and (c) assemblage-level attributes. Hem = Hemiptera, Hom = Homoptera, Hym = non-ant Hymenoptera, Psoc = Psocoptera; other figure details and abbreviations as in Figure 2.6.

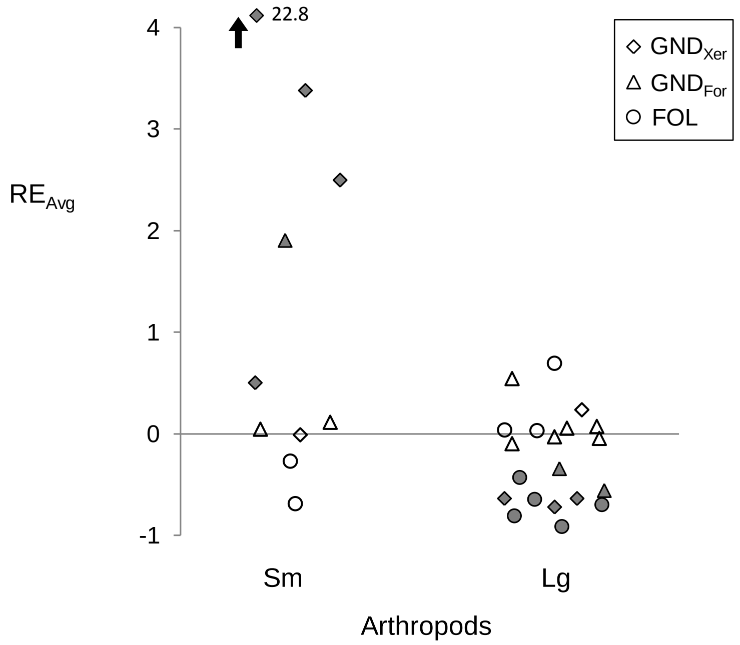

Figure 2.8 Model-averaged replacement effects (RE_{Avg}) for arthropod order abundances, grouped according to predominant species size. For species-rich orders permitting separate analyses of both small (Sm) and large (Lg) species abundances, RE_{Avgs} for both size classes are plotted. For all other orders, RE_{Avg} was plotted if, on average, > 80% of the individuals in the samples were either small species or large species. Shaded symbols indicate that BA_{Abund} significantly explained unique variation in at least one of the anole, best, or full models.

APPENDIX S1:

SUPPLEMENTARY METHODS

Table of Contents

Island marsh connections and habitat characteristics

Many of the islands used in this study had projections of marsh habitat extending towards neighboring islands. In some cases, particularly in the southern half of the island array where islands were deposited in shallow water, marsh extensions physically connected neighboring islands; in other cases, neighboring marshes approached to within a few dozen meters but were not connected, or were only connected by exposed mudflats during seasonal periods of low water levels. I assumed that the effect of connected marshes on arthropods in the xeric and forest habitats was negligibly small, and thus that marsh-connected islands could reasonably be considered independent sampling units. If, however, marsh connections linked together arthropod populations in neighboring xeric or forest habitats, or served as dispersal corridors between them, then various processes (e.g., source–sink or metapopulation dynamics) could have generated increased community similarities between marsh-connected islands.

I tested the assumption of negligible connection effects using the eleven study islands that had both a marsh-connected and a nearby, unconnected neighbor. I used one-way Wilcoxon signed-rank tests to assess whether ground (GND_{Xer}, GND_{For}), foliage-dwelling (FOL), or aerial (AER_{Xer}, AER_{For}) arthropod communities were more similar on marsh-connected neighbors than on corresponding unconnected neighbors. Wilcoxon signed-rank tests were better suited than paired *t*-tests for these comparisons because similarity differences were not normally distributed. As a measure of community similarity, I used Bray–Curtis distances calculated from community data sets in which rare species were trimmed and species abundances were square-root transformed (see Methods: *Multivariate community composition analyses*). Several islands were excluded from the forest aerial arthropod data set (AER_{For}) due to insufficient arthropod captures; as a result, only seven focal islands were available for AER_{For} neighbor comparisons.

Communities were not more similar on marsh-connected neighbors than unconnected neighbors ($n = 11$, one-way exact P values: GND_{Xer}, $V = 31$, $P = 0.45$; GND_{For}, $V = 51$, $P = 0.95$; FOL, $V = 38$, $P = 0.68$; AER_{Xer}, $V = 40$, $P = 0.74$; $n = 7$, one-way test with continuity correction: AER_{For}, $V = 10$, $P = 0.29$). These tests were conservative with respect to assumed negligible connection effects because marsh-connected neighbors tended to be closer and more similar in both habitat characteristics and brown anole abundances than their unconnected counterparts. Since community similarities are often negatively correlated with distance, and both habitat characteristics and anole abundances are expected to influence arthropod communities, the comparisons were likely biased towards greater community similarity on marsh-connected neighbors.

Blocks of two or more marsh-connected islands are denoted in Table S1.1, which also contains island habitat characteristics and other study-relevant data.

Table S1.1 Island locations, sampling start dates, anole counts, and selected structural characteristics. ICW = Intracoastal Waterway.

Island[1]	ICW position (km)	Latitude Longitude	Sampling start date[2]	Brown anole class	Total brown anole count[3]	Total green anole count[3]	Island area (ha)	% Xeric habitat[4]	% of xeric vegetated	% Open xeric perimeter	% Forest habitat[4]	Mean forest width (m)	Forest type
1	0.00	28.8571° N 80.8268° W	5	Rare	2	2	2.67	32.9	30	1	30.1	12.5	1
2	0.24	28.8554° N 80.8255° W	5	Rare	2	4	1.57	43.9	24	12	27.6	7.0	1
3	0.72	28.8516° N 80.8227° W	5	Abundant	15	2	1.25	46.8	26	29	17.0	6.7	1
4	1.13	28.8483° N 80.8211° W	19	Abundant	26	7	0.98	56.8	32	47	28.9	8.8	1
5	1.63	28.8445° N 80.8184° W	22	Abundant	67	0	1.06	41.9	18	20	32.4	7.7	1
6	1.92	28.8422° N 80.8169° W	22	Abundant	43	1	0.99	50.9	31	31	28.3	10.1	2
7	2.12	28.8407° N 80.8160° W	22	Abundant	55	3	1.02	32.2	47	14	32.4	11.6	2
8	3.00	28.8336° N 80.8120° W	22	Absent	0	0	0.60	28.0	43	15	44.1	10.8	2
9	3.29	28.8303° N 80.8103° W	14	Absent[5]	0	0	0.90	11.2	44	4	58.3	14.6	2
10	5.62	28.8123° N 80.7981° W	14	Absent	0	0	0.79	11.2	63	6	38.7	19.1	2
11	5.99	28.8092° N 80.7964° W	14	Rare	2	2	2.32	17.2	35	0	43.5	26.3	3
12	6.28	28.8071° N 80.7948° W	14	Absent	0	0	1.29	25.9	33	6	33.0	16.9	2
13	8.18	28.7922° N 80.7854° W	27	Abundant	20	3	1.61	11.3	59	0	54.9	23.3	3
14[A]	8.65	28.7884° N 80.7832° W	28	Abundant	12	0	1.24	18.5	43	16	33.2	19.6	2
15[A]	8.87	28.7865° N 80.7825° W	27	Abundant	8	3	1.12	21.2	38	33	20.1	11.5	2
16[B]	9.31	28.7828° N 80.7806° W	27	Abundant	16	1	2.00	36.8	25	21	28.8	22.5	2
17[B]	9.48	28.7816° N 80.7793° W	20	Abundant	22	1	1.13	36.1	25	18	34.5	14.4	2
18[B]	9.58	28.7810° N 80.7785° W	20	Abundant	25	2	0.68	19.9	28	33	38.1	14.9	2

Table S1.1 (continued)

Island[1]	ICW position (km)	Latitude Longitude	Sampling start date[2]	Brown anole class	Total brown anole count[3]	Total green anole count[3]	Island area (ha)	% Xeric habitat[4]	% of xeric vegetated	% Open xeric perimeter	% Forest habitat[4]	Mean forest width (m)	Forest type
19[C]	10.08	28.7769° N 80.7765° W	20	Absent	0	3	2.48	37.4	41	21	32.8	17.0	2
20[C]	10.30	28.7752° N 80.7753° W	20	Absent	0	2	1.24	30.6	28	12	36.6	17.9	2
21[C]	10.45	28.7738° N 80.7749° W	9	Absent	0	3	1.30	23.2	23	0	39.1	16.5	2
22[C]	10.66	28.7724° N 80.7736° W	9	Absent	0	1	2.01	27.6	35	3	31.8	20.4	2
23[D]	11.01	28.7696° N 80.7719° W	9	Absent	0	3	1.65	18.5	30	1	46.4	19.3	3
24[D]	11.19	28.7681° N 80.7712° W	9	Absent	0	4	2.09	16.5	40	0	46.2	25.4	3
25[D]	11.53	28.7655° N 80.7693° W	7	Absent	0	3	3.60	21.4	30	0	50.5	31.7	3
26[D]	11.88	28.7626° N 80.7674° W	16	Absent	0	1	1.73	20.1	38	0	46.4	23.0	3
27[D]	12.14	28.7607° N 80.7662° W	16	Absent	0	1	1.36	12.0	30	0	49.8	20.9	3
28	12.38	28.7589° N 80.7647° W	16	Abundant	11	3	1.21	35.1	26	8	44.9	14.8	2
29	12.70	28.7563° N 80.7631° W	16	Abundant	37	0	1.13	43.9	30	0	41.3	15.7	2
30[E]	13.11	28.7535° N 80.7603° W	7	Rare	1	0	1.85	20.9	41	0	57.1	23.4	3
31[E]	13.30	28.7523° N 80.7592° W	29	Absent	0	0	2.44	13.5	46	0	63.2	36.0	3
32	13.60	28.7501° N 80.7573° W	29	Absent	0	2	1.57	20.2	46	0	47.0	20.8	3
33[F]	13.97	28.7477° N 80.7543° W	29	Rare[6]	0	2	1.92	16.6	18	0	41.8	29.6	3
34[F]	14.18	28.7465° N 80.7526° W	29	Rare	1	5	2.42	24.0	39	0	56.1	29.2	3

[1] Islands denoted by the same letter belong to the same block of marsh-connected islands

[2] Day in June, first of two sampling days

[3] Brown anole counts are adjusted for observer bias; green anole counts are unadjusted

[4] Percent of total island area

[5] Island 9 lacked both anole species and was excluded from data analyses; green anoles were observed on every other island at some point during the study

[6] Classification based on brown anoles observed subsequent to the counts

Data collection sites

To facilitate sampling, I established a longitudinal sampling transect through each island that paralleled the Intracoastal Waterway and crossed through the approximate center of the xeric habitat. In the few cases where this transect did not pass through forest habitat at one or both ends of an island, the nearest suitable forest habitat was used for forest sampling activities.

For pitfall and sticky trap sampling, islands were visually bisected perpendicular to their sampling transect into northern and southern halves, and sampling stations were sited along the transect at habitat midpoints in each of the two island halves (Figure S1.1).

For sweep net sampling and anole counts, sweep/search routes began at each of the two points where the sampling transect intersected the xeric–forest edge, and continued outward (one eastward and the other westward) along the forest edge (Figure S1.1).

Islands were divided into four quadrants (using the sampling transect and a visually estimated north–south bisecting line) for forest density and plant composition estimates. Forest density sites were located approximately 5 m into the forest at the "outer corner" of each quadrant (Figure S1.1). Plant composition vantage points were sited to provide the best view of the quadrant's xeric and forest edge vegetation, and thus their locations on each island were somewhat dependent on xeric habitat size and vegetational configuration (approximate locations are shown in Figure S1.1).

Species-based arthropod size classification

From previous brown anole gut content studies, I expected that brown anoles would prey predominantly on larger arthropods (length > 2mm), and therefore that the negative effects of

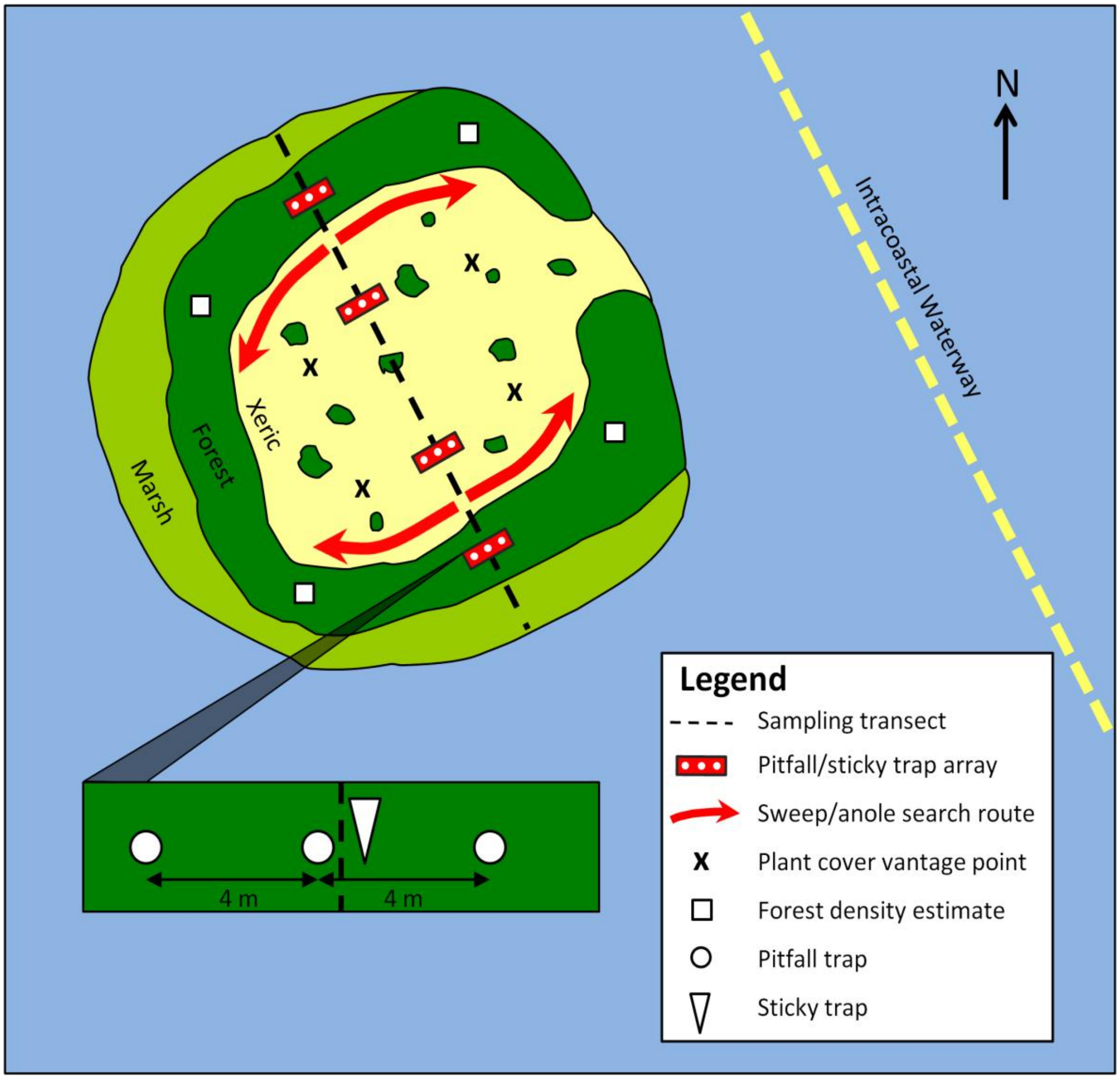

Figure S1.1 Sampling scheme for a typical study island.

increased anole predation following brown anole invasion would be focused on larger arthropods.

Under this expectation, there are distinct advantages to assigning arthropod size classes on the basis of adult body length for the species rather than captured specimen lengths. These advantages revolve around the fact that predation-driven declines in large arthropods could, through the reduction of population densities and total reproductive output in the consumed species, also reduce densities for small juveniles of those species. Thus, all else equal, anole predation on large arthropods could lead to a negative association between anole abundance and small arthropod abundance. Though the net effects of anoles on ambient small arthropod densities might be of primary interest in some studies (e.g., a study of competition between anoles and spiders), in this study the focus was the species-level impacts of differential dominant anole regimes, and potential impact mechanisms were of more concern than ambient arthropod availabilities.

One advantage to the species-based size classification is that it allows negative anole effects on large arthropod species to be detected even when large individuals of those species are not represented in samples (assuming that small juvenile densities are affected by reduced adult densities). For example, large individuals of large-bodied arthropod species might be missing in samples due to seasonal growth patterns or differential habitat occupancies among small and large individuals.

In the current study, the greatest advantage of the species-based size classification scheme was probably the greater detection probabilities it permitted for association patterns between BA_{Abund} and small arthropod species. Since small arthropod species are presumably less likely to serve as anole prey, they might indirectly benefit from increased anole predation on their larger arthropod predators or competitors. Signals from such effects, however, could be counteracted or obscured with the inclusion of small individuals of large species into measures of small arthropod abundance.

Anole counts: precision, adjustments, density relationship, and displacement relationship

Count precision

Anole searches were opportunistically repeated on three islands representing the range of brown anole invasion states observed in this study—absent, rare, and abundant (Table S1.2). Due to time constraints and observer availability, some routes were not searched on some visits. The same observer repeated the searches for a given route on a given island, with one exception (the June 24 searches on Island 1). The repeated searches demonstrated that counts were repeatable to within a few anoles (Table S1.2), but for counts to serve as a useful measure of anole abundance, it was necessary that their variation (1) could be distinguished from sampling error, and (2) reflected underlying variation in anole densities. For brown anoles, this first condition was clearly met—total adjusted brown anole counts on invaded islands ranged 0–67 and averaged 19.2, so sampling error uncertainties of 1–3 anoles at the lower end of this range and 5–15 anoles at the upper end were unlikely to have greatly affected the general position of islands in the ranked order of total counts (although the exact order was likely affected) or the results of statistical analyses (especially after counts were log-transformed). In contrast, total counts of green anoles ranged only 0–7 and averaged 1.9; sampling error uncertainties of 1–3 anoles at the lower end of the range and likely at least 2–3 at the upper end probably obscured any true differences in green anole relative abundance that may have existed. Whether counts reflected anole densities is addressed below (see *Count–density relationship*).

Table S1.2 Anole count totals and measures of dispersion for repeatedly searched islands. Brown anoles were absent on Island 8, rare on Island 1, and abundant on Island 7. Tabulated means are across-visit averages. SD = sample standard deviation, CV = coefficient of variation. The SD and CV were not calculated for routes searched only once, nor was the CV calculated for routes with count SD or mean equal to zero. Search dates were in 2006.

Species	Island	Route	Observer	Visit dates and counts					Mean	SD	CV,%
Brown anoles											
				5-Jun	24-Jun						
	1	NW	Author	1	-				1.0	-	-
		NE	Asst. 2[1]	0	1				0.5	0.71	141
		SW	Author	1	-				1.0	-	-
		SE	Asst. 1[1]	0	0				0	0	-
		Total		2	-				2.0	-	-
				19-Jun	23-Jun	26-Jun	1-Jul	2-Jul			
	7	NW	Author	8	6	12	10	7	8.6	2.41	28
		NE	Asst. 1	14	18	16	15	-	15.8	1.71	11
		SW	Asst. 2	8	11	7	5	-	7.8	2.50	32
		SE	Author	-	20	18	17	16	17.8	1.71	10
		Total		-	55	53	47	-	51.7	4.16	8
Green anoles											
				5-Jun	24-Jun						
	1	NW	Author	2	-				2.0	-	-
		NE	Asst. 2[1]	0	1				0	0	-
		SW	Author	0	-				0	-	-
		SE	Asst. 1[1]	0	0				0	0	-
		Total		2	-				2.0	-	-
				19-Jun	23-Jun	26-Jun	1-Jul	2-Jul			
	7	NW	Author	0	1	1	1	0	0.6	0.55	91
		NE	Asst. 1	0	0	0	0	-	0	0	-
		SW	Asst. 2	1	0	0	0	-	0.2	0.50	200
		SE	Author	-	2	0	1	0	0.8	0.96	128
		Total		-	3	1	2	-	2.0	1.00	50
				19-Jun	23-Jun	24-Jun	25-Jun				
	8	NW	Asst. 1	1	0	-	0		0.3	0.58	173
		NE	Asst. 2	0	0	-	0		0	0	-
		SW	Author	2	0	0	1		0.8	0.96	128
		SE	Author	-	0	0	0		0	0	-
		Total		-	0	-	1		0.5	0.71	141

[1] Searches on 24-Jun conducted by author

The repetition of search routes by the same observer may have biased the counts towards similarity due to observer familiarity with perch sites previously occupied by anoles. Although observers attempted to conduct searches without the use or consideration of such prior knowledge, it is possible that prior experience introduced unintentional bias into the counts. If so, the magnitude of the bias was likely small compared to the variation introduced by sampling error.

Count adjustments

Anole search routes on each island were haphazardly assigned among the author and two assistants. Since there were four routes (NW, NE, SW, SE) and three observers, it was necessary for one observer to search two routes on each island; because the identity of the two-route observer differed among islands, relative inter-observer effort was not equivalent across islands. If observers differed in their ability to detect anoles, differences in their relative effort across islands would have introduced bias into relative anole abundance estimates. I looked for evidence of differential brown anole detection probabilities among observers (green anole counts were too low to provide such evidence) and corrected for their effects using minor count adjustments.

Prior to investigating differential detection probabilities, I verified that route frequencies were not biased among observers ($X^2 = 5.86$, df = 6, $P = 0.44$).

To test for evidence of differential detection probabilities, I used paired *t*-tests to compare island-matched brown anole counts for each pairwise combination of observers. Given unbiased route assignments, if observers differed in their detection probabilities, then one or more observers should have counted more brown anoles, on average, than the remaining observer(s). I used only brown anole islands (i.e., those with abundant brown anoles) for the comparisons because (1) count differences on islands with rare brown anoles were likely driven by chance events rather than detection probabilities, and (2) islands without brown anoles were incapable of providing evidence for differential brown anole detection. For the two-route observer on each island, I used the mean of the two counts in comparisons. Counts did not significantly differ between the two assistants (mean difference [MD] = 0.2, $t = 0.15$, df = 12, $P = 0.88$), but my counts were greater on average than assistant counts ($MD_1 = 2.4$, $t = 2.93$, df = 12, $P = 0.012$; $MD_2 = 2.1$, $t = 2.15$, df = 12, $P = 0.053$). Since the counting efforts of the two assistants could be considered equivalent, relative counting effort across brown anole islands differed only by the author–assistant route number ratio (either 1:3 or 2:2).

To equilibrate counting effort across islands, it was necessary only to convert an assistant count to an author count for the islands on which I searched a single route. Although matched-count differences were useful for determining that I tended to count more brown anoles than did assistants, these differences were not as useful for converting counts among observers. Differences in counts were affected both by differences in detection probabilities and differences in underlying anole densities, so expected count differences should have varied with brown anole density across islands. In contrast, expected ratios of island-matched observer counts should—in the absence of other factors—depend only upon detection probabilities and remain constant across islands with differing anole densities. Count ratios thus offered (in theory) a relatively simple solution for converting observer counts: (1) calculate the mean author–assistant count ratio across brown anole islands, and (2) multiply an assistant count by this ratio to convert it to an author count for islands on which I counted a single route.

I used observer count ratios to make bias-correcting adjustments to brown anole counts. For each brown anole island, I pooled all assistant counts and calculated the ratio of the mean author count to mean assistant count. The mean of these ratios across brown anole islands was 1.88 (95% CI = 1.25–2.50), but inspection of the scatter plot of count ratio versus mean assistant count revealed a pattern of lower ratios at higher mean assistant counts; this pattern was approximately linear on the $\log_{10}$(mean assistant count) scale (Figure S1.2). Thus, all observers were approximately equivalent when brown anoles were extremely abundant, but I consistently counted more brown anoles where their abundance was more moderate. My best explanation for this pattern—based on anecdotal observations made in this system and elsewhere—is that average brown anole conspicuousness increased with density, and author–assistant detection inequalities decreased as anoles became more conspicuous. I assumed the pattern was real and used it to adjust brown anole count totals for brown anole islands on which I searched a single route. For a given island and its mean assistant count, I used the regression shown in Figure S1.2 to generate an expected author–assistant count ratio. Next, I multiplied this expected ratio by the mean assistant count as a way of converting an assistant count to an author count. Finally, I calculated an adjusted count total by rounding the following sum to the nearest integer: (author count) + 2*(mean assistant count) + (converted assistant count). Original and adjusted total counts for brown anole islands are listed in Table S1.3 and plotted in Figure S1.3. Brown anole count totals on green anole islands were not adjusted.

Count–density relationship

Anole densities were estimated on the two invaded, repeatedly counted islands (Islands 1 and 7) using a modified version of Heckel and Roughgarden’s (1979) mark-resight technique. I

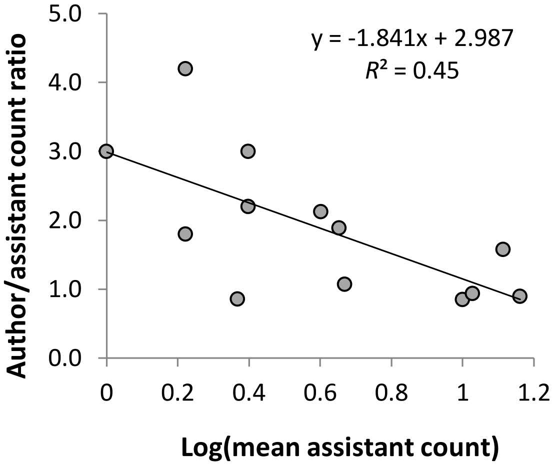

Figure S1.2 Linear regression of author/assistant count ratios on $\log_{10}$-transformed mean assistant counts for brown anoles on brown anole islands. Regression equation and explained variance (R^2) are displayed. $R^2_{\text{adj}} = 0.40$.

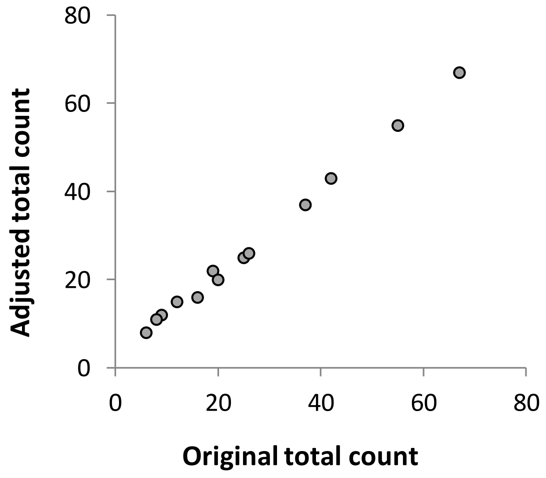

Figure S1.3 Original versus adjusted total brown anole counts for brown anole islands. Correlation (r) = 0.998.

Table S1.3 Author/assistant mean count ratios, number of author search routes, and count totals for brown anoles on brown anole islands.

Island	Author/asst. count ratio	Author searches	Original total count	Corrected total count
3	4.20	1	12	15
4	1.89	2	26	26
5	1.58	2	67	67
6	0.94	1	42	43
7	0.90	2	55	55
13	3.00	2	20	20
14	0.86	1	9	12
15	3.00	1	6	8
16	2.20	2	16	16
17	1.07	1	19	22
18	2.13	2	25	25
28	1.80	1	8	11
29	0.85	2	37	37

established a 15 x 4 m census plot along each of the search routes by staking off the first 15 m of the route and then conducting mark-resight activities in the forest to an estimated depth of 4 m from the marked forest edge. Plots were visited on three successive days in August 2006 between 0815–1100 h in sunny to partly sunny conditions, with the exception of the final census day for Island 1, which was conducted from 1200–1340 in cloudy conditions. Anoles were marked with a different color of India ink on successive census days, diluted with water and applied with a squirt gun (Vincent 2002); markings were applied to the posterior half of anoles so that markings would not hit their eyes. In addition to the anole searches conducted at the xeric–forest edge for this study, searches were also conducted at the outer marsh edges of each island as part of an unpublished related study, and I incorporated marsh count data into the assessment of anole count–density relationships. Marsh search methods were analogous to the methods used in forest searches, and both marsh and forest repeated counts and density estimates were performed on the same islands and dates. The assumption of independence between census days was verified with chi-squared goodness-of-fit tests for all density-estimating models except one—the NE marsh on Island 7, for which a lack of independence in days 2 and 3 was identified and modeled as described by Heckel and Roughgarden (1979). Note that since anole searches were conducted in June and density estimates in August, density-to-count ratios may have been underestimated to the extent that mortality reduced adult population sizes between June and August (only adult anoles were censused, and no new adult anoles were added to the population in the intervening time because the yearly cohort of juveniles matures between September and April in this system). It is possible, however, that the edge environments where anoles were counted and censused provided optimal territory locales, and that mortality along habitat edges was offset by anoles immigrating from sub-optimal territories in, for example, the forest interior.

To model the relationship between brown anole counts and estimated densities, I examined the scatter plot of route density estimate versus projected total count and attempted to construct a reasonably well-fitting model for the observed pattern. Projected total counts (Table S1.4) were the counts expected if all four routes were identical to the route(s) under consideration, using the repeated count mean for each route (see Table S1.2). For Island 7, projected totals were derived by multiplying mean route count by four; for Island 1, numbers of marked lizards were too small to allow separate density estimates for each route, so mark-resight data were pooled within habitats to estimate densities and projected counts were based on the mean totals of the pooled routes (forest = mean count x 1; marsh = mean count x 2). Counts were not adjusted for observer bias in this process because author–assistant count ratios were expected to be approximately 1:1 on Island 7, on which brown anoles were extremely abundant, and Island 1 was exempted from adjustment due to the rarity of its brown anoles (see *Count adjustments* above). The pattern present in the examined scatter plot suggested a linear relationship between densities and log-transformed projected counts, so I applied a $\log_{10}$(count +1) transformation to the projected total counts and obtained a well-fitting linear model ($R^2 = 0.87$; Figure S1.4).

Count correspondence to green anole displacement

To determine the approximate brown anole count magnitudes corresponding to green anole displacement from island food webs, I used the count–density regression derived above to convert relevant brown anole density estimates from Campbell's (2000) introduction experiment into expected total counts. Campbell introduced brown anoles onto three spoils islands in Mosquito Lagoon and monitored an unaided invasion on a fourth island; of these, only one of the introduction islands ("LT", Island 6 in this study) and the unaided invasion island ("L2C", Island 3) were of the same type as the islands used in the current study (i.e., islands with an open interior), and I used only the data pertaining to those two islands for the steps below. By 1998, the final year of Campbell's (2000) study, "the only habitat [on LT] in which green anoles could consistently be found was dense forested edge habitat bordering on dense shrub-marsh habitat, which was the only habitat in which green anoles could be found in large numbers on [L2C]" (p. 179). From these and other results reported by Campbell, I inferred that by 1998 green anoles had effectively been replaced in, and no longer substantially affected the food web dynamics of, xeric and forest (except forest–marsh edge) habitats on LT and L2C.

Table S1.4 Counts and density estimates used to evaluate the count–density relationship. Confidence interval lower bounds were constrained by the number of individual lizards physically marked in censuses.

Island	Habitat	Route	Mean count (samples; range)	Projected total count	Density estimate, per ha (95% CI)
1	F	NW+NE+SW+SE	2.0 (1; N/A)	2.0	272 (167–618)
	M	NW+NE	0 (2; 0–0)	0	545 (333–1236)
7	F	NW	8.6 (5; 6–12)	34.4	4768 (3667–6232)
	F	NE	15.8 (4; 14–18)	63.0	4164 (3667–4968)
	F	SW	7.8 (4; 5–11)	31.0	5400 (5000–6053)
	F	SE	17.8 (4; 16–20)	71.0	5833 (5500–6406)
	M	NW	3.3 (3; 3–4)	13.3	3509 (2500–5103)
	M	NE	7.5 (4; 5–10)	30.0	4400 (3000–6576)
	M	SW	18.7 (3; 11–24)	74.7	6182 (5667–6952)
	M	SE	17.3 (3; 10–28)	69.3	6782 (5667–8078)

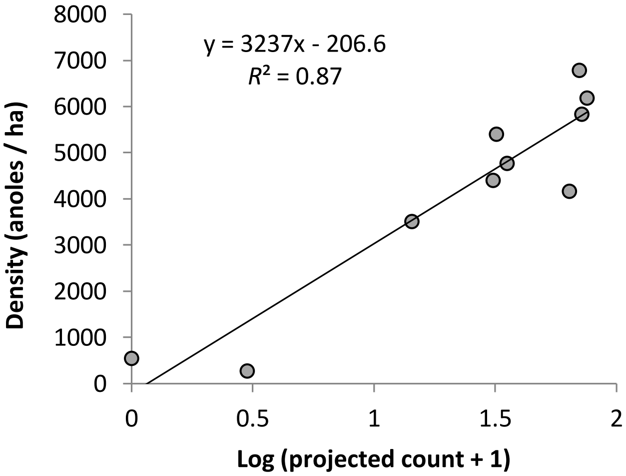

Figure S1.4 Estimated brown anole density versus log-transformed projected total counts. Linear regression equation and explained variance (R^2) are shown. $R^2_{adj} = 0.85$.

Whole-island, vegetated area brown anole densities in 1998 were estimated at 2515 [95% CI: 1930–3371] lizards/ha on LT and 1521 [984–2588] lizards/ha on L2C (Campbell 2000); I took this density range (1500–2500 lizards/ha) as an indicator of green anole displacement from the xeric and forest (except forest–marsh edge) habitats of similar islands. Correspondence of Campbell's whole island, vegetated area densities to the xeric–forest edge densities estimated in this study was, however, indirect. Approximately 60% of the brown anoles Campbell observed on LT (final year) and L2C (all years) were in forest habitat, with the remaining observations split about evenly between the xeric and marsh habitats (p. 181). Xeric, forest, and marsh habitats contained 23%, 39%, and 38% of the vegetated area on LT, respectively, and 34%, 40%, and 26% on L2C (Table 4.2 in Campbell 2000). Combining xeric and forest habitats and averaging between the two islands, 80% of the brown anoles were observed in 68% of the vegetated area; if densities mirrored these observation frequencies, then brown anoles were 80%/68% = 1.2 times denser in the combined xeric and forest habitats than the whole-island density estimates. Since more detailed information regarding the percentage of brown anoles observed at the xeric–forest edge was not reported, I used the above observation-to-area ratio for combined xeric and forest habitats to translate total vegetated area densities into xeric–forest edge densities. Xeric–forest densities expected to coincide with green anole replacement were thus 1500–2500 * 1.2 = 1800–3000 lizards/ha.

The count–density relationship modeled in this study yielded expected counts of 3.2–8.8 for brown anole densities of 1800–3000 lizards/ha (Figure S1.4). Thus the gap in the ordered set of total brown anole counts between 2 and 8 served well as a delimiter between islands dominated by green versus brown anoles. The resulting dominant anole assignments matched exactly my qualitative impressions concerning the dominant anole on each island.

Environmental covariable construction

Data for variables used in habitat structure PCAs were gathered using field observations and digital, aerial imagery. Field observations were used to class xeric and forest vegetation into basic types and estimate forest understory densities. Based on my experience working in this system, I categorized the xeric vegetation on each island as relatively short and scrubby (= 0) or taller and more forest-like (= 1). I also classed the forest on each island as relatively short and scrubby (= 0), intermediate (= 1), or tall, well-developed and/or mature (= 2). For forest understory density estimates, I used the mean value of four density estimates (Figure S1.1) in which the understory was classed as relatively open and easy to walk through (= 0), somewhat open and moderately passable (= 1), or nearly impenetrable without trail blazing (= 2). The remaining habitat structure variables were assembled using digital orthophotos from the Florida Land Boundary Information System (http://data.labins.org/2003/) that were taken in 2000 and provided as 1 m^2 resolution JPEG files. I collected data from these using ArcView (pixel counts) and Adobe Photoshop (all other processes). To estimate total island area and the areas of xeric, forest, and marsh habitats, I manually extracted images of each habitat on each island and summed the pixels in each image (1 pixel = 1 m^2; dithering was turned off to prevent pixel additions from automatic color simulation). For xeric habitats, I also selected and extracted (using the “magic wand” tool) the areas of open ground in order to calculate the vegetated proportion of xeric habitat area. Since exposure of xeric habitats to marsh or shorelines without a buffering band of forest likely affects both xeric microclimate and dispersal of shore arthropods into xeric areas, I estimated the proportion of the xeric habitat perimeter that was open to marsh and/or the shore (distances were measured in pixels, which corresponded to meters). I also estimated the mean width (i.e., depth) of forest bands because forest depth affected how far into the forest sampling stations were sited (since stations were established at forest band midpoints), which could have influenced arthropod community composition in a number of ways (e.g., microclimate variation and arthropod influx from edge habitats). Means were calculated from measurements of forest depth at six locations: the two points where the sampling transect intersected the forest, and both 15 m to the east and to the west of those two points; together, these six locations approximately bracketed the regions of the forest that were sampled in this study.

Plant cover estimates for xeric and forest vegetational composition PCAs were made from four non-overlapping vantage points on each island (see *Data collection sites*). At each vantage point, I surveyed the visible xeric vegetation and outer 5 m of forest vegetation and estimated for each the proportion of vegetated area (classed 0, < 0.10, 0.10–0.25, 0.26–0.75, or > 0.75) covered by each common plant species (i.e., those listed in Methods: *Study system* plus *Conocarpus erectus*, as lateral branches of *C. erectus* occasionally projected from marsh habitats through significant portions of the thinnest forests). Since the canopies of different plant species often overlapped, coverages summed across species for a given point estimate frequently totaled greater than 100%. Class midpoints were assigned to cover estimates prior to calculating habitat means for each species, which were subsequently used for PCA.

Habitat structure PCAs were performed on correlation matrices (due to differences in measurement types and scales) and plant composition PCAs on variance–covariance matrices. The first two principal components were retained from these PCAs as environmental covariables, summarizing 74–85% of the variation present in habitat structure variables and 74–84% of the variation in vegetational composition. Interpretations for these principle components are given in Table S1.5.

Table S1.5 Principal components retained as environmental covariables.

Principle component[1]	% Variance	Interpretation
Xhab_1	47.8	xeric scrubbiness; higher values = shorter, scrubbier xeric vegetation surrounded by thinner, less continuous forest
Xhab_2	26.1	tradeoff between xeric habitat size and plant cover; higher values = larger, less vegetated xeric habitats
Fhab_1	63.9	forest size and extent; higher values = larger, deeper, more mature and continuous forests
Fhab_2	20.8	forest understory density; higher values = denser understories
FEhab_1	56.0	island “forestedness”; higher values = taller xeric vegetation and larger, deeper, more mature and continuous forests
FEhab_2	21.3	tradeoff between xeric habitat size and plant cover; higher values = larger, less vegetated xeric habitats
Xveg_1	58.4	tradeoff between cedar and palm dominance; higher values = greater palm, less cedar cover[2]
Xveg_2	17.2	higher values = greater palmetto cover[2]
Fveg_1	54.1	dominance of cedar; higher values = greater cedar, less palm and Brazilian pepper cover[2]
Fveg_2	20.0	higher values = greater palm and palmetto, less myrtle cover; possibly related to substrate grain size[2]
FEveg_1	53.4	tradeoff between cedar and palm dominance; higher values = more cedar, less palm in swept vegetation[2]
FEveg_2	30.9	degree of dominance by cedar and palm; higher values = more cedar and/or palm, less Brazilian pepper, myrtle, and stopper[2]

[1] Codes imbedded in principle component names: X = xeric, F = forest, FE = xeric–forest edge, hab = habitat structure PCA, veg = vegetation composition PCA

[2] Referenced plant species: Brazilian pepper = *Schinus terebinthifolia*, cedar = *Juniperus virginiana*, myrtle = *Morella cerifera*, palm = *Sabal palmetto*, palmetto = *Serenoa repens*, stopper = *Myrcianthes fragrans*

Both weather data from a nearby weather station and rainfall observations from the field were used in a PCA to model xeric and forest habitat sampling conditions. Variables obtained or calculated from the Titusville NOAA weather station data included sampling date minimum temperature, maximum temperature, and five-day weighted rainfall totals (weights = $1/d$, where d = days from sampling date with range 1 [sampling day] to 5 [4 days prior]). Since rainfall coverages from afternoon thunderstorms were often spotty, whether a rainfall event was observed for an island during sampling (no = 0, yes = 1) was also included as a variable in the weather PCA. The first weather principle component (WTHR_1), representing 60% of the variance, was retained for the xeric and forest environmental covariable sets. Higher values of WTHR_1 were associated with more moderate temperatures (higher minimum temperatures and lower maximum temperatures) and greater regional rainfall (i.e., higher weighted rainfall totals at the weather station); interestingly, WTHR_1 was negatively associated with observed island rainfall events. This apparent discrepancy in rainfall trends occurred because rainfall was not observed on study islands on or soon after the dates that major rainfall events (> 0.75 inches) were recorded at the weather station. Since rainfall was recorded only five times for spoils islands (compared to 12 times at the weather station) and rainfall totals on spoils islands were unknown, it is probably best to regard WTHR_1 as an indicator of general weather conditions.

Spatial covariable selection

As recommended by Dray et al. (2006), I generated a set of candidate spatial weighting matrices as the first step in selecting spatial covariables that maximized explained arthropod community dissimilarities. I generated 126 unique spatial weighting matrices using two different neighborhood algorithms and the distance–similarity function:

$$f = 1 - \left(\frac{d_{ij}}{\max\left(d_{ij}\right)} \right)^{\alpha/\beta},$$

where d_{ij} was the distance between islands i and j, and α and β were parameters taking the integer values from 1 to 10. This function produces a variety of linear ($\alpha = \beta$), concave up ($\alpha/\beta < 1$), and concave down ($\alpha/\beta > 1$) distance–similarity relationships. Distances were calculated by considering the study islands as a linear array and measuring the distances between approximate island centers in this array (i.e., distances between the ICW positions listed in Table S1.1). Neighbor relationships were defined using (1) a distance criterion with the shortest distance required to keep all islands connected as the threshold (as is usually done in PCNM), or (2) a relative neighborhood graph (Jaromczyk and Toussaint 1992) connecting islands only to their nearest neighbor to the north and to the south.

The MEM with positive eigenvalues (i.e., eigenvectors representing positive autocorrelation patterns) generated from each unique spatial weighting matrix were retained as candidate predictor sets for explaining arthropod community variation, and the best-fitting of these MEM sets was separately assessed for each arthropod community. In each assessment, all possible MEM models were generated within each candidate MEM set, and the MEM set containing the model with the lowest AIC_C score across all sets was selected as the best fitting. Arthropod community variation was modeled using distance-based redundancy analysis (db-RDA) as described in Methods: *Multivariate community composition analyses*, but with one modification: db-RDA eigenvectors (i.e., the dependent variables) were detrended prior to spatial model selection to allow MEM full potential to model more complex spatial structures (Borcard and Legendre 2002). Detrending was accomplished by retaining the residuals of simple linear regressions of the eigenvectors on island position. For both $\mathrm{GND}_{\mathrm{Xer}}$ and $\mathrm{AER}_{\mathrm{For}}$, the best MEM set was derived using the distance criterion neighbor network with $\alpha = 1$ and $\beta = 10$. The relative neighborhood algorithm with $\alpha = 10$ and $\beta = 1$ produced the best MEM set for $\mathrm{GND}_{\mathrm{For}}$ and FOL, and this algorithm with $\alpha = 1$ and $\beta = 6$ yielded the best set for $\mathrm{AER}_{\mathrm{Xer}}$.

Only significant individual MEM within best-fitting sets were retained in final spatial covariable sets. Spatial covariables were relevant only to the extent that they captured autocorrelation patterns generated by environmental factors or ecological processes, and I assessed this relevancy with two tests. First, to determine whether individual MEM in a best-fitting set represented nonrandom autocorrelation patterns, I calculated Moran's *I* for each MEM and compared it to the distribution generated from 9999 permutations of MEM scores (MEM eigenvalues are linearly related to Moran's *I*; Dray et al. 2006, see also tutorial in Dray 2010); significant MEM (alpha = 0.10) were retained. Second, I used forward selection (alpha = 0.10) to identify remaining MEM that significantly explained variation in a detrended db-RDA of the relevant community (significance assessment and explained variation limits followed the procedures detailed in Methods: *Multivariate community composition analyses*). Final spatial covariable sets included these MEM (number retained: $\mathrm{GND}_{\mathrm{Xer}} = 4$, $\mathrm{GND}_{\mathrm{For}} = 3$, FOL = 3, $\mathrm{AER}_{\mathrm{Xer}} = 6$, $\mathrm{AER}_{\mathrm{For}} = 2$) as well as island position in the linear array (range 0–14.2 km). Spatial model analyses (except forward model selection) were performed using the packages 'vegan' (Oksanen et al. 2010), 'spdep' (Bivand et al. 2010), and 'spacemakeR' (Dray 2010) in R v2.11 (R Development Core Team 2010).

Distance-based redundancy analysis: suitability and explained variation calculations

I chose db-RDA over two constrained ordination alternatives, canonical correspondence analysis (CCA; ter Braak 1986) and RDA, because (1) spatial distances and environmental differences among islands were relatively small, leading me to expect linear—or at least monotonic—relationships between species abundances and spatial or environmental covariables (CCA is suited to unimodal relationships; McCune and Grace 2002), and (2) shared species absences do not contribute to site similarity in Bray-Curtis db-RDA as they do in RDA, making db-RDA a better choice for analyzing the sparse site–abundance matrices obtained in this study (see Legendre and Legendre 1998, pp. 253–254). Due to the semi-metric properties of Bray-Curtis distance matrices, some eigenvectors extracted in the PCoA step of db-RDA had negative eigenvalues, or sums of squares (SS). Since both positive and negative SS must be incorporated into db-RDA to prevent underestimating explained fractions (McArdle and Anderson 2001), in the RDA step of db-RDA I separately assessed the variation (SS) explained among positive and negative eigenvectors. Summing these two quantities yielded total explained SS (McArdle and Anderson 2001), which I divided by the total SS (i.e., the sum of all positive and negative eigenvalues) to obtain the unadjusted proportion of variation explained (R^2). As described in Methods: *Multivariate community composition analyses*, db-RDA R^2 values were adjusted to remove bias prior to variation partitioning. Db-RDAs were performed using the “wcmdscale” function in the R package ‘vegan’ for PCoA and CANOCO v4.5 (ter Braak and Šmilauer 2002) for RDA.

Negative binomial regression models: overdispersion parameter estimation

I used NB-2 negative binomial regression to model arthropod abundance responses that were overdispersed in, and therefore poorly modeled by, Poisson GLMs. I opted to use negative binomial (NB) rather than quasi-Poisson models for these responses because low and high counts are more evenly weighted in the fitting of NB models, whereas quasi-Poisson models heavily weight the highest counts (Ver Hoef and Boveng 2007); given the relatively limited sampling regimen of this study and the potential for sampling error to have substantially affected measured abundances, strong asymmetry in modeling weights would likely have resulted in less accurate parameter estimates. The NB-2 negative binomial model is a GLM if the overdispersion (or ancillary) parameter, θ, is considered a known constant (McCullagh and Nelder 1989, Hilbe 2008). In practice, θ is usually estimated from the data under the full (or global) model (Burnham and Anderson 2002, p. 26; Hilbe 2008). For a given abundance response variable, I obtained the full model maximum likelihood estimate of θ with the "glm.nb" function in the R package 'MASS' (Venables and Ripley 2002) and used that estimate in all NB models constructed for $R^2_{\mathrm{D,\ adj}}$ partitioning.

Adjusted *R*-squared measures for negative binomial regression models

I used simulated data to assess two adjusted R^2 deviance measures for NB-2 models. The first, given by Ricci (2010) as an asymptotically unbiased estimator of true population R^2 deviance (R^2_{D}) for exponential dispersion models when the null hypothesis of no association is true (i.e., regression coefficients = 0), was

$$R^2_{\mathrm{D,\,df}} = 1 - \left(\frac{n-1}{n-k-1} \right) \left(1 - R^2_{\mathrm{D}} \right),$$

where n is the number of observations and k the number of covariates. This measure is derived using model deviance divided by the degrees of freedom as an estimator of model dispersion (Ricci 2010), and it is analogous to the degrees of freedom correction used to calculate adjusted R^2 for ordinary least squares models (see Mittlböck and Waldhör 2000). Since Pearson residuals divided by the degrees of freedom produce less biased estimates of dispersion in Poisson models (Venables and Ripley 2002, Hilbe 2008) and have previously been used in adjusted R^2_{D} measures (Heinzl and Mittlböck 2003, Ricci and Martínez 2008), I also tested the measure

$$R^2_{\mathrm{D,\,P}} = 1 - \frac{D(\boldsymbol{y}, \hat{\boldsymbol{\mu}}) + k\varphi_{\mathrm{P}}}{D(\boldsymbol{y}, \bar{\boldsymbol{\mu}})} ,$$

where $\varphi_{\mathrm{P}} = \frac{1}{n-k-1} \sum \frac{(y_i - \hat{\mu}_i)^2}{\hat{\mu}_i + \hat{\mu}_i^2 / \theta}$,

$D(\boldsymbol{y}, \hat{\boldsymbol{\mu}})$ is the model deviance, $D(\boldsymbol{y}, \bar{\boldsymbol{\mu}})$ is the null deviance, and θ is the overdispersion parameter. To my knowledge, these measures have not previously been assessed for NB-2 models.

I used R to generate NB-2 distributed random variables with mean = μ_0 * exp[$\beta_1 x_1$] and θ = 1, 3, or 9, where x_1 was a normally distributed random variable $N(1, 0.2)$, μ_0 = 2, 5, or 20, and β_1 = 0, 1, or 2 (Hilbe 2011). The ranges of these parameter values were representative of most of the NB-2 models constructed for arthropod abundances in this study. For each set of modeled conditions, I calculated R^2_{D} for a sample size of 64,000 and used this value, denoted $R^2_{\mathrm{D,\,large}}$, as the true population R^2_{D} (bias in estimated R^2_{D} decreases with sample size). Smaller sample sizes of n = 16, 32, and 64 were created by partitioning the simulated data into 1,000 subsamples of n = 64 and using the first n observations in each subsample. To test the bias-correcting properties of $R^2_{\text{D, df}}$ and $R^2_{\text{D, P}}$, I calculated their values for each subsample for the NB-2 model containing x_1 (the generating variable) plus 1, 3, or 7 additional (and unassociated) normally-distributed random variables. I compared the means of these measures across subsamples to $R^2_{\text{D, large}}$ values, and considered smaller departures from $R^2_{\text{D, large}}$ to indicate better bias correction (though variation around mean adjusted R^2_{D} estimates is also of concern; see Heinzl and Mittlböck 2003).

These simulations are part of a larger study of NB-2 adjusted R^2_{D} measures that will be published elsewhere. In the larger study, I considered model conditions and estimation procedures that more closely resembled the modeling conducted in this food web study. Although the results of those additional simulations—which included other parameter values, additional generating variables either included or excluded from the full model, and the use of maximum likelihood θ estimates derived from either the current or full models—are not detailed here, they guided my selection of an adjusted R^2_{D} measure for this study.

Both adjusted R^2_{D} measures performed reasonably well under the modeling conditions considered here (Figure S1.5, Tables S1.6–9) and in additional simulations. In general, mean $R^2_{\text{D, df}}$ estimates tended to fall below true R^2_{D} (i.e., $R^2_{\text{D, large}}$) and mean $R^2_{\text{D, P}}$ estimates above, but the magnitudes of these departures were usually negligible with n = 64 and often negligible with n = 32. $R^2_{\text{D, P}}$ nearly always outperformed $R^2_{\text{D, df}}$ under more information-rich modeling conditions, for example greater n, smaller θ (= smaller variances), greater distribution means

(= fewer zeroes in the data), known rather than estimated θ, inclusion of all generating variables, and larger β values (= greater signal-to-noise ratios). Where less information was available, however, $R^2_{\mathrm{D,\,df}}$ performed at least as well as $R^2_{\mathrm{D,\,P}}$, and often better.

I opted to use $R^2_{\mathrm{D,\,df}}$ in this study for two reasons. First, arthropod abundance modeling in this study most closely resembled simulation conditions in which $R^2_{\mathrm{D,\,df}}$ performance was equal to or better than that of $R^2_{\mathrm{D,\,P}}$; specifically, sample sizes were moderately small (n = 33), mean abundances at the order level were typically low, θ values were estimated from the data, and unconsidered factors causally affecting abundances likely existed. Second, $R^2_{\mathrm{D,\,df}}$ values tended to fall below true R^2_{D}, as opposed to $R^2_{\mathrm{D,\,P}}$, and thus served as conservative estimates of R^2_{D}. Although this underestimating tendency may have rendered indistinguishable—through the truncation of reported $R^2_{\mathrm{D,\,df}}$ values at zero—cases in which the variation explained by brown anole abundance was very low and cases in which it was zero, because small fractions of explained variance were not statistically significant (i.e., distinguishable from zero) anyway, inferences were unlikely to be affected by the phenomenon.

R code used to generate NB-2 models and assess adjusted R^2_{D} measures is provided below.

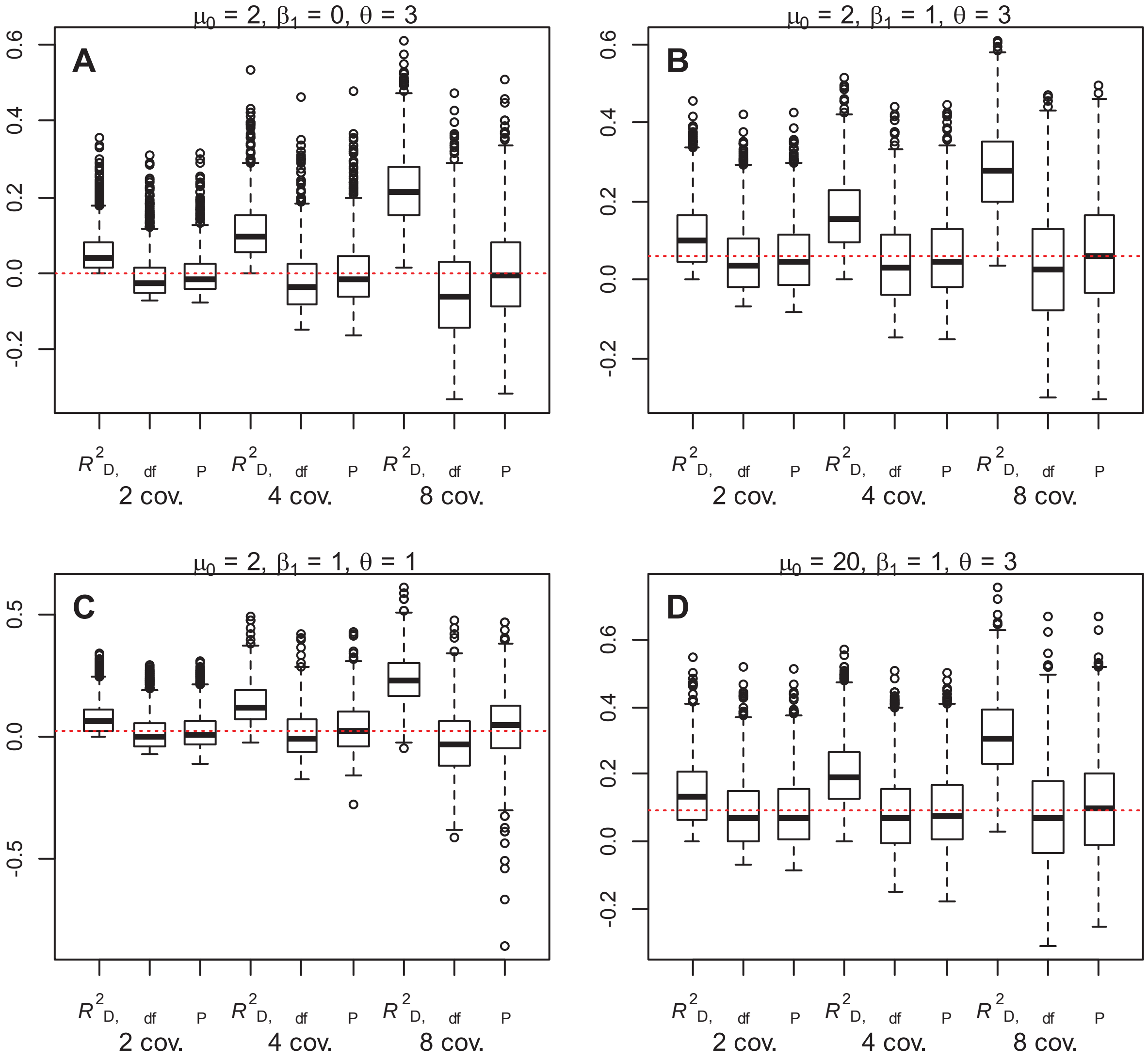

Figure S1.5 Boxplots of simulation results for selected models with n = 32 and 2, 4, or 8 covariates. Model parameters are listed above plots. Dashed lines represent $R^2_{\mathrm{D,\,large}}$, the estimated true population R^2_{D}.

Table S1.6 Simulation results for models with null β_1 and varying μ_0. These models correspond to the null hypothesis of no association.

									Estimated bias	
μ_0	β_1	θ	$R^2_{\text{D, large}}$	k	n	R^2_{D}	$R^2_{\text{D, df}}$	$R^2_{\text{D, P}}$	$R^2_{\text{D, df}}$	$R^2_{\text{D, P}}$
2	0	3	0.0000	2	16	0.1178	-0.0180	0.0068	-0.0180	0.0068
					32	0.0565	-0.0086	0.0013	-0.0086	0.0013
					64	0.0268	-0.0051	-0.0007	-0.0051	-0.0007
				4	16	0.2322	-0.0469	0.0082	-0.0469	0.0082
					32	0.1132	-0.0182	0.0037	-0.0182	0.0037
					64	0.0549	-0.0092	0.0003	-0.0092	0.0003
				8	16	0.4715	-0.1326	-0.0065	-0.1326	-0.0065
					32	0.2249	-0.0448	0.0062	-0.0448	0.0062
					64	0.1098	-0.0196	0.0018	-0.0196	0.0018
5	0	3	0.0000	2	16	0.1243	-0.0104	0.0071	-0.0104	0.0071
					32	0.0600	-0.0048	0.0027	-0.0048	0.0027
					64	0.0294	-0.0024	0.0010	-0.0024	0.0010
				4	16	0.2496	-0.0233	0.0166	-0.0233	0.0166
					32	0.1200	-0.0104	0.0060	-0.0104	0.0060
					64	0.0583	-0.0056	0.0017	-0.0056	0.0017
				8	16	0.5023	-0.0665	0.0318	-0.0665	0.0318
					32	0.2391	-0.0256	0.0149	-0.0256	0.0149
					64	0.1161	-0.0125	0.0044	-0.0125	0.0044
20	0	3	0.0001	2	16	0.1258	-0.0087	0.0040	-0.0087	0.0040
					32	0.0621	-0.0026	0.0027	-0.0026	0.0027
					64	0.0304	-0.0014	0.0008	-0.0014	0.0008
				4	16	0.2522	-0.0198	0.0099	-0.0198	0.0099
					32	0.1225	-0.0075	0.0046	-0.0075	0.0046
					64	0.0609	-0.0028	0.0021	-0.0028	0.0021
				8	16	0.5146	-0.0401	0.0291	-0.0401	0.0291
					32	0.2487	-0.0126	0.0175	-0.0126	0.0175
					64	0.1211	-0.0067	0.0051	-0.0067	0.0051

Table S1.7 Simulation results for varying $\beta_{1.}$

									Estimated bias	
μ_0	β_1	θ	$R^2_{\text{D, large}}$	k	n	R^2_{D}	$R^2_{\text{D, df}}$	$R^2_{\text{D, P}}$	$R^2_{\text{D, df}}$	$R^2_{\text{D, P}}$
2	0	3	0.0000	2	16	0.1178	-0.0180	0.0068	-0.0180	0.0068
					32	0.0565	-0.0086	0.0013	-0.0086	0.0013
					64	0.0268	-0.0051	-0.0007	-0.0051	-0.0007
				4	16	0.2322	-0.0469	0.0082	-0.0470	0.0082
					32	0.1132	-0.0182	0.0037	-0.0182	0.0037
					64	0.0549	-0.0092	0.0003	-0.0092	0.0003
				8	16	0.4715	-0.1326	-0.0065	-0.1326	-0.0065
					32	0.2249	-0.0448	0.0062	-0.0448	0.0062
					64	0.1098	-0.0196	0.0018	-0.0197	0.0018
2	1	3	0.0626	2	16	0.1726	0.0453	0.0621	-0.0173	-0.0005
					32	0.1139	0.0527	0.0593	-0.0098	-0.0032
					64	0.0876	0.0577	0.0606	-0.0049	-0.0019
				4	16	0.2857	0.0260	0.0649	-0.0365	0.0023
					32	0.1690	0.0459	0.0606	-0.0167	-0.0020
					64	0.1144	0.0544	0.0607	-0.0082	-0.0019
				8	16	0.5198	-0.0291	0.0620	-0.0916	-0.0005
					32	0.2831	0.0337	0.0692	-0.0288	0.0066
					64	0.1697	0.0490	0.0637	-0.0136	0.0011
2	2	3	0.2692	2	16	0.3324	0.2297	0.2401	-0.0395	-0.0291
					32	0.2980	0.2495	0.2536	-0.0197	-0.0156
					64	0.2835	0.2600	0.2617	-0.0093	-0.0075
				4	16	0.4276	0.2195	0.2446	-0.0497	-0.0246
					32	0.3433	0.2460	0.2555	-0.0233	-0.0137
					64	0.3060	0.2590	0.2629	-0.0102	-0.0063
				8	16	0.6289	0.2049	0.2628	-0.0644	-0.0065
					32	0.4380	0.2426	0.2663	-0.0267	-0.0029
					64	0.3508	0.2564	0.2654	-0.0128	-0.0038

Table S1.8 Simulation results for varying θ.

									Estimated bias	
μ_0	β_1	θ	$R^2_{\text{D, large}}$	k	n	R^2_{D}	$R^2_{\text{D, df}}$	$R^2_{\text{D, P}}$	$R^2_{\text{D, df}}$	$R^2_{\text{D, P}}$
2	1	1	0.0274	2	16	0.1416	0.0096	0.0406	-0.0179	0.0131
					32	0.0815	0.0181	0.0301	-0.0093	0.0027
					64	0.0527	0.0216	0.0267	-0.0058	-0.0008
				4	16	0.2604	-0.0085	0.0638	-0.0360	0.0363
					32	0.1388	0.0112	0.0396	-0.0163	0.0121
					64	0.0799	0.0175	0.0289	-0.0099	0.0014
				8	16	0.4965	-0.0789	0.0936	-0.1064	0.0661
					32	0.2434	-0.0197	0.0474	-0.0471	0.0200
					64	0.1336	0.0075	0.0346	-0.0199	0.0071
2	1	3	0.0626	2	16	0.1726	0.0453	0.0621	-0.0173	-0.0005
					32	0.1139	0.0527	0.0593	-0.0098	-0.0032
					64	0.0876	0.0577	0.0606	-0.0049	-0.0019
				4	16	0.2857	0.0260	0.0649	-0.0365	0.0023
					32	0.1690	0.0459	0.0606	-0.0167	-0.0020
					64	0.1144	0.0544	0.0607	-0.0082	-0.0019
				8	16	0.5198	-0.0291	0.0620	-0.0916	-0.0005
					32	0.2831	0.0337	0.0692	-0.0288	0.0066
					64	0.1697	0.0490	0.0637	-0.0136	0.0011
2	1	9	0.1129	2	16	0.2120	0.0908	0.0997	-0.0221	-0.0132
					32	0.1584	0.1004	0.1039	-0.0125	-0.0090
					64	0.1373	0.1090	0.1107	-0.0039	-0.0022
				4	16	0.3245	0.0788	0.0980	-0.0341	-0.0149
					32	0.2132	0.0966	0.1048	-0.0163	-0.0081
					64	0.1646	0.1080	0.1116	-0.0049	-0.0013
				8	16	0.5587	0.0544	0.0961	-0.0585	-0.0168
					32	0.3245	0.0896	0.1086	-0.0233	-0.0043
					64	0.2169	0.1030	0.1111	-0.0099	-0.0018

Table S1.9 Simulation results for varying μ_0.

									Estimated bias	
μ_0	β_1	θ	$R^2_{\mathrm{D, large}}$	k	n	R^2_{D}	$R^2_{\mathrm{D, df}}$	$R^2_{\mathrm{D, P}}$	$R^2_{\mathrm{D, df}}$	$R^2_{\mathrm{D, P}}$
2	1	3	0.0626	2	16	0.1726	0.0453	0.0621	-0.0173	-0.0005
					32	0.1139	0.0527	0.0593	-0.0098	-0.0032
					64	0.0876	0.0577	0.0606	-0.0049	-0.0019
				4	16	0.2857	0.0260	0.0649	-0.0365	0.0023
					32	0.1690	0.0459	0.0606	-0.0167	-0.0020
					64	0.1144	0.0544	0.0607	-0.0082	-0.0019
				8	16	0.5198	-0.0291	0.0620	-0.0916	-0.0005
					32	0.2831	0.0337	0.0692	-0.0288	0.0066
					64	0.1697	0.0490	0.0637	-0.0136	0.0011
5	1	3	0.0815	2	16	0.1857	0.0604	0.0729	-0.0211	-0.0085
					32	0.1324	0.0725	0.0776	-0.0089	-0.0039
					64	0.1067	0.0774	0.0795	-0.0041	-0.0019
				4	16	0.3030	0.0495	0.0789	-0.0320	-0.0026
					32	0.1882	0.0679	0.0796	-0.0136	-0.0018
					64	0.1348	0.0762	0.0810	-0.0053	-0.0005
				8	16	0.5427	0.0201	0.0881	-0.0614	0.0066
					32	0.3022	0.0594	0.0883	-0.0220	0.0068
					64	0.1902	0.0724	0.0837	-0.0091	0.0022
20	1	3	0.0945	2	16	0.1980	0.0747	0.0859	-0.0198	-0.0086
					32	0.1455	0.0866	0.0909	-0.0079	-0.0036
					64	0.1191	0.0902	0.0921	-0.0042	-0.0024
				4	16	0.3164	0.0678	0.0940	-0.0267	-0.0005
					32	0.2012	0.0829	0.0929	-0.0116	-0.0016
					64	0.1476	0.0899	0.0939	-0.0046	-0.0005
				8	16	0.5578	0.0525	0.1143	-0.0420	0.0198
					32	0.3173	0.0799	0.1056	-0.0146	0.0111
					64	0.2023	0.0863	0.0962	-0.0082	0.0017

```
## R code for generating NB-2 models and assessing adjusted R2 deviance measures:
## In the following simulations, the NB-2 response variable will be generated from a single independent random
## variable, which will be incorporated into all models.

## Generate eight sets of 1000 normally-distributed covariates of n=64
library(MASS)
set.seed(01134); Xcov <- matrix(rnorm(512000, 1, 0.2), ncol=8000)
Xgen <- Xcov[, 1:1000];      X2 <- Xcov[, 1001:2000]
X3 <- Xcov[, 2001:3000];   X4 <- Xcov[, 3001:4000]
X5 <- Xcov[, 4001:5000];   X6 <- Xcov[, 5001:6000]
X7 <- Xcov[, 6001:7000];   X8 <- Xcov[, 7001:8000]

## Make function to generate NB-2 response variates
nb <- function (mu_0, beta_1, theta, Xgen) {
    set.seed(01134)
    Xgen1 <- as.vector(Xgen)
    xb <- log(mu_0) + beta_1*Xgen1                      ##  linear predictor
    exb <- exp(xb)                                      ##  Poisson predicted value
    xg <- rgamma(64000, theta, theta, 1/theta)          ##  generate gamma variates given theta
    xbg <- exb*xg                                       ##  mix Poisson and gamma variates
    nby <- matrix(rpois(64000, xbg), ncol=1000)         ##  generate 1000 NB-2 variates with n=64
    }

##  Make functions to calculate adj-R2 deviance measures with 2, 4, and 8 covariates
R2_c2 <- function(reps, n, k, theta, NBresp) (
    sapply(1:reps, function(reps) {
    m <- glm(NBresp[1:n, reps] ~ Xgen[1:n, reps] + X2[1:n, reps], family=negative.binomial(theta))
    msum <- summary(m)
    R2 <- 1 - deviance(m)/m$null.deviance
    adjR2.df <-  1 - ((n - 1)/(n - k - 1))*(1 - R2)
    adjR2.P <- 1 - ((deviance(m) + k*msum$dispersion)/m$null.deviance)
    c(R2, adjR2.df, adjR2.P)
    }))
R2_c4 <- function(reps, n, k, theta, NBresp) (
    sapply(1:reps, function(reps) {
    m <- (glm(NBresp[1:n, reps] ~ Xgen[1:n, reps] + X2[1:n, reps] + X3[1:n, reps] + X4[1:n, reps],
      family=negative.binomial(theta)))
    msum <- summary(m)
    R2 <- 1 - deviance(m)/m$null.deviance
    adjR2.df <-  1 - ((n - 1)/(n - k - 1))*(1 - R2)
    adjR2.P <- 1 - ((deviance(m) + k*msum$dispersion)/m$null.deviance)
    c(R2, adjR2.df, adjR2.P)
    }))
R2_c8 <- function(reps, n, k, theta, NBresp) (
    sapply(1:reps, function(reps) {
    m <- (glm(NBresp[1:n, reps] ~ Xgen[1:n, reps] + X2[1:n, reps] + X3[1:n, reps] + X4[1:n, reps] + X5[1:n, reps] +
      X6[1:n, reps] + X7[1:n, reps] + X8[1:n, reps], family=negative.binomial(theta)))
    msum <- summary(m)
    R2 <- 1 - deviance(m)/m$null.deviance
    adjR2.df <-  1 - ((n - 1)/(n - k - 1))*(1 - R2)
    adjR2.P <- 1 - ((deviance(m) + k*msum$dispersion)/m$null.deviance)
```

```
   c(R2, adjR2.df, adjR2.P)
   }))

## Make function to tabulate mean R2 and adj-R2 measures from output of the above functions
Mtable <- function(R2_1, R2_2, R2_3) {
   R2means <- matrix(c(mean(R2_1[1, ]), mean(R2_1[2, ]), mean(R2_1[3, ]), mean(R2_2[1, ]), mean(R2_2[2, ]),
     mean(R2_2[3, ]), mean(R2_3[1, ]), mean(R2_3[2, ]), mean(R2_3[3, ])), ncol=3, byrow=TRUE)
   colnames(R2means) <- c("R2", "adj-R2_df", "adj-R2_P")
   rownames(R2means) <- c(deparse(substitute(R2_1)), deparse(substitute(R2_2)), deparse(substitute(R2_3)))
   R2means <- as.table(R2means)
   R2means
   }

## The following demonstrates the use of the above functions for mu_0=2, beta_1=0, and theta=3

## Generate NB-2 response and allocate into samples with n=16, 32, and 64;
## check overall mean and calculate R2.large
nb1 <- nb(2, 0, 3, Xgen)
nb1_16 <- nb1[1:16, ];  nb1_32 <- nb1[1:32, ];  nb1_64 <- nb1[1:64, ]
mean(nb1)
Lg.mod <- glm(as.vector(nb1) ~ as.vector(Xgen), family=negative.binomial(3))
Lg.mod_R2 <- 1 - deviance(Lg.mod)/Lg.mod$null.deviance
Lg.mod_R2

## Calculate R2 measures for models containing the generating variable plus a varying number
## of unrelated covariates; check R2 measure means.
## For n=16
cov2.16 <- R2_c2(1000, 16, 2, 3, nb1_16)
cov4.16 <- R2_c4(1000, 16, 4, 3, nb1_16)
cov8.16 <- R2_c8(1000, 16, 8, 3, nb1_16)
Mtable(cov2.16, cov4.16, cov8.16)

## For n=32
cov2.32 <- R2_c2(1000, 32, 2, 3, nb1_32)
cov4.32 <- R2_c4(1000, 32, 4, 3, nb1_32)
cov8.32 <- R2_c8(1000, 32, 8, 3, nb1_32)
Mtable(cov2.32, cov4.32, cov8.32)

## For n=64
cov2.64 <- R2_c2(1000, 64, 2, 3, nb1_64)
cov4.64 <- R2_c4(1000, 64, 4, 3, nb1_64)
cov8.64 <- R2_c8(1000, 64, 8, 3, nb1_64)
Mtable(cov2.64, cov4.64, cov8.64)

## Examine boxplots; note the differing y-axis scales
R2.labels <- expression({italic(R)^2}["D"], {italic(R)^2}["D, df"], {italic(R)^2}["D, P"], {italic(R)^2}["D"],
    {italic(R)^2}["D, df"], {italic(R)^2}["D, P"], {italic(R)^2}["D"], {italic(R)^2}["D, df"], {italic(R)^2}["D, P"])
win.graph(width=11, height=6)
par(mfrow = c(2, 2))
boxplot(cov2.16[1, ], cov2.16[2, ], cov2.16[3, ], cov4.16[1, ], cov4.16[2, ], cov4.16[3, ], cov8.16[1, ], cov8.16[2, ],
   cov8.16[3, ], names=R2.labels, cex.axis=0.7, boxwex=0.6)
```

```
    mtext(c("2 covariates", "4 covariates", "8 covariates"), adj=c(.14, .5, .86), side=1, line=2, cex=0.8)
    mtext(~mu[0]*" = 2, "*beta[1]*" = 0, "*theta*" = 3" , side=3, cex=0.8)
    abline(h=Lg.mod_R2, lty="dotted", col="red")
    title("n = 16", cex.main=0.9)
boxplot(cov2.32[1, ], cov2.32[2, ], cov2.32[3, ], cov4.32[1, ], cov4.32[2, ], cov4.32[3, ], cov8.32[1, ], cov8.32[2, ],
    cov8.32[3, ], names=R2.labels, cex.axis=0.7, boxwex=0.6)
    mtext(c("2 covariates", "4 covariates", "8 covariates"), adj=c(.14, .5, .86), side=1, line=2, cex=0.8)
    mtext(~mu[0]*" = 2, "*beta[1]*" = 0, "*theta*" = 3" , side=3, cex=0.8)
    abline(h=Lg.mod_R2, lty="dotted", col="red")
    title("n = 32", cex.main=.9)
boxplot(cov2.64[1, ], cov2.64[2, ], cov2.64[3, ], cov4.64[1, ], cov4.64[2, ], cov4.64[3, ], cov8.64[1, ], cov8.64[2, ],
    cov8.64[3, ], names=R2.labels, cex.axis=0.7, boxwex=0.6)
    mtext(c("2 covariates", "4 covariates", "8 covariates"), adj=c(.14, .5, .86), side=1, line=2, cex=0.8)
    mtext(~mu[0]*" = 2, "*beta[1]*" = 0, "*theta*" = 3" , side=3, cex=0.8)
    abline(h=Lg.mod_R2, lty="dotted", col="red")
    title("n = 64", cex.main=0.9)
```

Replacement effect calculations

The calculation of model-averaged replacement effects (RE_{Avgs}) involved three basic steps: (1) derive a model-averaged BA_{Abund} regression coefficient and its confidence limits, (2) multiply this averaged regression coefficient and its confidence limits by a change in BA_{Abund} that is representative of the shift in dominant anole species, and (3) convert the resulting expected change in response magnitude into an expected proportional change from green anole dominant conditions.

For the first of these steps, I generated all possible models for a given response variable and used the R package ‘AICcmodavg’ (Mazerolle 2010) to calculate the AIC_C-weighted model average of the BA_{Abund} regression coefficient (β_{BA}), as well as its unconditional standard error. Model-averaged β_{BA} estimates were computed using the “zero method”, in which β_{BA} and its error variance were defined as zero for models in the averaged set that lacked BA_{Abund} as a predictor (Burnham and Anderson 2002, Lukacs et al. 2010; see also Grueber et al. 2011).

Unconditional standard errors (Burnham and Anderson 2002, p. 345) were used to calculate the upper and lower 95% confidence limits of model-averaged β_{BA} estimates (as in Lukacs et al. 2010).

For the second $\mathrm{RE}_{\mathrm{Avg}}$ calculation step, I derived an expected change in $\mathrm{BA}_{\mathrm{Abund}}$ corresponding to the shift in dominant anole species by (1) averaging untransformed brown anole counts separately for green anole and brown anole islands, (2) $\log_{10}$(average count + 1) transforming these values to convert them into $\mathrm{BA}_{\mathrm{Abund}}$ averages for the two groups, and (3) taking the difference between the two $\mathrm{BA}_{\mathrm{Abund}}$ averages (1.308) as the expected increase in $\mathrm{BA}_{\mathrm{Abund}}$ associated with green anole replacement in this system. Next, I multiplied model-averaged β_{BA} estimates and their confidence limits by this expected increase in $\mathrm{BA}_{\mathrm{Abund}}$. For Gaussian GLMs, this multiplication yielded the magnitude of change in response variables predicted to occur following green anole replacement (with 95% confidence intervals); for Poisson and NB GLMs, it yielded the natural log of the predicted multiplicative effect on response variables.

In the final calculation step, I expressed $\mathrm{RE}_{\mathrm{Avgs}}$ in terms of their proportional equivalents under green anole dominant conditions to make them more intuitively meaningful and comparable across a common scale. For Poisson and NB GLMs, a value of 1 was subtracted from predicted multiplicative effects (and their confidence limits) to convert them into proportional gains or losses; for example, multiplicative effects of 0.6, 1, and 3 were proportional replacement effects of −0.4, 0, and 2 (i.e., 40% decrease, no change, and 200% increase), respectively. For Gaussian GLMs, predicted changes in response variables (and their confidence limits) were divided by the mean of the response among green anole islands to get proportional $\mathrm{RE}_{\mathrm{Avgs}}$. Replacement effects for variables that were transformed prior to Gaussian modeling were obtained by: (1) calculating the untransformed mean among green anole islands, (2) transforming this mean value, (3) adding in the model-averaged β_{BA} x 1.308 expected change in the transformed variable, (4) back-transforming the resulting value, (5) subtracting out the untransformed green anole island mean to yield the expected untransformed change, (6) dividing this value by the green anole island untransformed mean to produce the expected proportional RE_{Avg}, and (7) repeating steps 3–6 with the model-averaged β_{BA} confidence limits to define the RE_{Avg} 95% confidence interval.

Best model replacement effects (RE_{Best}) were calculated in the same manner using the best model β_{BA}, but RE_{Best} confidence intervals were not calculated.

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APPENDIX S2:

SUPPLEMENTARY RESULTS AND DISCUSSION

Table of Contents

Table S2.1 Mean percent large species composition in arthropod order abundances.

	Mean percent abundance large species[1]			
Order	GND_{Xer}	GND_{For}	FOL	AER_{Xer}
Collembola	0	0		
Blattodea	100	100	100	
Dermaptera	100	100		
Orthoptera	100	100	100	100
Homoptera	100	50	98	61
Hemiptera	100	100	100	75
Thysanoptera			50	0
Psocoptera		57	45	8
Lepidoptera	100	100	100	100
Coleoptera	100	95	63	63
Diptera	11	37	66	8
Hymenoptera:				
Non-ant	100	50	48	36
Formicidae	90	90	93	Omitted
Araneae	66	67	98	48
Isopoda	100	100		
Other	100	73	25	50
All Orders	89	85	83	21

[1] Mean percentages are the means of individual island percentages

Table S2.2 Partitioned variation fraction magnitudes and *P* values, RE estimates, and best model composition for GND_{Xer} responses.

Response[1, 2]	Model[3]	$R^{2,\,\text{BA}}_{\text{D, adj}}$	P	$R^{2,\,\text{BA−Best}}_{\text{D, adj}}$	P[4]	$R^{2,\,\text{BA−Full}}_{\text{D, adj}}$	P	RE$_{\text{Avg}}$[5]	[95% CI]	RE$_{\text{Best}}$[5]	Best model variables[6]
Rel A	db-RDA	**0.202**	**0.0001**	**0.197**	**0.0001**	**0.079**	**0.0005**	N/A		N/A	1, 2, 8
FORM Rel A	db-RDA	**0.251**	**0.0001**	**0.248**	**0.0001**	**0.095**	**0.0012**	N/A		N/A	1, 8
ARAN Rel A	db-RDA	**0.182**	**0.0016**	**0.069**	**0.0108**	0.020	0.3255	N/A		N/A	1, 5
B	G	0	0.7892	0	N/A	0	0.6657	0.04	[−0.34, 0.56]	0	Intercept
R	G	0	0.8195	0	N/A	0	0.2536	−0.02	[−0.22, 0.17]	0	*8*
E	G	0	0.4124	0	N/A	0.001	0.3196	0.00	[−0.13, 0.11]	0	*6*
A	NB	0	0.9703	0	N/A	0.013	0.9303	0.18	[−0.37, 1.20]	0	3, 6
Sm A	NB	**0.332**	**0.0005**	**0.110**	**0.0436**	0.110	0.0733	**1.55**	**[0.14, 4.73]**	1.33	1, 3
Lg A	NB	0	0.9889	0	N/A	0.004	0.9390	0.14	[−0.37, 1.06]	0	3, 6
COLLEM A	NB	**0.526**	**0.0056**	0	N/A	0.003	0.4952	0.50	[−0.76, 8.26]	0	3, *4*, 7
ORTH A	NB	0.023	0.1232	**0.076**	**0.0020**	**0.083**	**0.0073**	−0.64	[−0.87, 0.02]	−0.74	*1*, 2, *3*, 7
COL A	NB	**0.171**	**0.0234**	0.075	0.1031	0.078	0.1633	−0.64	[−0.93, 0.91]	−0.69	*1*, 6
COL Lg A	NB	**0.171**	**0.0234**	0.075	0.1031	0.078	0.1633	−0.64	[−0.93, 0.91]	−0.69	*1*, 6
DIPT A	NB	0.002	0.5578	**0.048**	**0.0418**	0.049	0.0612	3.38	[−0.14, 21.2]	3.90	1, 2, 3, 5, *7*, 8
DIPT Sm A	NB	0.004	0.2879	0.047	0.0623	0.051	0.0827	**3.64**	**[0.02, 20.2]**	4.25	1, 2, 3, 5, *7*, 8
FORM A	NB	0.034	0.9180	0	N/A	0.057	0.7692	0.29	[−0.40, 1.80]	0	3, 6
FORM Sm A	NB	**0.336**	**0.0014**	**0.158**	**0.0339**	0.125	0.0584	**2.50**	**[0.55, 6.87]**	1.96	1, 3
FORM Lg A	NB	0.008	0.9538	0	N/A	0.044	0.8305	0.24	[−0.42, 1.62]	0	3, 6

Table S2.2 (continued)

Response[1, 2]	Model[3]	$R^{2,\ \mathrm{BA}}_{\mathrm{D,\ adj}}$	P	$R^{2,\ \mathrm{BA-Best}}_{\mathrm{D,\ adj}}$	P[4]	$R^{2,\ \mathrm{BA-Full}}_{\mathrm{D,\ adj}}$	P	$\mathrm{RE_{Avg}}$[5] [95% CI]	$\mathrm{RE_{Best}}$[5]	Best model variables[6]
ARAN A	NB	0.090	0.0643	0.090	0.0643	0.015	1.0000	−0.44 [−0.82, 0.74]	−0.58	*1*
ARAN Sm A	NB	0	1.0000	0	N/A	0	1.0000	−0.01 [−0.43, 0.73]	0	Intercept
ARAN Lg A	NB	**0.165**	**0.0208**	**0.165**	**0.0208**	0.100	0.1593	−0.72 [−0.94, 0.20]	−0.75	*1*
Gnaph A	P	**0.138**	**0.0158**	**0.138**	**0.0158**	0.029	0.2894	−0.60 [−0.96, 2.72]	−0.79	*1*
Ther A	P	0	0.5338	0	N/A	0	1.0000	0.03 [−0.50, 1.12]	0	Intercept
Hunt A	NB	**0.263**	**0.0093**	**0.263**	**0.0093**	0.088	0.3235	−0.78 [−0.96, 0.44]	−0.85	*1*
Web A	NB	0	0.7883	0	N/A	0	1.0000	0.01 [−0.46, 0.88]	0	Intercept

[1] Rel A = relative abundances; B = biomass; R = species richness; E = evenness; A = abundance; Sm A = small species abundance; Lg A = large species abundance; COLLEM = Collembola; ORTH = Orthoptera; COL = Coleoptera; DIPT = Diptera; FORM = Formicidae; ARAN = Araneae; Gnaph = Gnaphosidae; Ther = Theridiidae; Hunt = hunting guild; Web = web-building guild

[2] For each response, variation fractions significant at $P < 0.05$ and $\mathrm{RE_{Avgs}}$ with confidence intervals excluding zero are indicated in bold

[3] db-RDA = distance-based redundancy analysis; G = Gaussian GLM; NB = negative binomial GLM; P = Poisson GLM

[4] Permutation tests for $\mathrm{BA_{Abund}}$ significance could not be conducted for best models lacking $\mathrm{BA_{Abund}}$

[5] RE were derived only for univariate responses

[6] Variable codes: 1 = $\mathrm{BA_{Abund}}$, 2 = Date, 3 = WTHR_1, 4 = Xveg_1, 5 = Xveg_2, 6 = Xveg_DIV, 7 = Xhab_1, 8 = Xhab_2, Intercept = intercept only model; for variable definitions and meanings, see Table 2.2 and Table S1.5; italicized variable codes indicate negative regression coefficients

Table S2.3 Partitioned variation fraction magnitudes and P values, RE estimates, and best model composition for GND$_{\mathrm{For}}$ responses.

Response[1, 2]	Model[1]	$R^{2,\ \mathrm{BA}}_{\mathrm{D,\ adj}}$	P	$R^{2,\ \mathrm{BA-Best}}_{\mathrm{D,\ adj}}$	P[3]	$R^{2,\ \mathrm{BA-Full}}_{\mathrm{D,\ adj}}$	P	RE$_{\mathrm{Avg}}$[3]	[95% CI]	RE$_{\mathrm{Best}}$[3]	Best model variables[4]
Rel A	db-RDA	**0.099**	**0.0001**	**0.042**	**0.0038**	**0.038**	**0.0177**	N/A		N/A	1, 4, 7
COL Rel A	db-RDA	0.024	0.2892	0	N/A	0	0.4279	N/A		N/A	Intercept
DIPT Rel A	db-RDA	0.042	0.0768	0	N/A	0	0.7673	N/A		N/A	Intercept
FORM Rel A	db-RDA	**0.180**	**0.0001**	**0.050**	**0.0105**	**0.064**	**0.0095**	N/A		N/A	1, 4, 7
ARAN Rel A	db-RDA	**0.129**	**0.0012**	**0.102**	**0.0013**	0.024	0.1781	N/A		N/A	1, 2
B	G	0.005	0.2844	0	N/A	0	0.6309	0.02	[−0.32, 0.45]	0	*4*, 7
R	G	0	0.4377	0.030	0.0909	0	0.3634	0.09	[−0.23, 0.41]	0.27	1, *5*
E	G	0	0.3340	0.041	0.0586	0.045	0.1442	0.07	[−0.13, 0.28]	0.16	1, *5*
A	NB	0	0.9715	0	N/A	0.006	0.9821	−0.16	[−0.50, 0.40]	0	2, 5, 7
Sm A	NB	0.013	0.8450	0	N/A	0	0.9374	0.20	[−0.34, 1.17]	0	4
Lg A	NB	0.002	0.9186	0	N/A	0.007	0.9509	−0.18	[−0.54, 0.48]	0	*4*, 5, 7
COLLEM A	NB	**0.237**	**0.0443**	**0.314**	**0.0073**	0.164	0.2073	**22.8**	**[1.04, 276.4]**	28.3	1, 4, 7
BLAT A	P	0	0.9784	0	N/A	0	0.8882	0.07	[−0.40, 0.91]	0	*3*, 8
ORTH A	NB	0	0.9955	0	N/A	0	0.9359	−0.03	[−0.46, 0.73]	0	6, 8
LEP A	P	0	0.9977	0	N/A	0	0.8554	−0.10	[−0.57, 0.88]	0	3
COL A	NB	0.063	0.1438	0	N/A	0	0.9391	−0.04	[−0.36, 0.43]	0	7
COL Lg A	NB	**0.063**	**0.0139**	0	N/A	0	0.8899	−0.07	[−0.42, 0.50]	0	7
DIPT A	NB	0	0.9865	0	N/A	0	0.9764	0.05	[−0.35, 0.69]	0	Intercept
DIPT Sm A	NB	0	0.9947	0	N/A	0	0.9801	0.04	[−0.43, 0.90]	0	Intercept
DIPT Lg A	P	0	0.8375	0	N/A	0	0.9985	0.06	[−0.37, 0.77]	0	Intercept

Table S2.3 (continued)

Response[1, 2]	Model[1]	$R^{2,\,\mathrm{BA}}_{\mathrm{D,\,adj}}$	P	$R^{2,\,\mathrm{BA-Best}}_{\mathrm{D,\,adj}}$	P [3]	$R^{2,\,\mathrm{BA-Full}}_{\mathrm{D,\,adj}}$	P	$\mathrm{RE}_{\mathrm{Avg}}$[3]	[95% CI]	$\mathrm{RE}_{\mathrm{Best}}$[3]	Best model variables[4]
FORM A	NB	0	0.9708	**0.047**	**0.0118**	0.047	0.0507	−0.31	[−0.64, 0.33]	−0.42	*1*, 5, 6
FORM Sm A	NB	0	1.0000	0	N/A	0	1.0000	0.11	[−0.43, 1.17]	0	4, *7*, *8*
FORM Lg A	NB	0	0.9599	**0.048**	**0.0097**	0.044	0.0513	−0.34	[−0.68, 0.34]	−0.45	*1*, 5, 6
ARAN A	NB	0.024	0.9727	0	N/A	0	0.9989	−0.07	[−0.38, 0.41]	0	2, *5*
ARAN Sm A	P	**0.217**	**0.0005**	**0.217**	**0.0005**	0.089	0.7152	**1.91**	**[0.26, 5.69]**	1.88	1
ARAN Lg A	NB	**0.247**	**0.0003**	**0.141**	**0.0013**	0.051	0.7742	−0.56	[−0.84, 0.20]	−0.64	Intercept
Gnaph A	P	**0.147**	**0.0237**	**0.237**	**0.0017**	**0.221**	**0.0084**	**−0.95**	**[−1.00, −0.55]**	−0.85	*1*, *2*, *5*
Liny A	P	**0.204**	**0.0011**	**0.204**	**0.0011**	**0.166**	**0.0052**	3.36	[−0.16, 21.7]	2.99	1
Lyc A	NB	**0.119**	**0.0130**	0	N/A	0	0.9402	−0.18	[−0.67, 1.04]	0	7
Oon A	P	**0.150**	**0.0031**	**0.097**	**0.0046**	0.023	0.8748	0.88	[−0.50, 5.95]	1.49	1, 2
Salt A	P	**0.441**	**0.0001**	**0.441**	**0.0001**	**0.210**	**0.009**	−1.00	[−1.00, 2.43]	−1.00	*1*
Hunt A	NB	**0.112**	**0.0014**	0.056	0.9144	0	0.9809	−0.25	[−0.64, 0.59]	−0.45	*1*, 2, *5*
Web A	P	**0.129**	**0.0092**	**0.142**	**0.0041**	**0.108**	**0.0171**	1.86	[−0.29, 10.6]	2.20	1, 4
ISOP A	NB	0	0.6674	0	N/A	0.007	> 0.05[5]	0.54	[−0.64, 5.65]	0	2, *4*, *6*

[1] Abbreviations as in Table S2.2 except: BLAT = Blattodea; LEP = Lepidoptera; Liny = Linyphiidae; Lyc = Lycosidae; Oon = Oonopidae; Salt = Salticidae

[2] For each response, variation fractions significant at $P < 0.05$ and $\mathrm{RE}_{\mathrm{Avgs}}$ with confidence intervals excluding zero are indicated in bold

[3] N/A causes as described Table S2.2

[4] Variable codes: 1 = $\mathrm{BA}_{\mathrm{Abund}}$, 2 = Date, 3 = WTHR_1, 4 = Fveg_1, 5 = Fveg_2, 6 = Fveg_DIV, 7 = Fhab_1, 8 = Fhab_2, Intercept = intercept only model; for variable definitions and meanings, see Table 2.2 and Table S1.5; italicized variable codes indicate negative regression coefficients

[5] Error encountered in permutation of regressor residuals test ("prr.test" routine in R package 'glmperm'), apparently due to instability in the model; non-significant p-value (> 0.05) assigned on basis of small explained variation fraction

Table S2.4 Partitioned variation fraction magnitudes and *P* values, RE estimates, and best model composition for FOL responses.

Response[1, 2]	Model[1]	$R^{2,\text{ BA}}_{\text{D, adj}}$	*P*	$R^{2,\text{ BA−Best}}_{\text{D, adj}}$	*P* [3]	$R^{2,\text{ BA−Full}}_{\text{D, adj}}$	*P*	RE_{Avg}[3] [95% CI]	RE_{Best}[3]	Best model variables[4]
Rel A	db-RDA	**0.094**	**0.0001**	**0.036**	**0.0030**	**0.040**	**0.0088**	N/A	N/A	1, 6, 8
DIPT Rel A	db-RDA	0	0.9702	0	N/A	0	0.7417	N/A	N/A	2
FORM Rel A	db-RDA	0.066	0.0866	0	N/A	0.062	0.0931	N/A	N/A	8
ARAN Rel A	db-RDA	**0.070**	**0.0052**	**0.075**	**0.0023**	**0.051**	**0.0333**	N/A	N/A	1, 5, 7
B	G	**0.190**	**0.0052**	**0.166**	**0.0057**	**0.109**	**0.0476**	−0.49 [−0.80, 0.04]	−0.50	*1*, 4, *9*
R	G	0.009	0.2644	0	N/A	0.053	0.1438	0.02 [−0.07, 0.11]	0	8
E	G	0.004	0.2972	0	N/A	0	0.6349	0.00 [−0.01, 0.02]	0	*5*, 9
A	NB	**0.194**	**0.0101**	**0.076**	**0.0437**	0	0.4973	−0.17 [−0.42, 0.19]	−0.25	*1*, *2*, 4
Sm A	NB	0.059	0.1853	0	N/A	0	0.8609	−0.07 [−0.44, 0.54]	0	*2*, 6
Lg A	NB	**0.181**	**0.0065**	**0.081**	**0.0310**	0	0.3497	−0.18 [−0.40, 0.12]	−0.23	*1*, *2*, 4
ORTH A	P	**0.307**	**0.0002**	**0.116**	**0.0069**	0.052	0.0815	**−0.64 [−0.83, −0.26]**	−0.61	*1*, *2*, 5, 7
HOM A	P	0	0.4947	0	N/A	0	0.5373	0.04 [−0.30, 0.55]	0	4, *5*, 6, *9*
HEM A	P	**0.233**	**0.0143**	**0.233**	**0.0143**	0.084	0.1606	−0.91 [−1.00, 2.03]	−0.94	*1*
PSOC A	P	0	0.8341	0	N/A	0.012	0.2190	0.23 [−0.47, 1.82]	0	*7*, *9*
LEP A	P	0.063	0.0785	0.063	0.0785	0.044	0.1536	0.69 [−0.49, 4.60]	1.11	1
COL A	P	**0.276**	**0.0013**	**0.247**	**0.0006**	0.075	0.0968	**−0.84 [−0.96, −0.37]**	−0.86	*1*, *2*, 4
COL Sm A	P	0.117	0.0588	0	N/A	0.010	0.2899	−0.69 [−0.98, 3.73]	0	*2*, 6, 9
COL Lg A	P	**0.234**	**0.0053**	**0.234**	**0.0053**	0.045	0.2109	−0.81 [−0.97, 0.16]	−0.85	*1*

Table S2.4 (continued)

Response[1, 2]	Model[1]	$R^{2,\ \mathrm{BA}}_{\mathrm{D,\ adj}}$	P	$R^{2,\ \mathrm{BA-Best}}_{\mathrm{D,\ adj}}$	P[3]	$R^{2,\ \mathrm{BA-Full}}_{\mathrm{D,\ adj}}$	P	$\mathrm{RE}_{\mathrm{Avg}}$[3] [95% CI]	$\mathrm{RE}_{\mathrm{Best}}$[3]	Best model variables[4]
DIPT A	NB	0.133	0.1073	**0.100**	**0.0320**	0.032	0.1827	−0.57 [−0.82, 0.01]	−0.61	*1*, *2*, 4, *5*, *7*
DIPT Sm A	NB	0.093	0.2353	0	N/A	0	0.6626	−0.27 [−0.77, 1.30]	0	*2*, 4, *5*, *7*
DIPT Lg A	P	**0.103**	**0.0326**	**0.072**	**0.0316**	0.031	0.1158	−0.43 [−0.77, 0.41]	−0.46	*1*, *2*, 4
FORM A	P	0.023	0.2954	**0.116**	**0.0037**	**0.069**	**0.0329**	−0.70 [−0.91, 0.02]	−0.78	*1*, 3, *6*, *8*
FORM Lg A	P	0.072	0.1044	**0.166**	**0.0016**	**0.125**	**0.0116**	**−0.80 [−0.94, −0.38]**	−0.84	*1*, 3, *6*, *8*
ARAN A	NB	0	0.7338	0	N/A	0	0.3899	0.03 [−0.18, 0.29]	0	*2*
ARAN Lg A	NB	0	0.8655	0	N/A	0	0.3076	0.06 [−0.20, 0.41]	0	*2*
Any A	P	0.005	0.4870	0	N/A	0.013	0.2538	0.15 [−0.37, 1.09]	0	*2*, 5, 7
Aran A	P	0.015	0.2956	0	N/A	0.030	0.1412	0.15 [−0.32, 0.93]	0	6
Phil A	P	0	0.5587	0	N/A	0	0.4993	−0.37 [−0.91, 3.53]	0	*2*, 3, *5*
Salt A	P	0.037	0.1163	0	N/A	0	0.3810	−0.13 [−0.52, 0.60]	0	5
Hunt A	P	0.095	0.0570	0	N/A	0	0.9061	−0.02 [−0.26, 0.28]	0	*2*, 5, 7
Web A	NB	0	0.3054	0.021	0.0736	0.003	0.2447	0.13 [−0.37, 1.05]	0.69	1, *2*, 6

[1] Abbreviations as in Table S2.2 except: HOM = Homoptera; HEM = Hemiptera; PSOC = Psocoptera; LEP = Lepidoptera; Any = Anyphaenidae; Aran = Araneidae; Phil = Philodromidae; Salt = Salticidae

[2] For each response, variation fractions significant at $P < 0.05$ and $\mathrm{RE}_{\mathrm{Avgs}}$ with confidence intervals excluding zero are indicated in bold

[3] N/A causes as described Table S2.2

[4] Variable codes: 1 = $\mathrm{BA}_{\mathrm{Abund}}$, 2 = Date, 3 = SWcond_1, 4 = RAINprev, 5 = FEveg_1, 6 = FEveg_2, 7 = FEveg_DIV, 8 = FEhab_1, 9 = FEhab_2; for variable definitions and meanings, see Table 2.2 and Table S1.5; italicized variable codes indicate negative regression coefficients

Table S2.5 Partitioned variation fraction magnitudes and *P* values, RE estimates, and best model composition for $\mathrm{AER}_{\mathrm{Xer}}$ responses.

Response$^{1,\ 2}$	Model^{1}	$R^{2,\ \mathrm{BA}}_{\mathrm{D,\ adj}}$	*P*	$R^{2,\ \mathrm{BA-Best}}_{\mathrm{D,\ adj}}$	P^{3}	$R^{2,\ \mathrm{BA-Full}}_{\mathrm{D,\ adj}}$	*P*	$\mathrm{RE}_{\mathrm{Avg}}{}^{3}$ [95% CI]	$\mathrm{RE}_{\mathrm{Best}}{}^{3}$	Best model variables^{4}
Rel A	db-RDA	**0.035**	**0.0434**	**0.052**	**0.0053**	**0.047**	**0.0098**	N/A	N/A	1, 2, 3, 4, 8
COL Rel A	db-RDA	0.024	0.2408	0	N/A	0.001	0.4326	N/A	N/A	5, 6
DIPT Rel A	db-RDA	0.045	0.0558	**0.082**	**0.0031**	**0.069**	**0.0113**	N/A	N/A	1, 4, 8
B	G	0	0.5498	0	N/A	0	0.8184	−0.05 [−0.42, 0.46]	0	*3*, 5
R	G	**0.182**	**0.0105**	**0.182**	**0.0105**	0.039	0.1644	0.28 [−0.13, 0.68]	0.36	1
E	G	**0.175**	**0.0115**	**0.175**	**0.0115**	0.065	0.1120	0.14 [−0.06, 0.35]	0.18	1
A	NB	0.088	0.0816	0.037	0.2073	0	0.3661	−0.17 [−0.52, 0.43]	−0.33	*1*, *3*
Sm A	NB	0.068	0.1102	0	N/A	0	0.4860	−0.12 [−0.47, 0.46]	0	*2*, *3*, *8*
Lg A	NB	0.030	0.2466	0	N/A	0	0.6487	−0.04 [−0.33, 0.38]	0	*3*, 6
PSOC A	P	0.008	0.3816	**0.077**	**0.0098**	0.042	0.0523	1.77 [−0.58, 17.5]	3.55	1, *3*, *7*
COL A	NB	0.045	0.2347	0	N/A	0	0.4189	−0.13 [−0.54, 0.63]	0	2, 6, 8
COL Sm A	P	0.056	0.1012	0	N/A	0	0.6555	0.29 [−0.54, 2.63]	0	7
COL Lg A	NB	0.137	0.0547	0.061	0.1022	0.008	0.2926	−0.38 [−0.81, 1.10]	−0.62	*1*, 2, 6
DIPT A	NB	0.100	0.0603	0	N/A	0.002	0.3457	−0.21 [−0.60, 0.54]	0	*2*, *3*, *8*
DIPT Sm A	NB	0.103	0.0568	0	N/A	0.010	0.2850	−0.25 [−0.64, 0.57]	0	*2*, *3*
DIPT Lg A	P	0	0.9992	0	N/A	0	0.6281	0.07 [−0.41, 0.93]	0	*5*, *8*
HYM A	P	0.021	0.3293	0.072	0.0688	0.059	0.1396	1.53 [−0.61, 15.6]	3.64	1, *2*, 6

Table S2.5 (continued)

Response[1, 2]	Model[1]	$R^{2,\,\mathrm{BA}}_{\mathrm{D,\,adj}}$	P	$R^{2,\,\mathrm{BA-Best}}_{\mathrm{D,\,adj}}$	P[3]	$R^{2,\,\mathrm{BA-Full}}_{\mathrm{D,\,adj}}$	P	$\mathrm{RE}_{\mathrm{Avg}}$[3] [95% CI]	$\mathrm{RE}_{\mathrm{Best}}$[3]	Best model variables[4]
ARAN A	NB	0.019	0.2827	0	N/A	0.011	0.3386	−0.27 [−0.78, 1.42]	0	Intercept
ARAN Sm A	NB	0.012	0.4244	0	N/A	0.020	0.4231	−0.29 [−0.85, 2.29]	0	Intercept
ARAN Lg A	P	0	0.4313	**0.060**	**0.0156**	0.053	0.0563	−0.72 [−0.99, 8.00]	−0.94	*1*, *2*, 6, 7
Web A	NB	0.001	0.4200	0	N/A	0	0.5712	−0.16 [−0.67, 1.14]	0	Intercept

[1] Abbreviations as in Table S2.2 except: PSOC = Psocoptera; HYM = non-ant Hymenoptera

[2] For each response, variation fractions significant at $P < 0.05$ and $\mathrm{RE}_{\mathrm{Avgs}}$ with confidence intervals excluding zero are indicated in bold

[3] N/A causes as described Table S2.2

[4] Variable codes: 1 = $\mathrm{BA}_{\mathrm{Abund}}$, 2 = Date, 3 = WTHR_1, 4 = Xveg_1, 5 = Xveg_2, 6 = Xveg_DIV, 7 = Xhab_1, 8 = Xhab_2, Intercept = intercept only model; for variable definitions and meanings, see Table 2.2 and Table S1.5; italicized variable codes indicate negative regression coefficients

Factors affecting brown anole invasion and abundance patterns

Additional support for the contingency hypothesis

Several additional pieces of evidence beyond those previously described (see Discussion: *Invasion patterns*) support the primacy of contingency in driving brown anole invasion and abundance patterns. Further evidence linking recreational use to introductions includes brown anole abundance patterns on the four study islands that were also National Park Service backcountry campgrounds (Islands 1, 4, 5, and 7) and the invasion history of Island 11. Campground islands likely received the heaviest use of all study islands, and the fact that brown anoles were present on all campground islands and highly abundant on three (including the two highest abundances observed in the study) is at least consistent with the hypothesis that introductions occurred earlier and more frequently on islands receiving greater use. On Island 11, I observed the initial stages and subsequent expansion of a brown anole invasion that almost certainly resulted from human recreational use of spoils islands. Island 11 was uninvaded in Todd Campbell's initial 1994 survey of spoils islands in this system (Stuart et al. 2014); while collecting preliminary data in June 2004, I observed an adult female brown anole near the northern xeric–forest edge of this island on lumber associated with a large and elaborate illegal campsite. In contrast to other illegal campsites that I discovered (they were common on islands in this system until at least 2006), this campsite contained large, permanent features (e.g., a plywood-topped table and large wooden benches) that appeared to have been constructed on-site, given the pieces of unused lumber remaining at the site. No other brown anoles were observed in a June 2004 survey of the entire xeric–forest margin. In the June 2006 sampling activities associated with the current study, one brown anole was observed in each of the two northern xeric–forest edge transect counts, but brown anoles were not observed elsewhere on the island.

In a July 2008 repetition of the xeric–forest edge transect counts, a single brown anole was observed in one of the northern and both of the southern counts, and additional brown anoles were seen on vegetation in the xeric habitat interior. This island ("North Twin") subsequently served as an invaded island in a study documenting the perch height shift and subsequent toepad size evolution of green anoles in response to brown anole invasion (Stuart et al. 2014). The initial sighting of brown anoles at a campsite in Island 11's xeric interior (separated by 40 m of dense forest and marsh vegetation from the nearest shoreline) and the subsequent, gradual spread of this population into other parts of the island together provide strong evidence that this invasion resulted from human recreational use.

The possibility that ecological sorting substantially influenced the observed invasion patterns is negated by evidence from successful introductions of brown anoles onto, and natural colonization of (i.e., not initiated in an experiment), a variety of island types and habitats in this system. In addition to the 100% introduction success rate noted by Stuart et al. (2014) for brown anoles on ten spoils islands of differing characteristics (at least one completely forested), I also obtained a 100% success rate for brown anole introductions onto four small, marshy islands in Mosquito Lagoon (Turnbough, unpubl. study). In the course of a variety of studies in the Mosquito Lagoon island system, I have observed brown anole populations occupying every type of habitat present on the spoils islands used in the current study, both on the study islands themselves and on smaller islands lacking extensive upland habitat (implying that brown anole occupation of marshy habitats on large spoils islands does not simply represent population spillover into sink habitat). Though the dense marsh and forest habitats that typically encircle the more heavily forested islands may represent suboptimal habitat for brown anoles, there is no reason to suspect that brown anoles were unable to colonize such habitats.

Habitat structure effects on latency to invade island interiors

Although marsh and forest habitats on heavily forested islands did not serve as a barrier to brown anole invasion, their characteristics may have increased the time required for nascent brown anole populations on island shorelines to colonize island interiors (where anole counts were conducted). It seems likely that most brown anole invasions begin at the edges of spoils islands, as propagules disembark from beached boats or unloaded cargo, or arrive via overwater dispersal. Since brown anoles favor relatively open environments and habitat edges and probably do not disperse into suboptimal habitats, like closed-canopy forest, while unoccupied space remains in better habitat (see Wright 2009), nascent populations probably remain in suitable marsh and forest–marsh edge habitat along island margins unless gaps or shallowness in the forest facilitate dispersal into island interiors. Forests on scrubby islands were about half as deep, on average, as those on heavily forested islands (13.5 vs. 24.2 m; $t = 6.06$, df = 31, $P < 0.0001$) and far more likely to have at least one gap (94% vs. 20%; Fisher's exact test, $P < 0.0001$), making it likely that colonizing brown anoles would disperse into island interiors more quickly on scrubby islands. Consistent with this possibility, islands on which brown anoles were abundant at the xeric–forest edge were more likely to have one or more forest gaps than islands on which brown anoles were present but rare (85% vs. 33%; Fisher's exact test, $P = 0.046$), and on average their forests were shallower (14.0 vs 21.3 m; $t = 2.20$, df = 17, $P = 0.042$).

Though the possibility also exists that habitat structure indirectly affected brown anole population growth by affecting anole predator assemblages (see Schoener and Schoener 1978, 1982a, Calsbeek and Cox 2010), the available evidence suggests that anole predators were not more abundant or active on heavily forested islands. Two anole predators were commonly observed on islands in this study: black racer snakes (*Coluber constrictor*), which frequently prey on anoles (Hamilton and Pollack 1956, Fitch 1963, Halstead et al. 2008), and raccoons (*Procyon lotor*), which probably opportunistically prey on them (especially at night). Since I have more frequently observed racers on invaded islands rather than heavily forested ones (Turnbough 2010), and since raccoons are regularly observed on both scrubby and heavily forested islands (Stuart et al. 2014, Turnbough unpubl. obs.) and their activity levels—as measured by the number of disturbed pitfall traps—did not differ between the two island types (Turnbough, unpubl. analyses), it does not appear that brown anole population growth was differentially slowed on heavily forested islands by predation.

Quicker brown anole colonization of scrubby island interiors may have affected the observed patterns of brown anole abundance, but it should not have much affected the results of this study. It is possible, for example, that equivalent brown anole propagules arrived on the shores of Islands 28 and 29 (abundant brown anoles) and Islands 30, 33, and 34 (rare brown anoles) within the same time frame, but because only Islands 28 and 29 were relatively scrubby (see Figure 2.2 and Table S1.1), it was only on those islands that brown anoles had proliferated to abundance along xeric–forest edges by the time this study was conducted. Since it is the density of brown anoles (reflected in the anole counts) and not the (unknown) trajectory of population growth followed to reach that density that is likely to be the primary driver of brown anole food web effects, differential latencies to abundance on different island types should not have greatly impacted the pattern or strengths of observed BA_{Abund}–response associations. However, it is possible that the impacts of dense brown anole populations change with increasing lengths of time, for example by causing extirpations for heavily preyed-on arthropod species.

Habitat structure effects on shoreline prey subsidies

Several mutually compatible mechanisms may give brown anoles on more scrubby islands greater access to, and ability to benefit from, prey subsidies deriving from shoreline wrack deposits. Such deposits have been shown to subsidize higher brown anole densities in the Bahamas by increasing arthropod prey abundances (Spiller et al. 2010), and similar subsidies have been observed for other lizards in xeric coastal habitats (Barrett et al. 2005, Catenazzi and Donnelly 2007).

First, the shallow and gappy tendencies of scrubbier island marshes and forests may facilitate the dispersal or windblown movement of shoreline arthropods (especially dipterans) through or around forest habitats into xeric interiors. The taller, deeper, more unbroken bands of vegetation encircling more heavily forested islands likely form a barrier to windborne shore arthropods (Cadenasso and Pickett 2001, Witman et al. 2004), and substantial shoreline subsidies are unlikely to penetrate by other means through tens of meters of relatively productive forest habitat (see Paetzold et al. 2008). As home range sizes, and thus densities, of female brown anoles may depend primarily on food resources (Schoener and Schoener 1982b), greater penetration of shoreline prey subsidies into island interiors on scrubbier islands may enable higher brown anole densities. Prey subsidies may also increase population growth rates on scrubbier islands by accelerating female growth to maturity, which can result in earlier—and thus greater—reproductive output during the limited window of the breeding season (Wright et al. 2013).

Second, even if prey derived from wrack inputs remain in shoreline habitats, the structure of such habitats tends to be more open on scrubby islands and thus better able to harbor dense populations of brown anoles. Most of the heavily forested islands in this study lie in shallow water and have relatively low elevation profiles; as a result, marsh habitats on the more forested islands tend to have poorly-drained, muck-infused soil substrates that support dense black mangrove (*Avicennia germinans*), saltwort (*Batis maritima*), and glasswort (*Salicornia spp.*) marshes. Although arthropod prey is abundant in these vegetational associations, they provide only marginal habitat for brown anoles, which occupy them only at low densities (Turnbough, unpubl. data). In contrast, the more elevated and steeply drained marsh habitats on scrubby islands in this system tend to be dominated by open stands of buttonwood (*Conocarpus erectus*), white mangrove (*Laguncularia racemosa*), and sea oxeye (*Borrichia frutescens*), which can support dense brown anole populations. Data to quantitatively compare brown anole densities among marsh habitat types are not yet available for this study system, but on South Bimini in the Bahamas, brown anole densities in habitats most comparable to scrubbier spoils island margins were 2–4 times greater than in habitat most comparable to heavily forested island margins (Low Scrub and Far Shrub versus Mangrove sites; Schoener and Schoener 1980). Brown anole populations inhabiting scrubbier island margins may thus be better able to translate shoreline subsidies into higher densities and greater fecundity, increasing the rate of invasion progression on scrubbier islands.

Finally, the shallow and gappy tendencies of scrubbier island marshes and forests may facilitate brown anole dispersal between shoreline habitats and xeric–forest edges. Forest depths at the northern and southern regions of spoils islands averaged 13.5 m on relatively scrubby islands and 24.2 m on relatively forested islands; given that brown anole adults and juveniles seldom dispersed more than 15 m and 30 m, respectively, in open habitat on one Bahamian island (Calsbeek 2009, Calsbeek et al. 2014), dispersal across forested habitat is probably much more common on scrubbier islands. Such dispersal may be particularly important in relation to the winter–spring dry season, as the declines in arthropod biomass that occur during this season in island interior habitats (Turnbough, unpubl. data; see Janzen 1973) may not occur, or be as severe, among shoreline arthropods. Where forests are shallow, some brown anoles may migrate during the dry season from xeric–forest edge areas to shoreline habitats with more abundant prey, and then move back into island interiors at the onset of breeding season. Indeed, in winter I have observed large numbers of brown anoles foraging among wrack and exposed shorelines (Mosquito Lagoon water levels typically drop in the dry season), in the open and far from vegetation, on more than one relatively scrubby island. Territoriality is reduced in brown anoles during the non-breeding season (Tokarz et al. 2002, Partan et al. 2011), which may enable them to aggregate at higher-than-normal densities near important food resources if prey become too scarce elsewhere in the habitat; farther north, winter suppression of territorial behavior in green anoles (Jenssen et al. 1995, 1996) enables them to aggregate around a different resource—rock bluffs providing shelter (Bishop and Echternacht 2004). Even if brown anoles do not aggregate in shoreline habitats, if reduced prey availability causes brown anoles in interior habitats to experience higher winter mortality than those occupying shoreline habitats, then a greater likelihood of dispersal between these habitats on scrubbier islands could facilitate quicker population recovery from winter die-offs on scrubbier islands.

If brown anoles are indeed subsidized to a greater extent on scrubbier islands, population densities at xeric–forest edges may have built up faster or to higher levels on scrubbier islands; neither of these possibilities is likely to have greatly affected findings in this study. Differential latency to population buildup is unlikely to have biased estimates of apparent anole effects in this study, as noted above. The impacts of brown anoles at high densities are not negated by the fact that brown anoles may not attain such densities on all islands, and because replacement effect estimates were calculated using the *average* difference in brown anole abundance between green anole islands and brown anole islands (as opposed to the *maximum* difference), RE estimates were based on brown anole abundance levels that were likely attainable even on heavily forested islands (an average of 27.4 brown anoles were counted on brown anole islands, and the count for heavily forested Island 13 was 20).

Red imported fire ant invasions

Overview

Co-occurring invasions of *Solenopsis invicta*, the red imported fire ant (RIFA), initially appeared to offer an alternative explanation for BA_{Abund}–response associations, but upon further investigation it became apparent that RIFA's potential to confound the results was relatively limited. RIFA were abundant only on brown anole islands, probably due in part to the proximity of these islands to mainland boat launches that provide suitable RIFA habitat, and it appears that they were in the process of invading the spoils island system at the time of this study. Although RIFA frequently alter the composition of ant assemblages in the southeastern U.S. (e.g., Wojcik 1994, Kaspari 2000, Calixto et al. 2007, LeBrun et al. 2012; but see Morrison and Porter 2003, King and Tschinkel 2013) and may, at high densities, impact the abundances of other arthropods (e.g., Porter and Savignano 1990, Allen et al. 2001, Calixto et al. 2006; but see Morrison 2002, King and Porter 2007), I treated them as a response rather than an explanatory variable because, theoretically, anoles could affect RIFA directly through predation or indirectly by consuming their competitors or shared arthropod prey.

Qualitatively, the potential for RIFA to explain generalities in BA_{Abund}–response association patterns was mixed. RIFA were more abundant in xeric than forest habitats, potentially explaining the stronger BA_{Abund}–response associations in xeric habitats, and their potential to negatively impact other arthropods initially seemed to offer an alternative explanation for the negative associations between BA_{Abund} and large arthropods. However, RIFA abundance does not appear to explain positive associations between BA_{Abund} and smaller arthropods: all else equal, smaller arthropods should be less able to escape RIFA predation, and at least some of the taxa in question (i.e., Collembola and Diptera) are both common in published RIFA diets (Wilson and Oliver 1969, Tennant and Porter 1991, Vogt et al. 2002a) and found to associate negatively with RIFA presence or abundance (Porter and Savignano 1990, Wickings and Ruberson 2011).

I used db-RDA variation partitioning and best model selection to determine the extent and nature of explanatory overlap among BA_{Abund}, log-transformed RIFA abundance, and environmental covariables for dissimilarity patterns in ground and foliage arthropod communities.

Invasion patterns

RIFA invasions were distributed similarly to brown anole invasions (Figure S2.1), and as a result there was a strong association between BA_{Abund} and log-transformed RIFA abundance ($\log_{10}$[per-trap RIFA abundance + 1/6], hereafter $RIFA_{Abund}$; Figure S2.2). Like brown anoles, RIFA invasions appear to have been affected by proximity to a boat launch, but the mechanism responsible for this pattern likely differed for RIFA. Boat launches probably served as disturbed habitat “islands” for RIFA along the mainland shoreline, which was otherwise mostly undisturbed and densely vegetated from the vicinity of Island 7 southward to past Island 34. In the absence of onshore winds, alate queens mating above boat launch habitats should easily be able to fly to nearby spoils islands, and RIFA colonies established on those islands could facilitate colonization of other islands even more distant from boat launches. The likelihood that RIFA were in the process of invading the spoils islands system when this study was conducted is supported by data from a concurrent brown anole removal study, in which arthropod communities on nine very small spoils islands were sampled (at the same locations) in both July 2005 and August 2007; over this timeframe, the number of RIFA-invaded islands increased from three in 2005 to six in 2007 (Turnbough, unpubl. data).

Variation partitioning analyses

I conducted separate db-RDA variation partitioning analyses for ant assemblages and non-ant arthropods in ground arthropod communities, but too few ants were present in foliage arthropod samples to permit separate analysis of FOL ant assemblages.

In each of the analyses, most of the dissimilarity jointly explained by $\mathrm{BA}_{\mathrm{Abund}}$ and $\mathrm{RIFA}_{\mathrm{Abund}}$ was also jointly explained by environmental covariables (Figure S2.3). These percentages were highest for non-ant ground arthropods (100%), followed by ground ant assemblages (83%, 91%) and then foliage arthropods (69%). Interestingly, in each analysis the dissimilarity uniquely explained by $\mathrm{BA}_{\mathrm{Abund}}$ was much greater than the dissimilarity uniquely explained by $\mathrm{RIFA}_{\mathrm{Abund}}$, which probably accounts for the priority of $\mathrm{BA}_{\mathrm{Abund}}$ over $\mathrm{RIFA}_{\mathrm{Abund}}$ in best model selections: $\mathrm{BA}_{\mathrm{Abund}}$ was a significant component of the best db-RDA model for each analyzed community or community fraction, but $\mathrm{RIFA}_{\mathrm{Abund}}$ did not enter any of the best models.

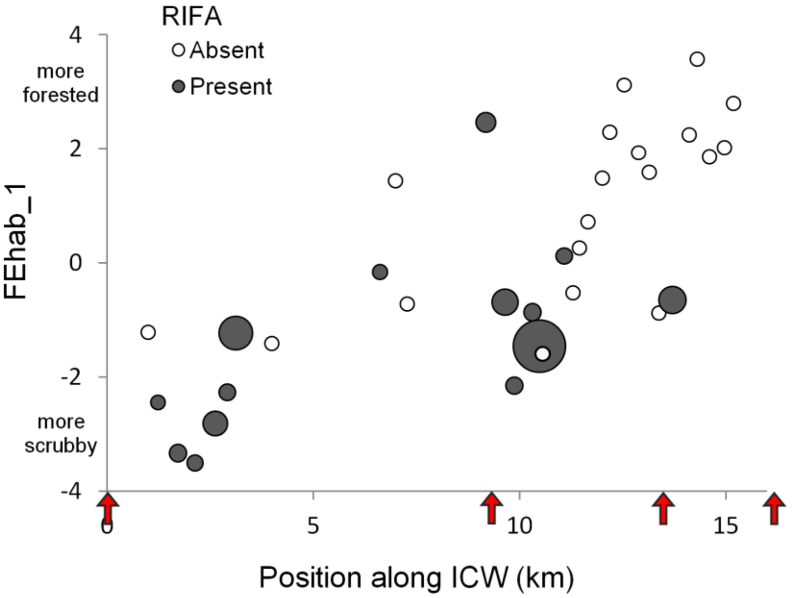

Figure S2.1 Island habitat structure and RIFA presence in xeric pitfall traps. Plot symbol areas are proportional to mean RIFA abundance per trap plus a constant of 5. Principle component scores (FEhab_1) reflect the extent and stature of xeric and forest vegetation. Arrows mark the locations of boat launches adjacent to the ICW; island and boat launch positions are offset by 1 km to aid visual presentation.

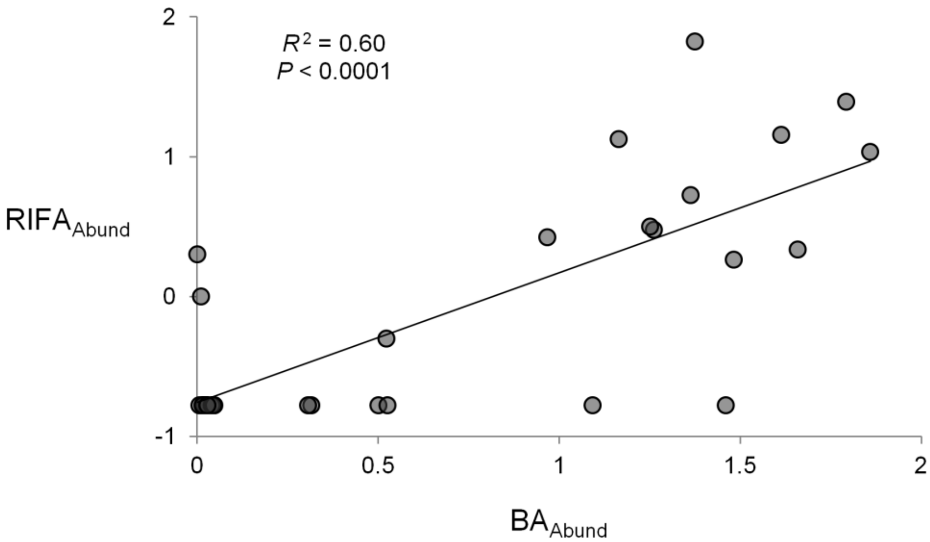

Figure S2.2 Scatterplot of BA_{Abund} versus $RIFA_{Abund}$. BA_{Abund} values include a small amount of added scatter (0 to 0.05) so that overlapping points can be observed. R^2 and P values for the linear regression line are shown.

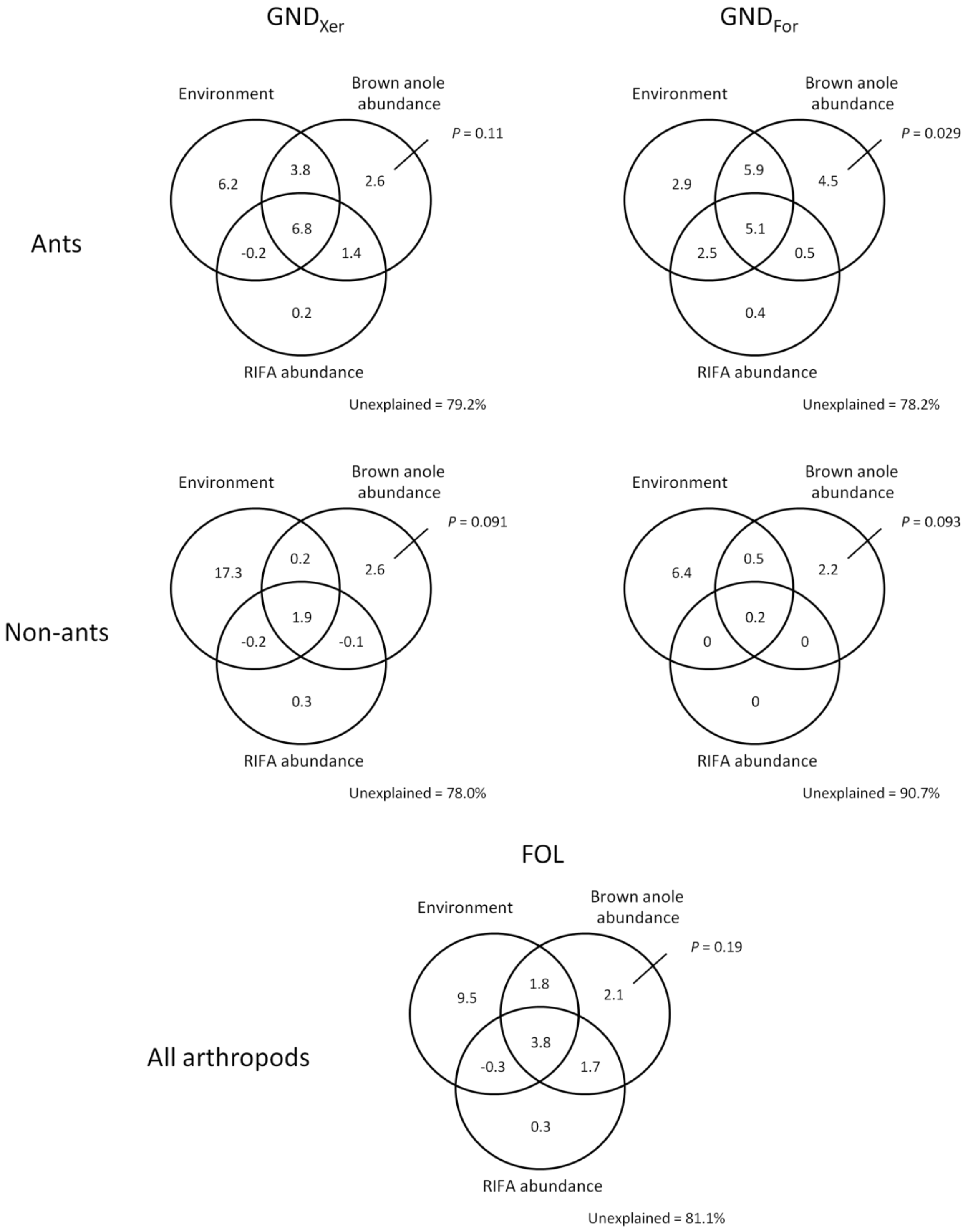

Figure S2.3 Community composition dissimilarity explained by RIFA abundance and other explanatory variable sets. Brown anole and RIFA abundances correspond to BA_{Abund} and $RIFA_{Abund}$, respectively. RIFA abundances were excluded from all response communities.

RIFA effects on inferential strength

The variation partitioning results suggest that RIFA's potential to offer competing explanations for apparent anole effects is primarily limited to best model evidence among non-ant ground arthropods. Observed $R^{2,\ \mathrm{BA-Full}}_{\mathrm{D,\ adj}}$ fractions, which offer the strongest form of statistical evidence for anole effects, should remain relatively unaffected by the inclusion of $\mathrm{RIFA_{Abund}}$ as an explanatory covariable, as partialling out the variation jointly explained by $\mathrm{BA_{Abund}}$ and environmental covariables should also partial out a great majority of the variation jointly explained by $\mathrm{BA_{Abund}}$ and $\mathrm{RIFA_{Abund}}$. The greater ability of $\mathrm{BA_{Abund}}$ than $\mathrm{RIFA_{Abund}}$ to explain composition variation in GND ant assemblages indicates that $R^{2,\ \mathrm{BA-Best}}_{\mathrm{D,\ adj}}$ fractions for this dominant group of ground arthropods would remain intact were $\mathrm{RIFA_{Abund}}$ incorporated as an explanatory covariable in the analyses. Although $\mathrm{BA_{Abund}}$ also outcompeted $\mathrm{RIFA_{Abund}}$ in the best db-RDA models for non-ant arthropods, it is possible that the pattern was driven by one or more of the most abundant response groups within those community fractions. It is thus possible that $\mathrm{BA_{Abund}}$ could be supplanted by $\mathrm{RIFA_{Abund}}$ in best models for some non-ant ground arthropod taxa, particularly those comprising a minor percentage of total non-ant arthropod abundance, and best model evidence for anole effects among these taxa should be considered with this limitation in mind.

Beyond the db-RDA evidence suggesting that $R^{2,\ \mathrm{BA-Best}}_{\mathrm{D,\ adj}}$ fractions for most (or at least the most abundant) FOL responses were unlikely to be affected by consideration of $\mathrm{RIFA_{Abund}}$ as an explanatory covariable, there is an additional reason to suspect that RIFA were not responsible for apparent anole effects on foliage arthropods: RIFA were never captured or observed in foliage on the study islands. Although it is possible that RIFA foraged arboreally only at night, diurnal arboreal foraging occurs in a variety of systems (e.g., Tedders et al. 1990, Forys et al. 2001, Ness 2003), and I have encountered RIFA in vegetation during the day on very small spoils islands. It is also possible that RIFA were simply not captured by sweep net samples, but if they were present in the vegetation it seems likely that I would have encountered them during anole counts or other sampling activities.

Adequacy of subsample sizes

Island arthropod communities were not intensively subsampled due to constraints imposed by logistics. Subsample sizes (i.e., samples per habitat per island, $n_{\text{subsample}}$) were 6, 4, and 2 for ground-active, foliage-dwelling, and aerially-active arthropod communities, respectively. To the extent that within-island variation among community subsamples was high, the error introduced into parameter estimates by small subsample sizes may have affected the qualitative findings of this study.

I assessed the adequacy of GND and FOL subsample sizes by evaluating, under two different resampling techniques, the relationship between subsample size and the proportion of community composition variation explained by BA_{Abund} (i.e., $R^{2,\text{BA}}$ for Bray-Curtis dissimilarities); the inadequacy of AER subsampling is acknowledged elsewhere (see Discussion: *Aerial arthropods*). I focused on community composition $R^{2,\text{BA}}$ because it was the fundamental measure of interest in this study, as it quantified the extent to which arthropod communities varied with brown anole abundance. The first resampling regimen was a form of jackknifing: community composition $R^{2,\text{BA}}$ was calculated for data sets generated by randomly selecting, without replacement, a given number of the subsamples collected on each island (between 1 and $n_{\text{subsample}} - 1$). For GND data sets, when the number of subsamples to be selected exceeded the number recovered for a given island (some pitfall traps on some islands were lost to raccoon interference), the total number of subsamples collected (without duplication) served as the island's contribution to the resampled data set. The second resampling regimen employed bootstrapping: $R^{2,\text{BA}}$ was calculated for data sets generated by randomly selecting, *with* replacement, a given number of subsamples for each island (between 1 and 10). In both resampling routines, random subsamples were selected via the "strata" function in the R package 'sampling' (Tillé and Matei 2015), and 10,000 data sets were generated for each subsample size. $R^{2,\text{BA}}$ values were calculated with PERMANOVA (see Methods: *Multivariate community composition analyses*) and left unadjusted; adjusted $R^{2,\text{BA}}$ values would add noise to the pattern of interest (the adequacy of subsample sizes) because adjustment magnitudes (both absolute and proportional) are affected by the value of the unadjusted measure.

Subsample sizes appear to have been adequate for GND_{Xer} and GND_{For}, but not FOL (Figure S2.4). Together, the jackknife and bootstrap resampling analyses suggested that $R^{2,\text{BA}}$ magnitudes were relatively stable once subsample sizes reached 5–6 for GND_{Xer} and 4–5 for GND_{For} (Figure S2.4 a–d, Table S2.6). Bootstrap analyses suggested that FOL $R^{2,\text{BA}}$ magnitudes would also stabilize around 5–6 subsamples (Figure S2.4 f), but only 4 FOL subsamples were collected on each island.

Although foliage-dwelling arthropod communities were likely undersampled, the effects of this undersampling appear to have been conservative, in that $R^{2,\text{BA}}$ was biased downwards. In all GND and FOL resampling analyses, $R^{2,\text{BA}}$ values increased in magnitude (and decreased in

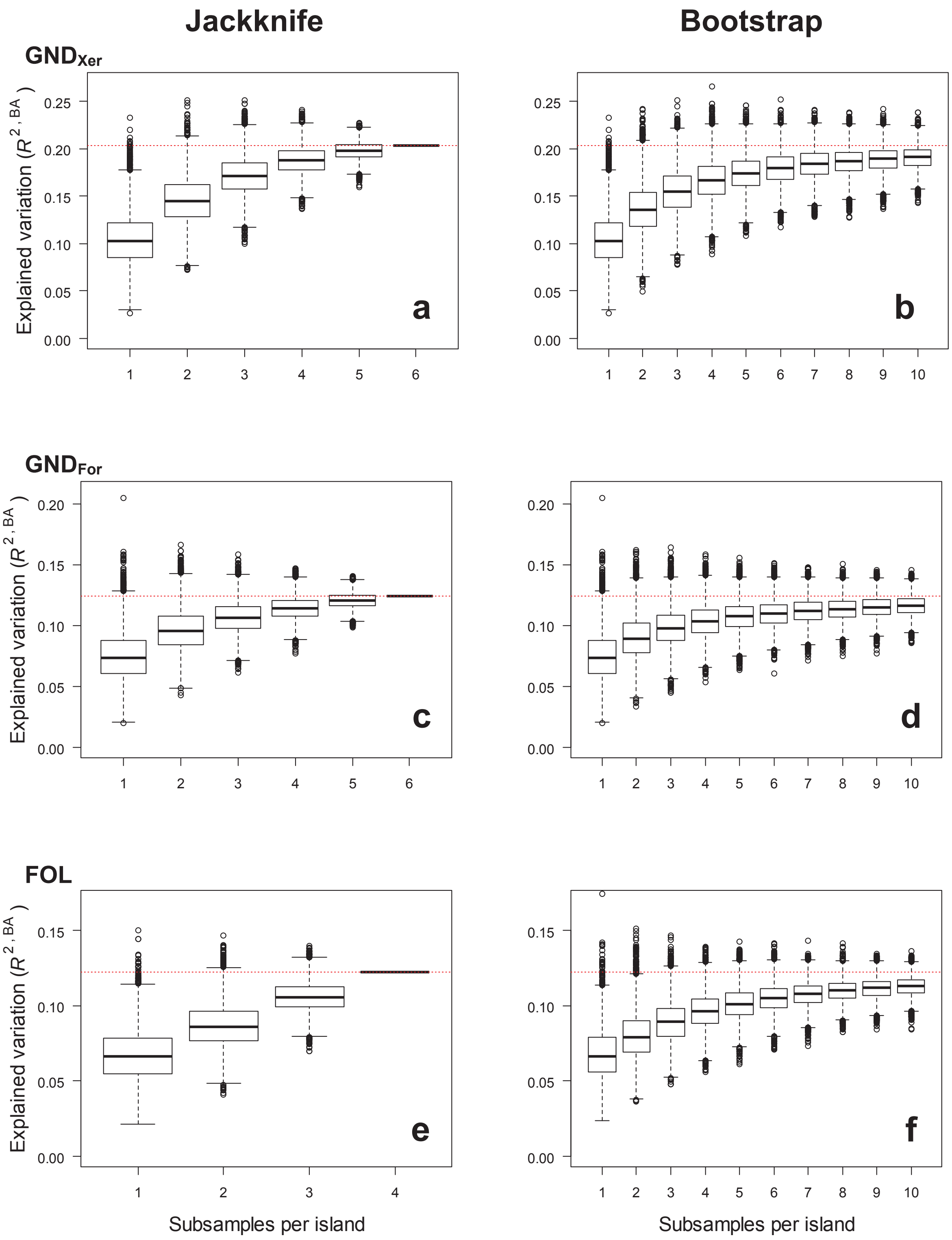

Figure S2.4 Boxplots showing the relationship between explained community composition variation ($R^{2,\,\mathrm{BA}}$) and subsample size in jackknife and bootstrap resampling analyses of (a, b) $\mathrm{GND}_{\mathrm{Xer}}$, (c, d) $\mathrm{GND}_{\mathrm{For}}$, and (e, f) FOL. Dotted lines indicate the actual $R^{2,\,\mathrm{BA}}$ values obtained in the study.

Table S2.6 Attributes of jackknifed and bootstrapped $R^{2,\,\mathrm{BA}}$ distributions.

			Jackknife		Bootstrap	
Community	Subsample size	$R^{2,\,\mathrm{BA}}$:	Median	2.5th, 97.5th percentiles	Median	2.5th, 97.5th percentiles
$\mathrm{GND}_{\mathrm{Xer}}$	1		0.103	0.056, 0.162	0.103	0.056, 0.162
	2		0.145	0.099, 0.197	0.136	0.086, 0.192
	3		0.172	0.133, 0.212	0.155	0.108, 0.204
	4		0.188	0.160, 0.217	0.167	0.125, 0.210
	5		0.198	0.179, 0.216	0.174	0.138, 0.213
	6		0.204	–	0.180	0.146, 0.214
	7		–	–	0.184	0.152, 0.215
	8		–	–	0.187	0.158, 0.215
	9		–	–	0.190	0.162, 0.215
	10		–	–	0.191	0.166, 0.216
$\mathrm{GND}_{\mathrm{For}}$	1		0.073	0.040, 0.119	0.073	0.040, 0.119
	2		0.096	0.065, 0.132	0.089	0.057, 0.128
	3		0.106	0.082, 0.133	0.098	0.069, 0.130
	4		0.114	0.096, 0.133	0.103	0.076, 0.131
	5		0.120	0.108, 0.133	0.107	0.084, 0.132
	6		0.124	–	0.110	0.088, 0.131
	7		–	–	0.112	0.092, 0.133
	8		–	–	0.114	0.095, 0.132
	9		–	–	0.115	0.098, 0.132
	10		–	–	0.116	0.100, 0.132
FOL	1		0.066	0.038, 0.109	0.066	0.038, 0.110
	2		0.086	0.060, 0.117	0.079	0.053, 0.114
	3		0.106	0.088, 0.125	0.089	0.064, 0.117
	4		0.122	–	0.096	0.073, 0.121
	5		–	–	0.101	0.081, 0.122
	6		–	–	0.105	0.086, 0.123
	7		–	–	0.108	0.091, 0.124
	8		–	–	0.110	0.096, 0.124
	9		–	–	0.112	0.098, 0.124
	10		–	–	0.113	0.100, 0.125

variability) with greater subsample size. Conservative or not, the error introduced by undersampling into estimates of BA_{Abund}-explained FOL variation was probably too small to have qualitatively affected the results of at least the community-level composition analyses. For example, median bootstrapped $R^{2,\,BA}$ values for FOL subsample sizes of 4 and 6 differed by less than 0.01, and maximum difference among the central 95% of bootstrapped $R^{2,\,BA}$ values for these subsample sizes was only 0.05 (Table S2.6, comparing the 2.5th percentile of the 4-subsample distribution to the 97.5th percentile of the 6-subsample distribution). However, it is possible that analysis results for within-FOL responses, particularly those involving a relatively small proportion of the community (e.g., Hemiptera abundance), were qualitatively affected by undersampling-induced error.

In conclusion, there is little reason to suspect that the qualitative results of GND and FOL analyses were much influenced by small subsample sizes. For community composition analyses, at least, ground arthropods appear to have been adequately subsampled, and the effects of foliage arthropod undersampling were probably minor in magnitude and conservative with respect to the patterns of interest. It should be noted, however, that the ultimate basis for these inferences was the observed subsample data, and it is possible that these inferences would change with different or additional subsample data.

Potential effects of brown anole predation on *Pheidole* ants

Overview

In addition to positive associations with RIFA abundance, strong associations between BA_{Abund} and GND ant assemblage compositions were largely driven by negative associations between

BA_{Abund} and the abundances of large *Pheidole* species (*P. dentata* and *P. morrisi*; hereafter "*Pheidole*"). These association patterns do not appear to be caused by environmental differences among islands, as habitat characteristics correlated with BA_{Abund} (e.g., composite measures of scrubbiness) were not as strongly associated with either RIFA or *Pheidole* abundances as was BA_{Abund}. Concerning *Pheidole*, for example, the highest GND_{For} abundances and the fourth highest GND_{Xer} abundances were on Island 8 ("Hornet" in Stuart et al. 2014), a scrubby uninvaded island, and conversely *Pheidole* were absent in GND samples from Island 13, a heavily forested island with abundant brown anoles. Further, GND_{Xer} *Pheidole* abundances on Island 9—a scrubby, uninvaded island that was excluded from analyses due to its lack of green anoles—were almost three times greater than the highest abundance among all other islands.

RIFA invasions do not appear to be primarily responsible for the BA_{Abund}–*Pheidole* associations, though they may contribute to the pattern. Given RIFA's propensity to negatively impact *Pheidole* ants (Wojcik 1994, King and Tschinkel 2013), the possibility that RIFA invasions secondarily (through similar invasion contingencies) generated the observed BA_{Abund}–*Pheidole* association is certainly plausible. However, BA_{Abund} explained 1.2 (GND_{Xer}) to 2.6 (GND_{For}) times more variation ($R^2_{D,\ adj}$) in *Pheidole* abundance patterns than did $RIFA_{Abund}$, and specific aspects of the patterns provide qualitative support for brown anole invasion as the main causal agent behind the association. For example, in GND_{Xer}, RIFA were absent on two of the brown anole islands that lacked *Pheidole*, and *Pheidole* abundances on the two islands invaded by RIFA but not brown anoles were higher than those of any brown anole island (Figure S2.5a). Evidence against RIFA-generated *Pheidole* declines was even stronger for GND_{For}, as RIFA were absent from the majority of brown anole islands (Figure S2.5b). Though RIFA do not

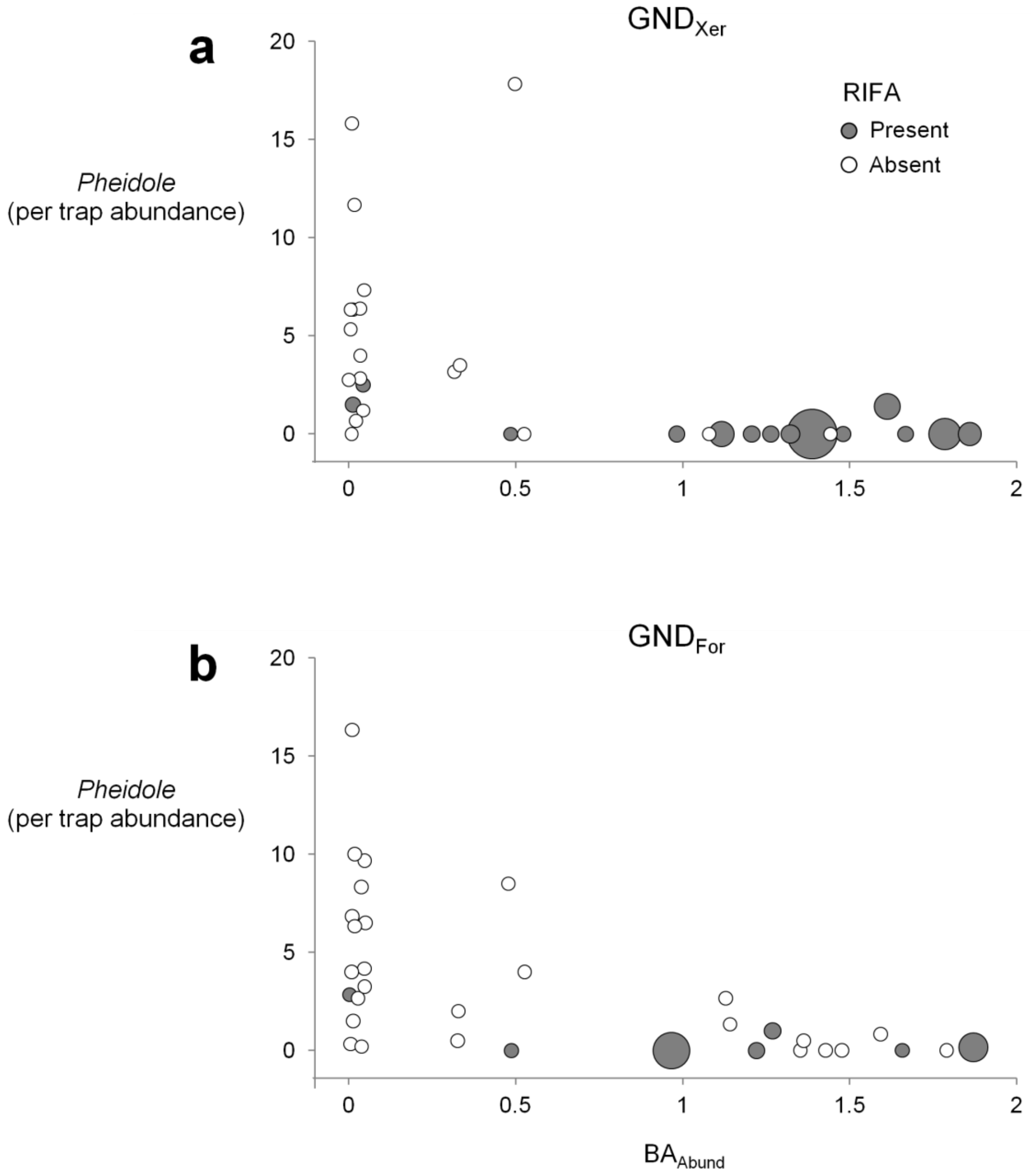

Figure S2.5 Per-trap *Pheidole* abundances versus BA$_{Abund}$ and RIFA presence/absence for (a) GND$_{Xer}$ and (b) GND$_{For}$. Plot symbols are proportional to per-trap RIFA abundance plus a constant of 5.

appear to have been the primary driver for $\mathrm{BA}_{\mathrm{Abund}}$–*Pheidole* associations, they may aid the primary causal agent—possibly brown anole predation—in reducing *Pheidole* abundances. I found no evidence for an additive or synergistic RIFA effect in *Pheidole* abundance models, however, as neither the $\mathrm{RIFA}_{\mathrm{Abund}}$ nor the $\mathrm{BA}_{\mathrm{Abund}}$–$\mathrm{RIFA}_{\mathrm{Abund}}$ interaction terms were significant in models with $\mathrm{BA}_{\mathrm{Abund}}$ (Turnbough, unpubl. analyses).

Brown anole predation appears to best explain the apparent response of *Pheidole* ants to brown anole invasion. This hypothesis requires that *Pheidole* are (1) palatable prey, (2) consumed in greater numbers by brown anole populations than green anole populations, and (3) negatively impacted by increased anole predation. The relative palatability (due to a reliance on physical defense) of *Pheidole* to anoles and high frequencies of *Pheidole* in brown anole diets have already been established (see Discussion*: Ground arthropods*); I discuss here and below points (2) and (3) of the anole predation hypothesis.

Data from Giery et al.'s (2013) study of syntopic anoles in Florida support the assertion that brown anoles selectively prey on *Pheidole* ants. In standardized habitat (isolated *Ficus aurea* "tree islands"), bark anoles consumed more and a greater diversity of ants than did brown anoles (24 bark anole stomachs contained an average of 26.5 ants and 14 total species, compared to 0.5 ants on average and 4 species total in 32 brown anole stomachs), but proportionally fewer *Pheidole* (7% vs. 75% of the ants consumed by bark and brown anoles, respectively). Given that bark and brown anoles overlapped broadly in perch height distributions and shared important terrestrial prey (e.g., lygaeid bugs), and the fact that bark anoles ate ground-nesting ant species that were absent in brown anole diets (e.g., RIFA), Giery et al.'s (2013) results suggest that brown anoles preferentially consumed *Pheidole* over at least some of the other ant species they encountered (assuming that bark anoles do not actively avoid eating *Pheidole*). No data are currently available to assess a potential green anole preference for *Pheidole* ants, but even if such a preference exists, brown anole populations are likely to consume greater numbers of *Pheidole* ants than green anole populations because brown anoles (1) perch closer to the ground and are therefore more likely to encounter *Pheidole,* which are mostly ground nesters and foragers (Wilson 2003); (2) tend to consume more ants per-capita (Hamilton and Pollack 1961, Schoener 1968, Lister 1976, Campbell 2000, Whitaker et al. 2012), though this pattern may be influenced in areas of sympatry by the upward shift in green anole perch use; and (3) attain much higher densities (Campbell 2000).

Direct effects on Pheidole

Greater predation pressure on *Pheidole* resulting from brown anole invasion could very well negatively impact populations of these ants. In the only study to date of anole effects on ant assemblages, Huang et al. (2008a) found that brown anoles altered the composition of ant assemblages in betelnut palm plantations in Taiwan, primarily by reducing *Pheidole fervens* abundance by 45%. Although they could not rule out *P. fervens* behavioral avoidance of sub-enclosures containing anoles, Huang et al.'s results were consistent with predation-driven declines in *Pheidole* density, and reasonable assumptions applied to the available data suggest that brown anole predation could cause even greater declines on Florida spoils islands.

Under the conservative assumption that green and brown anoles are identical in their per-capita ant consumption, I estimate that *P. dentata* and *P. morrisi* worker populations in mature colonies could suffer monthly losses of 30% and 22%, respectively, from the increase in anole density that accompanies brown anole invasion. Median estimated brown anole density among brown anole islands in this study was 0.420 lizards/m^2 (using the count–density equation in

Appendix S1) whereas average (across years) green anole density on one of the green anole islands in a previous study was only 0.096 lizards/m^2 (Campbell 2000); an increase of 0.324 lizards/m^2 may therefore be taken as a typical result of brown anole invasion in this system. An expected per-capita rate of brown anole ant predation equal to 2.3 ants/day can be derived from Campbell's (2000) analysis of brown anole stomach contents from similar spoils islands (using island-weighted averages, assuming a 1:2 male-to-female population sex ratio, and assuming a 2-day gastric evacuation rate [Windell and Sarokon 1976]); if 85% of consumed ants are *Pheidole* (Norval et al. 2011, Giery et al. 2013), then a conservative estimate of increased *Pheidole* predation following brown anole invasion is 0.639 ants/m^2/day. Converting this predation rate into increased worker mortality rates requires colony size and foraging area data. Colony sizes for *P. dentata* and *P. morrisi* (the species affected in this study) in Florida are approximately 800 and 2,500 workers, respectively (King 2010). Foraging or territorial areas for these species are not reported in the literature, but in Florida *P. morrisi* workers forage up to 4.3 m or even 8 m away from the nest area (Van Pelt 1958, Johnson 1988), *P. dentata* has been observed to forage long distances from wooded areas into soybean fields (Whitcomb et al. 1972), and several other *Pheidole* species have foraging ranges of 4 m or greater (Naves 1985); given these distances, foraging areas approximated by circles with radii of 2 m and 3 m seem to be reasonably conservative estimates for *P. dentata* and *P. morrisi*, respectively (the greater area of the latter owing to its greater colony size). Multiplying these areas by the conservatively estimated increased predation rate yields expected colony losses of 8.0 ants/day for *P. dentata* and 18.1 ants/day for *P. morrisi*, which correspond to daily losses of 1.0% and 0.7% of the worker populations of these respective species and, assuming no compensatory production of workers, monthly losses of 30% and 22%. Such losses may not be sustainable, especially if *Pheidole* colonies are competing with, and defending against, ant species advantaged by lesser palatability to anoles.

Under a less conservative scenario of increased anole predation, in which only brown anoles, and not green anoles, are assumed to prey on *Pheidole*, estimated monthly worker population losses rise to 39% and 28% for *P. dentata* and *P. morrisi*, respectively.

Actual increases in predation following brown anole invasion are likely to be greater than these estimates. Anole hatchlings and juveniles were not included in brown anole density estimates, but these age classes are seasonally abundant and likely to consume *Pheidole* ants—perhaps more so than adult anoles, as their lower perch heights (Schoener 1968, Treglia et al. 2008) and smaller sizes should, relative to adults, reduce the cost of pursuit and increase the energetic value of *Pheidole* prey. Furthermore, if brown anoles negatively impact syntopic *Pheidole* populations and do not compensate for reduced *Pheidole* availability by consuming other ant genera, then ant predation frequencies derived from long-established brown anole populations may substantially underestimate those occurring in the early stages of invasion. That individual brown anoles can and do consume very large numbers of *Pheidole* ants is evidenced by the presence of 47, 77, 129, and 160 *Pheidole megacephala* in the stomachs of individual brown anoles in recently invaded Taiwan (Norval et al. 2011; but note that such large numbers may be prompted by aspects of *P. megacephala* foraging behavior).

Although *Pheidole* ants could, if the necessary behavioral plasticity mechanisms exist, avoid anole predation by reducing or eliminating aboveground activity during times or conditions of anole activity (e.g., by foraging exclusively nocturnally), such a behavioral shift could reduce their ability to compete with other ant species and potentially result in negative impacts comparable to those caused by anole predation. A change in foraging time cannot account for the observed $\mathrm{BA}_{\mathrm{Abund}}$–*Pheidole* associations, however, as pitfall traps were deployed for 24 hours.

Indirect effects on RIFA invasion success

Brown anole predation of *Pheidole* ants may even aid RIFA invasion success and contribute to the positive $\mathrm{BA}_{\mathrm{Abund}}$–RIFA association. Resident ant faunas can hinder RIFA colonization of new areas by killing alighting RIFA queens and by raiding newly-founded RIFA nests (Whitcomb et al. 1973, Nickerson et al. 1975, Vinson and Rao 2004), and the available evidence suggests that *P. dentata* and *P. morrisi* are important contributors to such resistance. Both species have been observed to attack newly mated RIFA queens in the field (Whitcomb et al. 1972, Kaspari and Vargo 1994), *P. dentata* attacks founding queens in simulated nests in the field and destroys incipient colonies in the lab (Nichols and Sites 1991, Rao and Vinson 2004), and *P. morrisi* raids and destroys colonies of a closely related and ecologically similar fire ant, *Solenopsis geminata*, in natural settings (Johnson 1988). Thus, negative effects of brown anoles on these *Pheidole* species may, depending upon the responses of other ants in the assemblage, create a more favorable environment for RIFA colony establishment.

Though it is possible that any reduction in *Pheidole* abundance would be compensated for by an increase in the abundance of other ant species that offer similar or greater levels of resistance to RIFA colonization, such a scenario does not appear to have occurred on spoils islands in this study: among islands where RIFA was absent or relatively uncommon (mean per-trap RIFA abundance ≤ 2), there was no abundance compensation, on average, from other non-RIFA ant species to lower *Pheidole* abundances, both within and among islands and in both xeric and forest habitats (Figures S2.6, S2.7). In addition to potentially increasing the odds of successful RIFA colony establishment, this lack of compensation also suggests that incipient RIFA colonies would have fewer competitors for resources on islands with lower *Pheidole* abundances, leading perhaps to more rapid or complete RIFA dominance in local ant assemblages. Once established, RIFA colonies are unlikely to be negatively impacted by brown anoles, as fire ant workers appear to be relatively unpalatable ants (Vogel and von Brockhusen-Holzer 1984) that are avoided as prey by brown anoles (Giery et al. 2013), in contrast to fire ant queens (Norval et al. 2011). Relationships between brown anole and RIFA invasions and the nature of their combined effects on both ant assemblages and arthropod faunas are clearly deserving of further study.

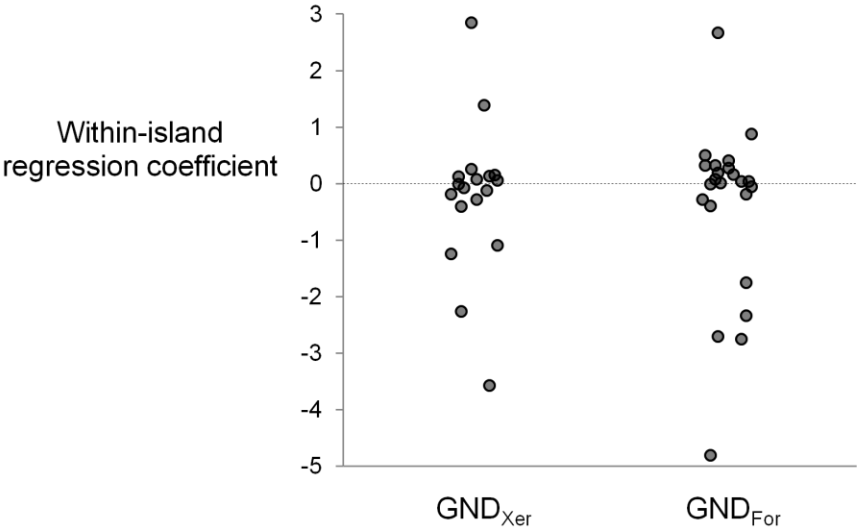

Figure S2.6 Coefficients for within-island (trap-level) regressions of non-RIFA, non-*Pheidole* ant abundance against *Pheidole* abundance. A coefficient of zero indicates a complete lack of abundance compensation from other non-RIFA ant species to lower *Pheidole* abundance levels; a value of −1 indicates 1:1 abundance compensation. Only traps in which RIFA were absent or rare (≤ 2 captured RIFA individuals) were used for analyses. Islands with < 3 useable traps and islands lacking *Pheidole* in all useable traps were not analyzed.

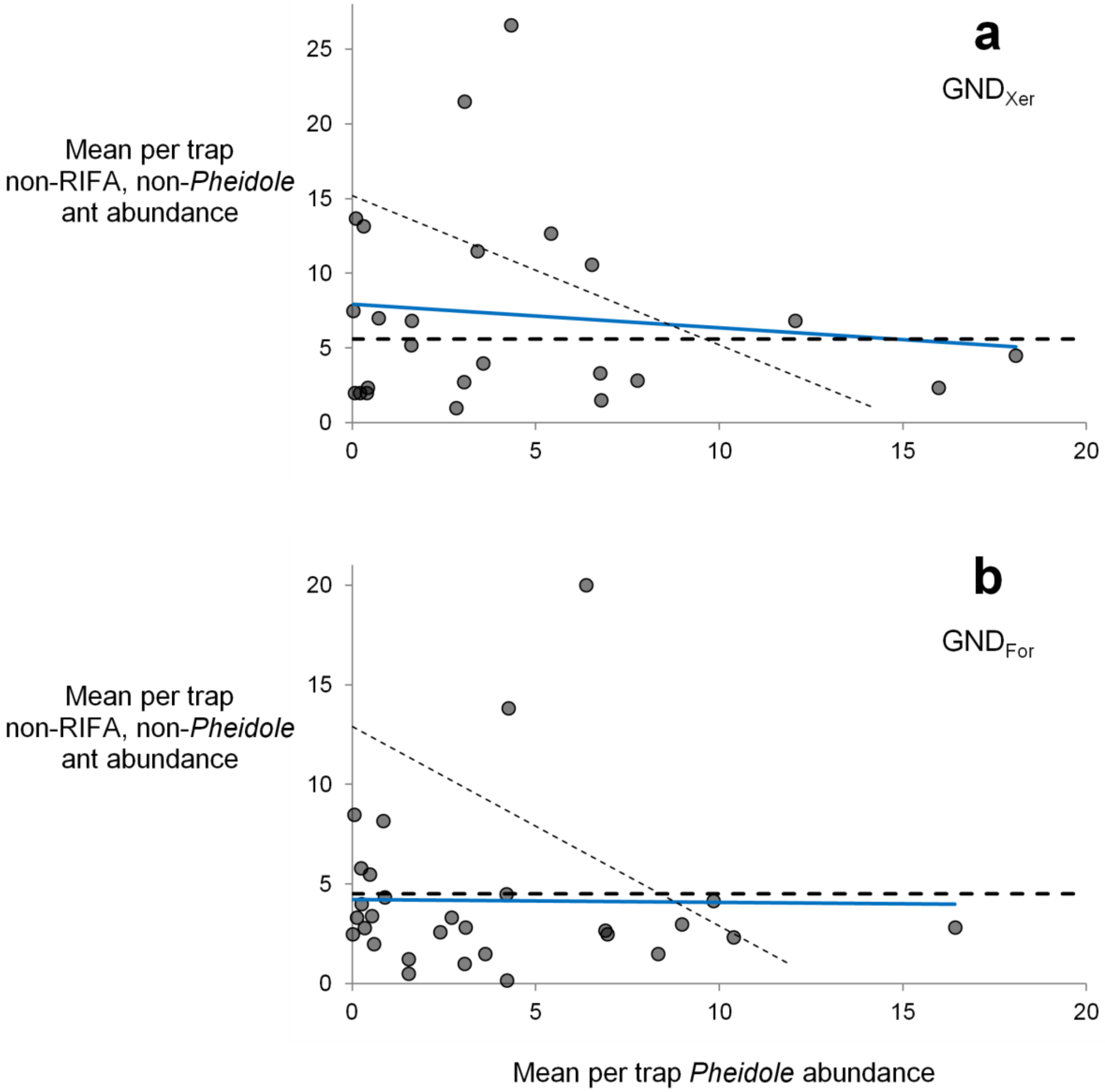

Figure S2.7 *Pheidole* versus non-RIFA, non-*Pheidole* ant abundances (per-trap island means) for (a) GND_{Xer} and (b) GND_{For}. Thick and thin dotted lines represent patterns expected to result from, respectively, the absence of abundance compensation and 1:1 replacement levels of other non-RIFA ant species in response to lower *Pheidole* abundances, as extrapolated from mean *Pheidole* and mean non-RIFA, non-*Pheidole* ant abundances among islands comprising the upper 50th percentile of non-zero *Pheidole* abundances. Solid lines show the linear regression of the plotted points. Only islands with mean per-trap RIFA abundances ≤ 2 were included in the analyses.

Ground arthropod total abundances: discrepancy with previous studies

Total ground arthropod abundances were not negatively associated with BA_{Abund}, in contrast to two other studies in which ground-trapped arthropod abundances were negatively affected by anoles. These discrepancies may be reasonably explained. The sticky traps that Pacala and Roughgarden (1984) placed on the forest floor of their enclosures were dominated by dipterans (mostly phorids), an order poorly sampled by spoils island pitfall traps, and it is possible that ground-placed sticky traps on spoils islands would yield results similar to Pacala and Roughgarden's. More likely, however, is the possibility that the negative effects of predation on small, ground-alighting flies are stronger for *A. wattsi* (one of the two anole species in Pacala and Roughgarden's enclosures) than for brown anoles due to the former's smaller body size, smaller typical prey size, and lower perch height (Schoener 1968, Lister 1976, Pacala and Roughgarden 1985, Rummel and Roughgarden 1985). Schoener et al.'s (2002) pitfall-sampled islands were simpler and much smaller than islands used in the current study, with vegetation that rarely exceeded 2 m in height and covered an area only about 0.01 that of the average spoils island, and it is likely that ground-directed foraging was more intense on these islands because their relatively dense brown anole populations (probably subsidized by shoreline resource inputs) were constrained to low perch heights by the vegetation. Concentrated foraging near the ground probably caused brown anoles to have stronger negative effects on the ground arthropod communities of Schoener et al.'s islands than on those of spoils islands in the current study.

Ground arthropod associations: potential mechanisms

Direct effects

Many of the morphospecies comprising ground arthropod orders that were negatively associated with BA_{Abund} belonged to genera or families that normally remain hidden and inactive (at least on the surface) during the day, which raises the question as to how they might be exposed to diurnal, visually-oriented *Anolis* predators. This was most noticeable for Orthoptera, of which 98.9% were *Gryllus* crickets. That brown anoles do indeed prey on *Gryllus* and other typically nocturnal arthropods like *Parcoblatta* roaches is evidenced by gut content studies (e.g., Giery et al. 2013), and two classes of mechanisms may facilitate such interactions.

The most obvious mechanism for anole predation of mostly nocturnal prey is that periods of anole and prey activity overlap during certain parts of the day or year. *Gryllus* crickets, for example, can be active around sunrise and sunset (French and Cade 1987), as are brown anoles during at least the warm breeding season (Ord 2008); on spoils islands, some brown anoles move from their arboreal sleeping perches to the ground—perhaps to forage—even before sunrise (Turnbough, unpubl. obs.). *Gryllus* and other nocturnal arthropods (e.g., some carabid beetles) may also switch to diurnal activity when nights become too cool for activity, and even during warmer weather some individuals in predominantly nocturnal populations may exhibit some degree of diurnal activity (Alexander and Meral 1967, Lövei and Sunderland 1996, Tuf et al. 2012). Since brown anoles do not hibernate and are active year-round in favorable weather, diurnally active arthropods in any season are potentially exposed to anole predation.

It is also possible that nocturnal prey may be exposed through disturbance. Predatory ants, especially those that mob larger prey, are particularly likely to flush out hidden arthropods, as they can maneuver through the litter layer to find potential prey and arthropods sufficiently large and mobile to escape often do so by rapidly fleeing (e.g., Otis et al. 1986). Anoles and other lizards prey on arthropods flushed by swarming neotropical army ants (Willis and Oniki 1978), and it is safe to assume that brown anoles would opportunistically consume palatable arthropods flushed singly and sporadically by more diffuse ant foraging. Further, because the anole- and ant-specific defenses of many prey are conflicting (i.e., remain hidden vs. flee), brown anoles and predatory ants may have synergistic effects on ground-dwelling prey (Sih et al. 1998). Synergistic effects of brown anoles and ants have been inferred from measures of herbivory on small Bahamian islands (Piovia-Scott et al. 2011), though the postulated mechanism differed in that a combination of diurnal anoles and nocturnal ants was suggested to deny herbivores a temporal refuge for feeding activities. Particularly worthy of consideration is the potential for RIFA to act synergistically with brown anoles, given RIFA's sheer abundance in some environments (Tschinkel 2006), diurnal foraging (Porter and Tschinkel 1987), and tendency to aggressively attack large prey (Allen et al. 1994, Allen et al. 2004). However, I found no evidence for such a synergism in this study, as the interaction between BA_{Abund} and $RIFA_{Abund}$ was never significant when these two variables were used to model the individual or combined abundances of orthopterans, large beetles, and large spiders (Turnbough, unpubl. analyses).

Indirect effects

If brown anole predation on ants or spiders indirectly benefited small-bodied arthropod groups, then ant or spider assemblage variation should overlap with BA_{Abund} in explaining the abundances of these small arthropod responses. I extracted principle components (PCs) from ant and spider assemblages (using square-root transformed per-trap abundances for species captured on at least 3 islands) and used them in variation partitioning analyses to determine the percentage of $R^{2,\,\mathrm{BA}[...]}_{\mathrm{D,\,adj}}$ fractions that were also explained by ant or spider assemblage PCs. Retained PCs explained 75–88% of the variation in ant assemblages and 63–80% of the variation in spider assemblages. For each response group, I partitioned variation for the model (anole or best) that provided the greatest $R^{2,\,\mathrm{BA}[...]}_{\mathrm{D,\,adj}}$ magnitude. For small ant and small spider responses, PCs for the corresponding assemblage were derived using only the large species. To determine the important PCs for each response, I used them in stepwise variable selection procedure that added and removed variables from the model on the basis of AIC improvement. Consideration of the ant or spider species that loaded heavily on selected PCs allowed greater mechanistic insight to be gleaned.

For Collembola, these analyses supported the plausibility of both ant- and spider-mediated indirect effects, though the pathway with greater support differed between $\mathrm{GND}_{\mathrm{Xer}}$ and $\mathrm{GND}_{\mathrm{For}}$ (Table S2.7). However, when species-level associations are considered, the spider-mediated pathway appears to be the better of the two. Among spiders, collembolans were negatively associated (through PCs) with gnaphosid ($\mathrm{GND}_{\mathrm{Xer}}$, $\mathrm{GND}_{\mathrm{For}}$), lycosid ($\mathrm{GND}_{\mathrm{For}}$), salticid ($\mathrm{GND}_{\mathrm{For}}$), and theridiid ($\mathrm{GND}_{\mathrm{Xer}}$) species abundances, and positively associated with the abundance of a small oonopid ($\mathrm{GND}_{\mathrm{For}}$), which may itself be responding to reduced intraguild predation (see below); except for the theridiid and the oonopid, these spiders belonged to families that were negatively associated with $\mathrm{BA}_{\mathrm{Abund}}$ (see Spider assemblage analyses, below). Collembola are an important prey resource for many lycosids and other cursorial ground spiders (Nentwig 1986, Sanders and Platner 2007), and cursorial spider assemblages comprised in large part by lycosids have been shown to reduce collembolan abundances in several habitat types (Wise 2004, Sanders and Platner 2007, Sanders et al. 2011). Among ants, Collembola were positively associated with RIFA and negatively associated with large *Pheidole* in both GND_{Xer} and GND_{For}. Although data are not available to assess the extent or effects of *Pheidole* predation on collembolans, RIFA frequently prey heavily on them in open habitats (Wilson and Oliver 1969, Tennant and Porter 1991, Vogt et al. 2002a) and RIFA suppression can lead to positive collembolan responses (Wickings and Ruberson 2011; but see Tschinkel and King 2007 for the potential confounding effects of broadcasting ant bait for RIFA reduction). Fire ant predation of collembolans might therefore be expected to counteract any effects of reduced *Pheidole* predation, and thus spider-mediated effects appear to offer a better explanation for positive BA_{Abund}–collembolan associations. It is of course possible that predation by *Pheidole* and cursorial spiders worked in concert to produce the observed Collembola patterns, or that RIFA

Table S2.7 Percent explanatory overlap of ant and spider assemblage principle components for variation uniquely explained by BA_{Abund} in positive BA_{Abund}–response group associations. For each response, the model supplying the greatest $R^{2,\,\text{BA}[...]}_{\text{D, adj}}$ value was analyzed.

Response		Model	$R^{2,\,\text{BA}[...]}_{\text{D, adj}}$	Explanatory overlap (%) Ants	Spiders
GND_{Xer}	Collembola	Anole	0.526	72.2	40.8
	Diptera	Best	0.094	0.0	3.1
	Small ants	Anole	0.336	7.6	0.0
GND_{For}	Collembola	Best	0.391	28.3	78.1
	Small spiders	Anole	0.217	43.7	42.6

negatively impacted arthropods that prey heavily on Collembola but were not well represented in GND samples (e.g., *Strumigenys* ants; Hölldobler and Wilson 1990, Calixto et al. 2007), or even that unmeasured environmental factors generated the patterns (e.g., ground substrate characteristics or moisture levels; see Shultz et al. 2006).

Support for ant- and spider-mediated anole effects on small spiders in $\mathrm{GND}_{\mathrm{For}}$ was weaker, but equivalent between the two pathways. These spiders, comprised mostly of an oonopid (*Heteroonops spinimanus*) and several unidentified linyphiids, were negatively associated (through PCs) with *P. dentata*, RIFA, a salticid (*Anasaitis canosa*), and a gnaphosid (*Gnaphosa sp.*), all of which are likely to prey on small spiders to some extent. *Pheidole dentata* prey on a wide variety of invertebrates (Calabi and Traniello 1998 and references therein), and at least one Brazilian *Pheidole* species has been observed to associate negatively with several cursorial ground spiders in forest fragments (Haddad et al. 2011). RIFA frequently consume spiders, and although most studies of their impacts on ground arthropods fail to demonstrate significant negative effects on linyphiids, hunting spiders, or total spiders (e.g., Wickings and Ruberson 2011, Vogt et al. 2002b, Diaz 2003, Seagraves et al. 2004, Womack 2006, Rice 2007; but see Howard and Oliver 1978, Nichols and Sites 1989, Porter and Savignano 1990), this trend may be influenced by the use of toxic baits for RIFA suppression (see Tschinkel and King 2007). *Anasaitis canosa* appear to prefer ant prey, but they will also prey on a variety of insects (Jackson and van Olphen 1991) and may prey on smaller spiders, as do many other salticids (Nentwig 1986, Nyffeler 1999). Gnaphosid spiders prey on smaller spiders in laboratory settings (Wise and Chen 1999, Lensing and Wise 2004), and stable isotope studies suggest that they also do under natural conditions (Hladilek 2008, Mestre et al. 2013). Except for RIFA, all of these potential intraguild predators were negatively associated with BA_{Abund} and may have been involved in mediating positive, indirect effects of brown anoles on small ground spiders.

No support was provided by the explanatory overlap analyses for ant- or spider-mediated indirect effects on small ants or dipterans in GND_{Xer}. Given the importance of competition in structuring ant assemblages (Hölldobler and Wilson 1990) and the potential for RIFA impacts, the inability of large ant assemblages to co-explain variation in small ant abundances associated with BA_{Abund} is surprising. Small ants in GND_{Xer} were almost entirely (98%) *Brachymyrmex spp.*, which seem to be relatively unaffected by RIFA (Cook 2003, Morrison and Porter 2003, Calixto et al. 2007, Stuble et al. 2009) and may similarly be unaffected by other larger ant species like *P. morrisi*. In the absence of mechanistic evidence for indirect anole effects on small ants, the most plausible explanation for the association may be environmental differences existing between green and brown anole islands, perhaps related to substrate grain size. In contrast, the positive association between BA_{Abund} and dipteran abundances was most likely an artifact driven by an outlying data point; removal of this outlier eliminated the significance of the association in the Diptera and small Diptera best models. An artifactual nature for the association is also suggested by the number of explanatory variables in these best models—six, more than any other best model in the study (nearly all others had four or fewer)—together with the fact that BA_{Abund} did not significantly explain unique variation in best models restricted to have fewer variables.

Aerial arthropod analyses

Overview and methods

Community dissimilarity db-RDA analyses suggested that BA_{Abund} might be a significant predictor of AER_{Xer} dissimilarity patterns once environmental covariables were incorporated into the model. To assess this possibility, I repeated the db-RDA variation partitioning analyses using only BA_{Abund} and environmental covariables. BA_{Abund} was in fact able to significantly and uniquely explain in the full model a small fraction of the overall pattern in AER_{Xer} dissimilarities ($R_{adj}^{2,\,BA-Full} = 0.029$, $F^* = 2.02$, $P = 0.032$), but it remained excluded from the best model.

Given the significance of BA_{Abund} in the full dissimilarity model, I proceeded to analyze anole-associated differences in AER_{Xer} as described and performed for GND and FOL (see Methods). The results (Figures S2.8, Table S2.4) reinforced the general trends observed for GND and FOL, except for components of arthropod diversity, which were associated with BA_{Abund} only in AER_{Xer}.

Results and discussion

Curiously, $R_{adj}^{2,\,BA[...]}$ fractions were significant for all three models (i.e., anole, best, and full) when community dissimilarities were derived from relative abundances rather than actual abundances (Figure S2.8a). Magnitudes of AER_{Xer} $R_{adj}^{2,\,BA-Best}$ and $R_{adj}^{2,\,BA-Full}$ were similar to their counterparts among GND_{For} and FOL, but AER_{Xer} $R_{adj}^{2,\,BA}$ was lower, reflecting the importance of environmental suppressor variables for BA_{Abund} explanatory power in this community.

At the community level, BA_{Abund} was not significantly associated with the abundance (small, large, or total) or biomass of aerial arthropods, but it was associated with components of their diversity: both richness and evenness were best and positively explained by BA_{Abund}. These patterns were largely driven by Diptera, which on average comprised 71% of AER_{Xer} individuals. Effects of anoles on arthropod diversity have rarely been studied, with the exception of a well-established negative effect on web spider richness on Bahamian islands (e.g., Schoener and Spiller 1996, Spiller and Schoener 1998, Schoener et al. 2002), and positive effects on diversity have never been reported. Murakami and Hirao (2010) assessed the effects of anole presence on the species–area curves of aerially-active insects on Bahamian islands, and found anoles to be negatively associated with the richness of all insects, dipterans, hymenopterans, and beetles. Wright (2009) detected no effect of brown anoles on aerial arthropod richness in an enclosure study on Hawaii, but the length of the experiment—only 40 days, with arthropod samples taken midway through it—was probably too short for the relatively low densities of anoles to generate detectable effects, especially indirect ones. It is important to note that in the current study, richness refers to sample-based rarefied estimates of richness for a given number of individuals, not species density. BA_{Abund} was not associated with species density (Turnbough, unpubl. analyses), and given that there was a marginally significant, negative association between BA_{Abund} and total arthropod abundance (see below), the anole-associated pattern was one of fewer arthropod individuals distributed among equivalent species numbers in a more equitable manner. Such an effect could occur if anoles negatively affected the abundance of the dominant dipteran species, but had neutral or positive effects on the abundances of rarer aerial arthropods. Since most AER_{Xer} dipterans were small (92%, on average), direct predation by

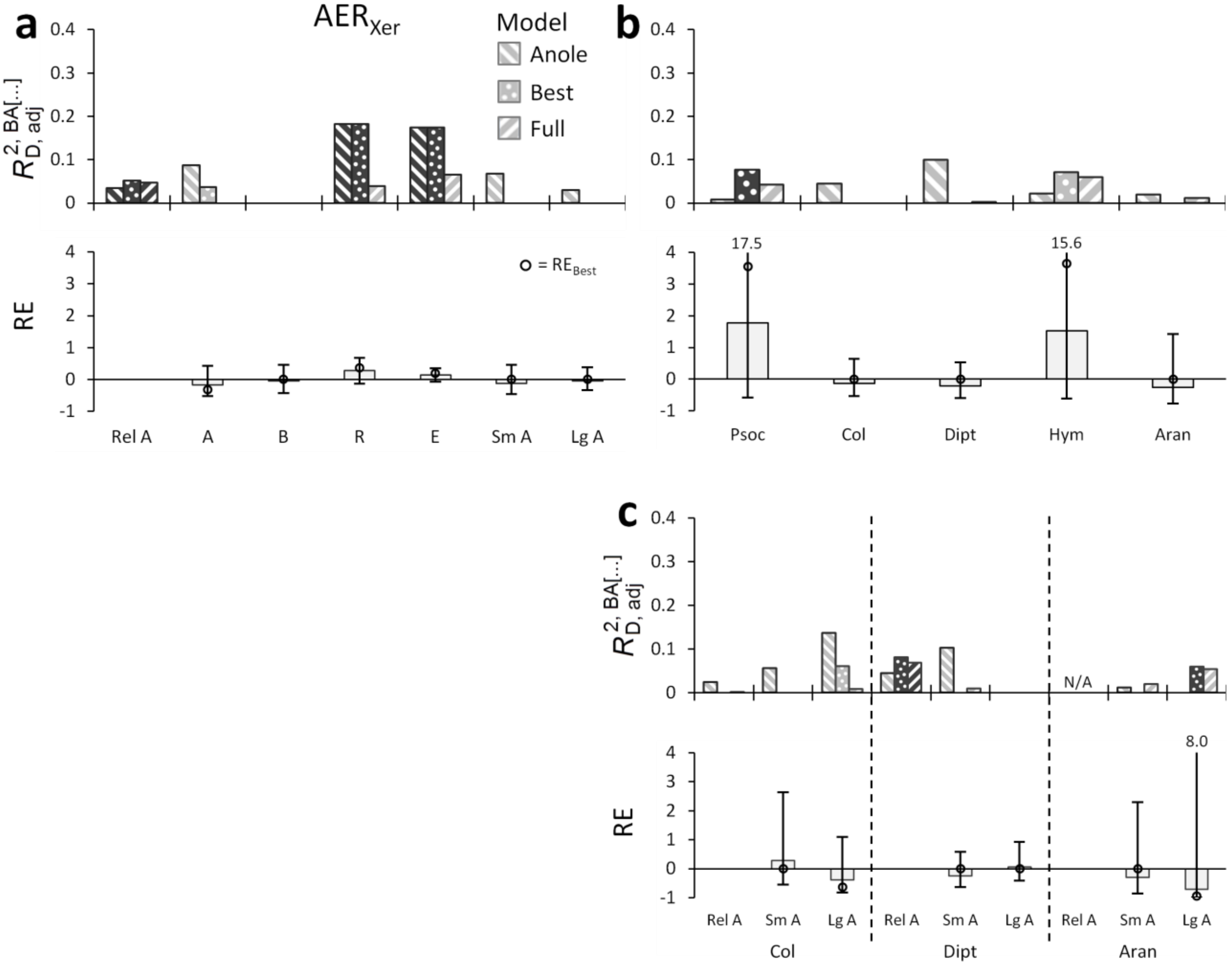

Figure S2.8 Uniquely explained variation fractions and modeled replacement effects (RE$_{Avg}$, RE$_{Best}$) for (a) AER$_{Xer}$ community-level attributes, (b) order abundances, and (c) assemblage-level attributes. Error bars denote 95% confidence intervals for RE$_{Avgs}$. Values exceeding figure scales are displayed. Significant $R^{2, BA[...]}_{D, adj}$ fractions are indicated by darker shading. Rel A = relative abundance, A = abundance, B = biomass, R = richness, E = evenness, Sm A = small species abundance, Lg A = large species abundance; Psoc = Psocoptera, Col = Coleoptera, Dipt = Diptera, Hym = non-ant Hymenoptera, Aran = Araneae; N/A = not analyzed.

brown anoles seems an unlikely mechanism for reducing their dominance. Explanations that invoke indirect effects, for example anole-induced changes in the composition of foliage spider assemblages that could somehow differentially impact the abundances of common versus rarer aerial arthropods, remain entirely speculative. Since BA_{Abund} could not explain diversity variation independently of all environmental covariables, it may be best to tentatively assume that the pattern was generated by environmental differences that were simply efficiently captured by BA_{Abund}.

The lack of significant associations with aerial arthropod abundance or biomass is at odds with the majority of relevant food web studies. Anoles are generally found to have positive effects on small aerial arthropod abundance or biomass (Schoener and Spiller 1999, Schoener et al. 2002), and negative effects on the abundance or biomass of large aerial arthropods (Dial and Roughgarden 1995, Spiller and Schoener 1988 cf. Schoener and Spiller 1999); interestingly, only one of these effects—never both—are found in the same study. When total aerial arthropod abundance or biomass are considered, anole effects can be positive (Pacala and Roughgarden 1984) or negative (Spiller and Schoener 1988, Dial and Roughgarden 1995), with the direction of the effect perhaps being influenced by the relative contribution of large arthropods to the totals or the degree to which web spiders were reduced by anoles. A lack of significant anole effects on total, small, or large aerial arthropod abundance or biomass has occurred in only two studies; in one of these (Spiller and Schoener 2001), anoles had marginally significant positive effects on small aerial arthropod abundance, and in the other (Spiller and Schoener 1994), anole effects on web spiders (the probable link mediating indirect effects to aerial arthropods) were relatively weak, probably due to low rainfall (Spiller and Schoener 1995). In the current study, the association between BA_{Abund} and total arthropod abundance was actually marginally significant and negative. The pattern was not driven by the contribution of large arthropods to the total abundance: most aerial arthropods were small (79%, on average), and BA_{Abund}'s nonsignificant association with their abundance was more strongly negative than was its nonsignificant association with large arthropod abundance. As negative associations with small aerial arthropods (primarily dipterans) are unlikely to be driven by anole predation, the pattern probably resulted from habitat differences that tended to exist between green and brown anole islands. For example, the greater scrubbiness of brown anole islands likely increased the risk of desiccation for small aerial arthropods, and may have driven down their abundance.

Although $R^{2,\,BA[...]}_{D,\,adj}$ magnitudes were relatively small for ordinal-level responses, BA_{Abund} was still significantly associated in some way with the majority of analyzed orders, and all orders were at least marginally associated with BA_{Abund} (Figure S2.8b, c, Table S2.5). For the majority of the orders, associations were dependent upon the incorporation of environmental covariables into the model. The relative weakness of these associations likely reflects both the small number of samples taken per island and relatively weak interaction strengths between anoles and aerial arthropods.

For Diptera, the dominant order in AER_{Xer}, patterns of association with BA_{Abund} were similar to, but slightly stronger than, the community-wide patterns. Dissimilarities in dipteran assemblage relative abundances were significantly explained by BA_{Abund} once environmental covariables entered the model. Total dipteran abundance was marginally associated with BA_{Abund} ($R^{2,\,BA}_{D,\,adj}$ = 0.100, D = 4.40, P = 0.060), but the pattern was entirely driven by a marginally significant negative association with small dipteran abundance ($R^{2,\,BA}_{D,\,adj}$ = 0.102, D = 4.64, P = 0.057). Negative anole effects on aerially-captured dipterans have been observed only for large dipteran abundance (Dial and Roughgarden 1995) and dipteran richness (Murakami and Hirao 2010); in other studies, total dipteran abundance and biomass in aerial communities have not been affected by anoles (Spiller and Schoener 1994, Schoener and Spiller 1999). As discussed above for total arthropod abundance, it seems unlikely that anoles were causally responsible for the observed associations with dipterans.

Associations with the remaining orders fit the pattern expected for anole effects: negative associations with orders comprised mostly of large species, and positive associations with orders comprised mostly of small species. It is important to bear in mind that with the exception of beetles, non-dipterans were poorly represented in $\mathrm{AER}_{\mathrm{Xer}}$ samples, and their associations with $\mathrm{BA}_{\mathrm{Abund}}$ should therefore be considered particularly tenuous.

Negative associations with large arthropod abundances were significant for spiders and marginally significant for beetles ($R^{2,\,\mathrm{BA}}_{\mathrm{D,\,adj}} = 0.137$, $D = 4.96$, $P = 0.055$). Model-averaged predictions for the effect of brown anole invasion on the abundances of these groups were reductions of 72% and 38%, respectively, but confidence intervals for these predictions were wide and broadly overlapped zero. Captured large spiders were primarily small, presumably ballooning individuals of large web spider species. Neither total web spider abundance nor the abundances of web-building spider families were negatively associated with $\mathrm{BA}_{\mathrm{Abund}}$ in any sampled community, and given the poor representation of this order in $\mathrm{AER}_{\mathrm{Xer}}$, it seems probable that the observed association was due simply to the vagaries of the small sample. By contrast, large beetles were fairly well represented in $\mathrm{AER}_{\mathrm{Xer}}$ samples and their marginally negative association with $\mathrm{BA}_{\mathrm{Abund}}$ matched significant negative associations with large beetles in $\mathrm{GND}_{\mathrm{Xer}}$ and FOL. Negative anole effects on large aerially-active beetles were observed in the only other study analyzing this response (Dial and Roughgarden 1995); in studies assessing the total abundance or biomass of aerially-active beetles (Spiller and Schoener 1994, Schoener and Spiller 1999), anoles had no detectable effect.

Positive associations with orders predominantly comprised of small species were significant for Psocoptera (92% small spp.) and marginally significant for non-ant Hymenoptera (64% small spp.; $R^{2,\text{ BA-Best}}_{\text{D, adj}} = 0.072$; $D = 6.25$, $P = 0.067$). RE_{Avg} predictions for psocid and hymenopteran abundances were increases of 177% and 153%, but again confidence intervals were wide and overlapped zero. The response of aerially-captured psocids to anoles has not been examined in previous food web studies, but Dial and Roughgarden (1995) found no significant anole effects on the abundances of large or small psocids in rainforest canopy foliage. Some evidence exists that anoles can positively affect the abundances of hymenopteran parasitoids on Bahamian islands (Schoener et al. 1995), but no further support for this effect or for an effect on hymenopteran biomass was detected in subsequent studies in this system (Spiller and Schoener 1994, Schoener et al. 2002). In Dial and Roughgarden's (1995) rainforest canopy experiment, anoles negatively affected the abundances of large aerially-active hymenopterans, but had no effect on small hymenopterans. The most obvious way that anoles could positively affect psocid and aerial hymenopteran abundances is by reducing the abundances of spiders that prey on them. However, BA_{Abund} was not associated with the abundances of FOL web spiders, which are likely to prey on flying psocids and hymenopterans, nor was it associated with the abundances of FOL cursorial spiders, which are more likely to prey on feeding or resting psocids. If the associations are anole-generated, they may result from alterations to the species composition of spider assemblages that happen to benefit psocids and non-ant hymenopterans. Another possibility, at least for psocids, is a release from ant predation, which could result from anole predation on, or exploitative competition with, foliage-foraging ants.

The associations observed between BA_{Abund} and AER_{Xer} arthropods should be considered tentative. Aerial arthropods were (seemingly) insufficiently sampled in this study, and therefore little confidence should be placed in the obtained results. Greater resolution of aerial arthropod differences in food webs dominated by green versus brown anoles awaits a better sampling of this community.

Spider assemblage analyses

Overview and methods

Anoles are consistently found to negatively impact web spiders, and brown anoles have been the focal species in most of the studies documenting these impacts (e.g., Spiller and Schoener 1988, Schoener and Spiller 1996). I therefore expected the increase in anole density that follows brown anole invasion of spoils islands to negatively impact, at the least, foliage web spiders.

To better characterize the relative effects of green and brown anoles on spider assemblages, I used Poisson and negative binomial GLMs (see Methods) to calculate $R^{2,\text{ BA[...]}}_{\text{D, adj}}$ and RE magnitudes for spider foraging guild and family abundances in ground and foliage assemblages. For guild assignment, spiders were characterized as either hunting or web-building following Uetz et al. (1999); families not treated in that study were assigned to a guild based on natural history information (e.g, Kaston 1978, Ubick et al. 2005).

Results

Spider family and foraging guild abundances were significantly associated with $\mathrm{BA}_{\mathrm{Abund}}$ in $\mathrm{GND}_{\mathrm{Xer}}$ and $\mathrm{GND}_{\mathrm{For}}$, but not FOL (Figure S2.9, Tables S2.1–3). With the exception of $\mathrm{GND}_{\mathrm{Xer}}$ Theridiidae, $\mathrm{BA}_{\mathrm{Abund}}$ significantly explained abundance variation in every analyzed family of ground spider assemblages.

Hunting spiders in $\mathrm{GND}_{\mathrm{Xer}}$ and $\mathrm{GND}_{\mathrm{For}}$ were predominantly negatively associated with $\mathrm{BA}_{\mathrm{Abund}}$. In $\mathrm{GND}_{\mathrm{Xer}}$, gnaphosid spiders were the largest component of the hunting guild (Table S2.8) and the only family with sufficient occurrences for analysis; their abundance was negatively associated with $\mathrm{BA}_{\mathrm{Abund}}$, and this pattern grew stronger when all other $\mathrm{GND}_{\mathrm{Xer}}$ hunting spiders (primarily Lycosidae and Salticidae) were included. In $\mathrm{GND}_{\mathrm{For}}$, lycosids were the largest component of the hunting guild, and their abundances were negatively, but weakly, associated with $\mathrm{BA}_{\mathrm{Abund}}$; gnaphosid and salticid abundances were more strongly negatively associated. Interestingly, though overall $R^{2,\,\mathrm{BA}[...]}_{\mathrm{D,\,adj}}$ fractions for $\mathrm{GND}_{\mathrm{For}}$ salticids were the highest of any response in the study, standard errors for $\mathrm{BA}_{\mathrm{Abund}}$ regression coefficients in salticid abundance models were large—likely due to the absence of salticids in $\mathrm{GND}_{\mathrm{For}}$ samples from all but one of the invaded islands—and confidence intervals for the strongly negative $\mathrm{RE}_{\mathrm{Avg}}$ overlapped zero. The abundance of a fourth $\mathrm{GND}_{\mathrm{For}}$ hunting spider family, Oonopidae, was positively associated with $\mathrm{BA}_{\mathrm{Abund}}$, which weakened the negative relationship between $\mathrm{BA}_{\mathrm{Abund}}$ and total $\mathrm{GND}_{\mathrm{For}}$ hunting spider abundance.

Web-building spider abundances were positively associated with $\mathrm{BA}_{\mathrm{Abund}}$ in $\mathrm{GND}_{\mathrm{For}}$, but no such association was present in $\mathrm{GND}_{\mathrm{Xer}}$. Linyphiids dominated the $\mathrm{GND}_{\mathrm{For}}$ web-building guild and were responsible for its association with BA_{Abund}; in GND_{Xer}, theridiids dominated the guild.

Among the spider families and guilds associated with BA_{Abund}, most $R^{2,\ \text{BA-Best}}_{\text{D, adj}}$ and several $R^{2,\ \text{BA-Full}}_{\text{D, adj}}$ fractions were significant. In the presence of all environmental covariables, BA_{Abund} remained a significant predictor of unique variation in the abundances of GND_{For} gnaphosids, salticids, linyphiids, and web spiders.

As was the case for arthropod orders, spider families with abundances negatively associated with BA_{Abund} were comprised primarily of large species, and positively-associated families were comprised primarily of small species (Figure S2.10).

Discussion

The lack of an association between BA_{Abund} and foliage-inhabiting web spider abundances was one of the more surprising outcomes of this study. The lack of association with FOL hunting spider abundances was surprising as well, given that brown anole populations frequently consume more hunting spiders than web spiders (Spiller and Schoener 1990a, Norval et al. 2007, Giery et al. 2013). It is very unlikely that these results are explained by a lack of interaction between anoles and the spider species involved, for several reasons. First, conspecifics or congeners of several collected web spider species, including the two most common (*Metepeira datona* and *Eustala sp.* [Araneidae], together comprising about 40% of FOL web spiders), are known to be both consumed and negatively impacted by brown anoles in the Bahamas (Spiller and Schoener 1988, 1990a, 1998, Schoener and Spiller 1995). Second, arboreal members of the second most frequently collected hunting spider family, Salticidae, are consumed by brown

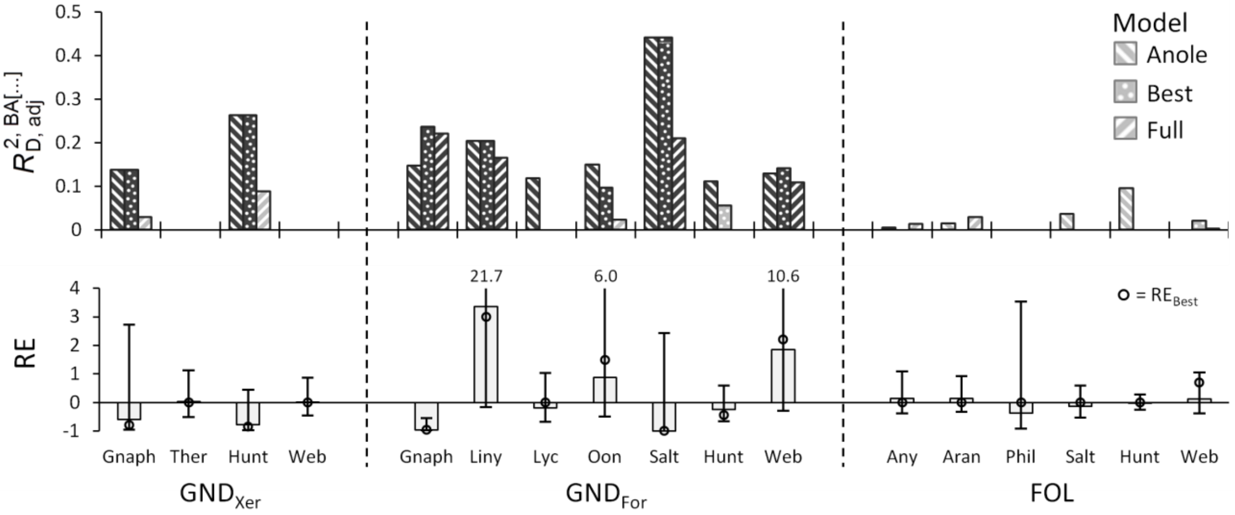

Figure S2.9 Uniquely explained variation fractions and modeled replacement effects (RE_{Avg}, RE_{Best}) for spider family and foraging guild abundances in GND_{Xer}, GND_{For}, and FOL. Any = Anyphaenidae, Aran = Araneidae, Gnaph = Gnaphosidae, Liny = Linyphiidae, Lyc = Lycosidae, Oon = Oonopidae, Phil = Philodromidae, Salt = Salticidae, Ther = Theridiidae; Hunt = hunting guild, Web = web-building guild; other figure details as in Figure 2.6.

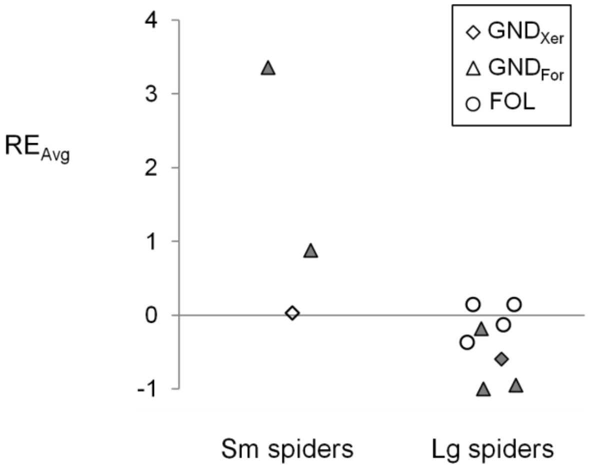

Figure S2.10 Model-averaged replacement effects (RE_{Avg}) for spider family abundances, grouped according to predominant species size. Families were plotted if > 80% of their comprising individuals were either small species or large species. Shaded symbols indicate that BA_{Abund} significantly explained unique variation in at least one model (anole, best, or full).

Table S2.8 Mean percent abundance and species richness for spider foraging guilds and families.

	Mean percent abundance[1]				Species richness				
Guild: Family	$\mathrm{GND}_{\mathrm{Xer}}$	$\mathrm{GND}_{\mathrm{For}}$	FOL	$\mathrm{AER}_{\mathrm{Xer}}$	$\mathrm{GND}_{\mathrm{Xer}}$	$\mathrm{GND}_{\mathrm{For}}$	FOL	$\mathrm{AER}_{\mathrm{Xer}}$	All
Hunting:	**56.8**	**84.2**	**56.5**	**11.5**	**10**	**26**	**10**	**3**	**42**
Anyphaenidae		0.4	26.1	7.7		1	1	2	2
Clubionidae		2.1				2			2
Corinnidae		2.5				1			1
Ctenidae	4.5				1				1
Gnaphosidae	18.0	9.8	0.4		2	5	1		6
Lycosidae	12.5	32.1			2	10			11
Mimetidae			2.0				1		1
Oonopidae	6.8	16.7			1	1			1
Philodromidae			4.4				1		1
Salticidae	13.6	13.2	22.6	3.8	2	2	4	1	9
Sparassidae	0.8	3.6			1	1			1
Thomisidae		2.1				1			1
Other	0.6	1.7	1.0		1	2	2		5
Web:	**43.1**	**15.9**	**43.5**	**88.5**	**8**	**12**	**26**	**8**	**42**
Araneidae	2.9	0.2	33.8	13.1	2	1	12	3	12
Dictynidae		3.6					1		1
Linyphiidae	6.4	10.9	0.8	15.4	3	9	2	2	14
Tetragnathidae			4.7	19.2			3	1	3
Theridiidae	33.8	1.0	3.7	40.8	3	1	6	2	9
Other		0.2	0.5			1	2		3
Total A, R[2]	**58**	**142**	**225**	**25**	**18**	**38**	**36**	**11**	**84**

[1] Mean of individual island percentages

[2] Total number of individuals (A) and species (R) pooled across islands

anoles in Florida (Giery et al. 2013) and presumably negatively impacted by them in Taiwan (Huang et al. 2008b; ground and foliage samples were apparently combined in this study). Finally, $\mathrm{BA}_{\mathrm{Abund}}$ significantly explained FOL spider assemblage dissimilarity patterns (Figure 2.7), which suggests the existence of species-level associations not evident in the feeding guild- and family-level results.

The best explanation for these unexpected results appears to be that green anoles are more efficient predators of foliage spiders than are brown anoles, so that the effects of increased anole density following brown anole invasion are offset by the weaker per-capita interaction strengths between brown anoles and foliage spiders. Most FOL spiders were relatively inconspicuous species that probably would not be highly visible to anoles unless they were perched in the spider's immediate vicinity. With the exception of *M. datona*, most FOL web spiders were nocturnal species that generally spend the day hidden in vegetation at the edge of the web; *M. datona* reside in a debris-encased retreat constructed within a barrier web, though they will emerge diurnally to feed (e.g. Spiller and Schoener 1990a). Among the hunting spiders, the sole anyphaenid (*Hibana sp.*) remains diurnally hidden within a silken retreat in leaves, and both the sole philodromid (*Philodromus sp.*) and dominant salticid (*Hentzia palmarum*) appear to forage, in this system, predominantly on palm leaves. Because green anoles perch and actively forage on leaves and thin branches more frequently than do brown anoles (Schoener 1968, 1975, Mattingly and Jayne 2004, Turnbough unpubl. study), they are probably more likely to encounter spiders resting or foraging in the vegetation and observe those subduing prey. Furthermore, green anoles possess larger toepads with more lamellae than do brown anoles (Collette 1961, Lister 1976b), and the greater clinging ability this gives them (Irschick et al. 1996) presumably increases their maneuverability on foliage and may enable them to more effectively launch attacks on detected spiders. It is important to note here that the overall effects of brown anole invasion might be greater for foliage spider assemblies located closer to the ground (FOL sample heights were 1–2 m) or dominated by larger and more conspicuous species (e.g., *Argiope spp.*).

Contrasting species-level associations within spider families lend some support to the hypothesis that differential interaction strengths contributed to the lack of association at the guild and family levels. Of the two most frequently captured araneid web spiders, *M. datona* abundance was positively associated with $\mathrm{BA}_{\mathrm{Abund}}$ (Turnbough, unpubl. analyses: $\mathrm{RE}_{\mathrm{Avg}} = 1.65$

[−0.96 to 164]; $R^{2,\,\mathrm{BA}}_{\mathrm{D,\,adj}}$ = 0.287, D = 16.96, P = 0.006) and *Eustala sp.* abundance was marginally, negatively associated ($\mathrm{RE}_{\mathrm{Avg}}$ = −0.31 [−0.78 to 1.14], $\mathrm{RE}_{\mathrm{Best}}$ = −0.55; $R^{2,\,\mathrm{BA-Best}}_{\mathrm{D,\,adj}}$ = 0.042, D = 3.30, P = 0.094). The more negative direction of association with *Eustala sp.* may reflect the facts that juveniles of this species build webs lower in the vegetation and, in contrast to adults, diurnally occupy them; both of these factors probably increase their exposure to brown anole predation. On small Bahamian islands, the inclusion of diurnally unoccupied *E. cazieri* webs reduced the strength of this species' negative association with lizards—nearly all of which were brown anoles (Toft and Schoener 1983). The positive association between *M. datona* and $\mathrm{BA}_{\mathrm{Abund}}$ may indicate that green anoles are particularly more efficient at capturing this species, but since $\mathrm{BA}_{\mathrm{Abund}}$ was not in the best *M. datona* model (in contrast to *Eustala sp.*), it is safer to assume that environmental factors were responsible for the observed association. Among the salticids, the only other analyzed FOL spider family comprised of more than one species, the dominant species (*H. palmarum*, 72% of salticids) was not associated with $\mathrm{BA}_{\mathrm{Abund}}$ but the second most abundant species, *Phiddipus regius* (23% of salticids), was negatively associated (Turnbough, unpubl. analyses: $\mathrm{RE}_{\mathrm{Avg}}$ = −0.67 [−0.97 to 2.94], $\mathrm{RE}_{\mathrm{Best}}$ = −0.84; $R^{2,\,\mathrm{BA-Best}}_{\mathrm{D,\,adj}}$ = 0.145, D = 4.86, P = 0.022). Of the two species, *P. regius* are almost certainly more exposed to brown anole predation due to their much larger size (up to 22 mm [Edwards 1981]), bold coloration, and greater tendency to forage lower to the ground on palm "trunks" and other vegetation (Turnbough, unpubl. obs.). In addition, green anoles are less likely than brown anoles to attack adult and subadult *P. regius*, seemingly because this species' impressive antipredator display—involving facing the threat, raising the stout front legs in a threatening manner, and clearly displaying large, iridescent chelicerae—is more effective against the more cautious green anoles (Turnbough, unpubl. study; see also Chapter 3).

If the differential interaction strength hypothesis correctly explains the similarities in foliage spider assemblages on green and brown anole islands, why did not a similar balancing of effects occur for the for the FOL arthropod taxa that were negatively associated with BA_{Abund}? No single mechanism that can explain all the differences is readily apparent, and a variety of factors may be involved. Arthropods in several of the negatively associated taxa (Diptera, Coleoptera, and Hemiptera) use flight with varying degrees of frequency to move about the habitat, which may increase their visibility to, and probability of capture by, brown anoles, especially should they alight near one. Except for the salticids, diurnal movements among FOL spiders were probably infrequent, small, and restricted to the foliage. Arthropods that travel along larger branches to reach outer branches and leaves, for example ants, are probably also more likely to be consumed by brown anoles than spiders remaining in the foliage (though FOL ant workers seem relatively unlikely to serve as brown anole prey, as discussed above). Another potential factor is differing plant species associations. The large, broad leaves of cabbage palms better obscure arthropods from predators perched some distance away than do the small, scaly leaves of southern redcedars, the other dominant plant in spoils island vegetation. Most FOL spiders appeared to be associated with palms or palmettos, and may thus have been better protected from brown anole predation than arthropods frequently found in both palm and cedar foliage (e.g., *Cycloptilum* crickets) and arthropods primarily occupying cedar foliage.

In stark contrast to foliage spider assemblage patterns, BA_{Abund} was associated with the abundances of nearly all analyzed ground spider guilds and families. Anole impacts on ground spiders remain relatively unexplored, and the scope of the observed associations is unprecedented, though perhaps not surprising. Brown anoles perch near and on the ground far more frequently than do green anoles (Schoener 1968, 1975, Lister 1976a), and therefore their per-capita interaction rates with ground spiders are likely much higher. Stronger per-capita effects on ground spiders would only be compounded by the greater densities of brown anoles.

The negative associations observed between BA_{Abund} and GND hunting spiders are well explained as direct effects of anole predation. Hunting spiders comprise a large percentage—often the majority—of spiders identified in brown anole gut contents (Spiller and Schoener 1990a, Norval et al. 2007, Huang et al. 2008b, Giery et al. 2013), and in each of these studies the three most frequently consumed hunting spider families were the same as those negatively associated with BA_{Abund} in the current study—Gnaphosidae, Lycosidae, and Salticidae. Spiders in these families were primarily (81–100%) large species and therefore relatively likely to serve as brown anole prey, a probability supported by the fact that the only GND hunting spider family not negatively associated with BA_{Abund} was composed of a single small species (Oonopidae: *Heteroonops spinimanus*). The strongest of the these associations, and indeed in the entire study, was the negative association with Salticidae, which happens to be (1) the most diurnally active spider family in the study system, (2) the most abundant spider family in brown anole gut contents reported from Florida and the Bahamas (Spiller and Schoener 1990a, Giery et al. 2013), and (3) the only hunting spider family yet shown to be negatively impacted by brown anoles (Huang et al. 2008b) or other anole species (Dial 1992). Most GND_{For} salticids (80%) were *Anasaitis canosa*, a species that is particularly visible due to its frequent waving of pedipalps marked with a bright white patch. By contrast, the gnaphosids and lycosids appeared to be primarily nocturnal, which may explain the relatively weak evidence for anole effects on Lycosidae. A similar difference in family-level effects has been reported from Taiwan, where brown anoles reduced the abundance and richness of salticids but not lycosids (Huang 2007, Huang et al. 2008b). The comparatively strong evidence for large anole effects on spoils island gnaphosids is, however, difficult to reconcile with the lack of such evidence for lycosids. No general feature of gnaphosid behavior would appear to increase their risk of anole predation relative to lycosids, and the mechanism responsible for this pattern of results, if it is anole-driven, may depend on the behavioral ecologies of the particular species involved. Factors promoting anole predation of nocturnally active arthropods are unexplored and worthy of study.

The positive associations between BA_{Abund} and the abundances of GND_{For} linyphiids and oonopids may have resulted from a reduction in intraguild predation. Because both families were comprised only of small species, they probably rarely served as anole prey and could therefore benefit from anole-driven declines in other predators. Given the prevalence of other (usually smaller) spiders in the diets of cursorial hunting spiders (Nentwig 1986, Wise 1993, Nyffeler et al. 1994), the lower abundance of large hunting spiders on brown anole islands seems to offer the best explanation for higher linyphiid and oonopid abundances. In a *Spartina* marsh system, for example, the presence or increased abundance of a lycosid reduced, through predation, the abundance of a smaller linyphiid spider (Denno et al. 2004). Reduced competition for shared prey could also allow small spiders to benefit from a reduction in the densities of larger spiders, but exploitative competitive for prey does not appear to play a large role in structuring spider assemblages (Wise 1993). Another possibility is that BA_{Abund}-associated differences in GND_{For} ant assemblages, in particular the lower abundances of large *Pheidole,* released small linyphiids and oonopids from predation or competition with ants. Indeed, in explanatory overlap analyses there was equivalent support for the ant- and spider-mediated pathways for indirect anole effects on small spider abundance in GND_{For} (see Ground arthropod associations: potential mechanisms). Anole effects on linyphiid spiders have been assessed once before: Huang et al. (2008b) detected no effect of invading brown anoles on the abundance of (pooled) ground- and foliage-inhabiting linyphiids in a Taiwanese palm plantation, despite the fact that linyphiids represented the largest fraction (36%) of identified spiders in brown anole stomach contents in this system and nearby areas (Norval et al. 2007). The prevalence of linyphiids in Taiwanese brown anole diets probably reflects their dominance in the local spider assemblages (~30% of sampled spiders [Huang et al. 2008b], about 3x greater than in $\mathrm{GND_{For}}$) and may have been influenced by the size or web placement of the species consumed, which were not reported. Brown anole densities were somewhat low in Huang et al.'s study (0.22 lizards/m^2 compared to an estimated median of 0.42 lizards/m^2 among brown anole spoils islands), and as they suggest, the numbers of linyphiids consumed by brown anoles may have been too small to significantly impact the densities of such an abundant spider family.

Spiders in the only analyzed GND family not associated with $\mathrm{BA_{Abund}}$, Theridiidae, were mostly (77%) small species that probably infrequently served as brown anole prey. Similarly, infrequent predation probably explains the absence of anole effects on cryptically-colored theridiid spiders in rainforest canopy foliage (Dial 1992). Although brown anoles are known to negatively affect the abundance of the theridiid *Latrodectus mactans* in the Bahamas (Spiller and Schoener 1988, 1998), this interaction is likely facilitated by the large size (9–10 mm for adult females) of this species and its lack of cryptic coloration (especially in juveniles).

Spider assemblages on spoils islands are in need of further study. Most of the large and conspicuous web spiders commonly observed on the islands were absent or rare in sweep net samples (e.g., *Nephila clavipes, Gasteracantha cancriformis, Leucauge spp., Argiope aurantia*, and *Cyclosa sp.*), and further, the total numbers of spiders captured from ground and foliage communities were low enough that abundance analyses for several relatively common families were either based off of sparse data (i.e., zero counts for many islands) or not conducted due to insufficient occurrences. The role of intraguild predation in modulating the effects of multiple predators on shared prey is an active area of research (Janssen et al. 2007, Vance-Chalcraft et al. 2007); given the typical strength of anole–spider interactions and their potential to influence downstream food web elements (e.g., Spiller and Schoener 1990b, Schoener and Spiller 1999), the relative effects of green and brown anoles on spider assemblages are worthy of more focused study.

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CHAPTER 3:

FUNCTIONAL SIMILARITY IN THE PER-CAPITA EFFECTS OF NATIVE AND INVASIVE *ANOLIS* LIZARDS ON ARTHROPOD PREY

ABSTRACT

When invasive species displace an ecologically similar resident species, the wider impacts of invasion will depend in part upon the degree to which the invading and displaced species differ in their per-capita or per-biomass effects in the invaded system. The functional similarity of invading and displaced predators, and the trait differences that affect it, have seldom been studied for closely related (e.g., congeneric) species, and data for terrestrial vertebrates are particularly rare. I erected enclosures around small cabbage palms (*Sabal palmetto*) in Florida to assess whether differences in the perching and foraging behavior of native green anoles (*Anolis carolinensis*) and invading brown anoles (*Anolis sagrei*) cause these lizards to differ in their per-capita effects on arthropod prey species. In each of six separate experiments, I introduced a single adult male green anole or brown anole into treatment enclosures that had been cleared of all arthropods and stocked with a single prey taxon. Despite their differential use of canopy and below-canopy microhabitats, green anoles and brown anoles had similar per-capita effects on the six individually-tested and autecologically diverse focal prey taxa—planthoppers, scaly crickets, grasshoppers, anyphaenid spiders, jumping spiders, and orb web spiders. These results suggest that green and brown anoles foraging in spatially proximate locations will have similar interaction rates with prey species in their nearby vicinity, and thus that the net impacts of brown anole invasion and green anole displacement will be largely dependent upon differences in the population density and larger-scale vertical habitat use of these two species. More generally, these results suggest that it may be difficult, at least for some groups, to accurately predict the

relative importance of particular trait differences for the functional similarity of closely-related and ecologically-similar species.

INTRODUCTION

Invasive species impacts on local communities are a function of both their abundance (density or biomass) and per-capita or per-biomass effects (Parker et al. 1999). It therefore follows that when invading species displace an ecologically similar resident species (e.g., Race 1982, Porter et al. 1988, Gurnell et al. 2004), further impacts (beyond the initial displacement) will depend upon the degree to which the invading and displaced species differ in their abundance and per-capita effects in the invaded system. Though the total impacts of invader–resident displacements are justifiably of greatest concern in many conservation and invasive species management applications, there are good reasons to evaluate the contribution of differential per-capita effects. For instance, differences in invading and displaced species abundances may vary through time or across space (e.g., Lohrer and Whitlatch 2002), and knowledge of the species' relative per-capita effects permits invasion impact predictions to be made for such varying contexts. Further, understanding whether and how invading and displaced species differentially function in invaded communities can benefit invasion biology and other ecological subdisciplines in a variety of ways, for example by informing the search for species traits that confer greater invasion success rates or impacts (e.g., Kolar and Lodge 2001, Vilà et al. 2015) or by illuminating the relationship between trait similarities and functional equivalence (e.g., Chalcraft and Resetarits 2003a). For displacements involving predators, differential interactions with prey are probably most often the primary mechanism responsible for further impacts in the invaded system.

Although the per-capita effects of different predator species on shared prey have been assessed in a variety of systems, few studies have involved closely related (confamilial or congeneric) predators and even fewer have involved terrestrial vertebrates. These gaps in the current literature are significant for at least two reasons. First, invasive species often displace confamilial or congeneric residents (e.g., Case et al. 1994, Larson and Magoulick 2009, Santulli et al. 2014; see also Reitz and Trumble 2002), and though differences in the per-capita effects of ecologically similar predators seem likely to be, in general, inversely related to phylogenetic affinity (but see Chalcraft and Resetarits 2003a, Losos 2008, Best et al. 2013), studies are needed to identify the types of differential effects that commonly occur among closely related predators as well as the trait differences that cause them. Second, insights or generalities derived from the current literature may have limited applicability to displacements involving terrestrial vertebrate predators. Most studies comparing the relative effects of predator species have been in aquatic systems (e.g., Morin 1995, Resetarits and Chalcraft 2007, Griffen and Byers 2009), which differ fundamentally from terrestrial systems in food web structure and dynamics (Strong 1992, Polis and Strong 1996, Shurin et al. 2006), and the vast majority of terrestrial predator comparisons have involved invertebrates (e.g., Riechert and Lawrence 1997, Schmitz and Suttle 2001, Fagan et al. 2002), which likely function differently than vertebrates in food webs due to their great differences in size and phylogenetically-linked biological traits (Woodward et al. 2005, Brose et al. 2006, Bersier and Kehrli 2008). The relative effects of ecologically similar terrestrial vertebrates are clearly in need of additional study.

Displacements of native green anole lizards (*Anolis carolinensis*, Polychrotidae) by invading brown anoles (*Anolis sagrei*) in the southeastern U.S. offer an opportunity to assess both the potential mechanisms of impact in a particular invasion and the relative per-capita effects of closely-related vertebrate predators in a terrestrial system. Brown anoles from Cuba and the Bahamas were introduced onto mainland Florida beginning in the 1940s, and since that time the species has spread throughout peninsular Florida and into several surrounding states (Oliver 1950, Lee 1985, King et al. 1987, Thomas et al. 1990, Echternacht et al. 1995, Kolbe et al. 2004, Turnbough 2006). Anecdotal, observational, and experimental evidence together indicate that brown anoles displace green anoles from the near-ground portions of structurally complex or densely vegetated habitats and from the near entirety of structurally simple or open habitats (Figure 3.1; Christman 1980, Crews 1980, Echternacht 1999, Vincent 2002, Campbell 2000, Edwards and Lailvaux 2012, Stuart et al. 2014). In complex habitats, at least, brown anole invasion appears to establish the structural niche partitioning that occurs between brown anoles and green anole analogs in Cuba and the Bahamas (Schoener 1975, Rodríguez Schettino et al. 2010).

Though green anoles and brown anoles are ecologically similar and likely consume the same prey species, differences in their perching and foraging behavior may cause them to differentially interact with these prey. Both species are relatively small, diurnal, territorial, sexually dimorphic, generalist insectivores that perch at similar heights in the vegetation (when the other species is absent or rare; Edwards and Lailvaux 2012, Stuart et al. 2014) and overlap greatly in diet when syntopic, at least at a coarse (predominantly ordinal-level) taxonomic scale (Campbell 2000). However, green anoles and brown anoles belong to different ecomorph classes—groups of species that utilize microhabitats in similar ways and exhibit correlated morphological and behavioral attributes (Williams 1972, Losos 2009)—and vary in perching and foraging behavior accordingly. As trunk–ground anoles, brown anoles more frequently perch on or near the ground than do trunk–crown green anoles and their closely-related Caribbean analogs, which perch more frequently on leaves and thin branches in the vegetation than do brown anoles (Schoener 1968, 1975, Lister 1976, Stuart et al. 2014). These perch use differences may cause brown anole per-capita interaction rates to be, relative to green anoles, higher for ground-active prey and lower for foliage-active prey. Further, trunk–ground and trunk–crown anoles differ in movement behavior (which encompasses but is not restricted to foraging behavior) in ways that correspond to differences in the habitat visibility profiles of perches in their preferred microhabitats (Moermond 1979): brown anoles tend to perch in more open microhabitats and move less frequently than do green anoles and their closely-related analogs, which tend to perch in more foliage-cluttered microhabitats and exhibit a more active foraging mode (Jenssen et al. 1995, Mattingly and Jayne 2004, Johnson et al. 2008). As a result, green anoles may be more likely to detect hidden or cryptic prey (Huey and Pianka 1981).

In Florida, arthropod communities on islands invaded and dominated by brown anoles differ substantially from those on islands still dominated by green anoles (Chapter 2), but the extent to which anole behavioral differences contribute to these island faunal differences is unknown. Though brown anoles are similar in adult size to the green anoles they displace on these islands, they have a more robust body shape (weighing about 1.5 times more than green anoles of equal SVL) and also attain higher densities, so that total anole density and biomass are likely to be, respectively, about 3 times and 4–5 times greater on fully invaded islands than on uninvaded islands (Campbell 2000). These differences in anole abundance are sufficient to explain most of the observed anole-associated differences in island arthropod communities (Chapter 2). However, at least one important finding—the absence of an expected association between invasion status and the abundance of large foliage-dwelling spiders, in contrast to relatively strong associations with large ground spider abundances—suggests that green and brown anole behavioral differences may also play an important role in determining the pattern of invasion impacts.

To investigate the role of anole behavior in modulating effects on prey, I assessed the effects of individual green and brown anoles on single arthropod prey taxa in enclosures containing small cabbage palms (*Sabal palmetto*). I selected cabbage palms as a habitat substrate for experiments because (1) isolated cabbage palms are a ubiquitous and frequently anole-occupied feature of many natural and disturbed Florida habitats (e.g., Gilman and Irschick 2013); (2) the canopy arthropod faunas of small, isolated cabbage palms on islands dominated by green versus brown anoles differ in ways that reflect differences observed for island foliage arthropod communities (Turnbough, unpubl. study); and (3) differences in green and brown anole perch behavior are particularly evident on small cabbage palms, with green anoles most frequently perching in the canopy and brown anoles most frequently perching below the canopy on the intact petioles or broken-off spurs of dead fronds. Given these differences in perch use and associated differences in anole foraging behavior, I hypothesized that brown anoles would have, relative to green anoles, weaker per-capita effects on canopy-active prey species and stronger per-capita effects on ground-active prey species.

METHODS

Study system and field enclosures

This study was conducted in an abandoned citrus orchard within Merritt Island National Wildlife Refuge, Brevard County, Florida. The site (28°45.16'N, 80°46.16'W) had been periodically burned to maintain open scrub habitat on a soil substrate comprised primarily of fine sand.

Small, isolated cabbage palms were abundantly distributed throughout the site, and I selected 18 with similar dimensions for experimental enclosures. Maximum canopy heights (i.e., the upper tips of the highest fronds) averaged approximately 224 cm (SD = 18.5 cm) and "trunk" or bole heights—the distance from the ground to the base of the rosette of unexpanded leaves—averaged approximately 44 cm (SD = 9.6 cm). Vegetation surrounding palms was cleared except for sparse, isolated grasses and forbs of small stature (~ 10–20 cm in height), and this condition was maintained throughout the study. During the preparation of palm sites for enclosures, at least one green anole was removed from 13 (72%) of the experimental palms (overall sex ratio = 1:1) and one female brown anole was removed from an additional palm (brown anoles were still rare at the field site at the time of this study).

Cube-shaped enclosures were erected over the 18 experimental palms in May 2008 (Figure 3.2). Handmade nets constructed from a fine nylon mesh were suspended from anchored PVC frames to a height approximately 20–30 cm above maximum canopy height; net bottoms were anchored by burial in the sandy ground. Enclosure frames measured 2.21 m on each side, but the nets extended a short distance (up to approximately 40 cm at ground level) beyond the framed area on each side to facilitate investigator movement within enclosures. Nets had a hook-and-loop-secured slit to allow investigator entry. A 0.6 m-high chickenwire fence was installed around each enclosure to prevent damage from armadillos and other small mammals. Enclosed palms were trimmed as necessary to have 9 expanded live fronds and 3 dead fronds, and this condition was maintained throughout the study.

Arthropods were removed from enclosures over a several day period in June 2008. Canopy arthropods were removed with a handheld vacuum aspirator, followed by careful inspection and hand removal of remaining arthropods; an insecticidal soap spray (Garden Safe®, Schultz Co.) was afterwards applied to kill unseen canopy arthropods, followed by a water rinse to remove soap residues. An aerosol insecticide (Raid®, S.C. Johnson & Son, Inc.) was sprayed into the deep crevices surrounding palm trunk boles to eliminate inaccessible arthropods residing within them. To eliminate ant colonies, ant bait (Amdro®, Central Garden & Pet Co.) was sprinkled on the ground within and around enclosures. A residue-active insecticidal spray (Home Pest Control Insect Killer, Bayer CropScience LP) was occasionally applied to the ground around enclosures to prevent the approach of arthropods that might chew through the net or distract anoles by climbing on exterior net surfaces.

Non-focal arthropods and other animals were removed whenever they were observed throughout the study. In the course of experimental activities, enclosures were repeatedly carefully searched—often multiple times per week and during both day and night—, and 1–3 non-focal arthropods were typically discovered and removed in each search of each enclosure. In most cases these arthropods likely emerged from the ground or palm trunk crevices, but some may have entered through small insect chewing holes that were occasionally found (and subsequently fixed) in the nets. Spadefoot toads (*Scaphiosus holbrookii*) also emerged into enclosures in late June. Most toads emerged and were removed between the first and second experiments, but toads were discovered in three enclosures midway through the second experiment; excluding those enclosures from the second experiment analyses did not qualitatively change the results.

Experimental design

Six experiments with a common design were conducted from June to August 2008 (Table 3.1). By experimental Day 1, a given number of a single prey taxon had been stocked into each enclosure. On the morning of Day 2, a single male green anole, male brown anole, or no anole was introduced into the enclosures (n = 6 for each treatment). Behavioral data for experimental anoles were collected at least once during Days 3-6, and anoles and remaining arthropods were removed from enclosures on Day 7, beginning around 1100–1200 h with the anoles. Palms were also checked on subsequent days for arthropods missed on Day 7, frequently at night as well as during the day. Insecticidal soap sprays (followed by water rinses) were used to aid the removal of scaly crickets and anyphaenid spiders, which were difficult to capture by hand. Due to a scheduling restraint, anoles and arthropods were removed on Day 8 in the jumping spider experiment. Treatment assignments were randomized for each experiment.

Arthropod taxa used for experiments were selected to represent diversity in microhabitat use and diurnal behavior (Table 3.1). Prey taxa were collected by hand or sweep net (for grasshoppers) from the study area or nearby localities, and collection efforts generally took 2-3 days. Except for planthoppers, herbivores were added to the enclosures on a daily basis until the required numbers were attained; predators remained in vials until the total numbers needed were captured, and then were released at a single time into enclosures. Arthropods were released at multiple ground (grasshoppers) or palm canopy (all other taxa) locations. Size distributions of inserted arthropods were equivalent among enclosures.

As an exception to the above procedure, planthoppers were added to enclosures three days prior to experimental Day 1 and thereafter counted daily to assess the effectiveness of predatory arthropod removals. Additional planthoppers were added as necessary in these pre-experiment days and on Day 1 to maintain target stocking levels of 36 individuals. Due to planthoppers missed in the Day 1 counts, actual numbers of planthoppers present in enclosures were higher than 36 for at least two enclosures, from which 37 planthoppers were recovered.

Such departures from target levels were unlikely to be substantial or biased by treatment, and therefore were unlikely to have materially affected experimental results. Stocking numbers were considered to be 37 for planthopper analyses.

Adult male green anoles and brown anoles were captured from nearby localities and housed individually until their use in experiments. Green anole capture sites were flagged to facilitate post-experiment repatriation to territories and to prevent recapture for use in later experiments. Housing cages measured 34 x 20 x 14 cm or 51 x 23 x 53 cm (length x width x height) and were kept in a large, shaded, screened-in porch. Each cage had a screened top with a basking light (40 watt, daylight spectrum incandescent bulb) over one end, a wooden dowel for perching, and artificial foliage for a retreat site; the larger cages also had a screened front and additional lighting from fluorescent plant light bulbs. Lizards were misted daily and fed crickets *ad libitum*. Crickets were withheld from anoles for two days prior to their introduction into field enclosures in order to ensure empty stomachs and motivation to forage at the start of the experiment (Windell and Sarokon 1976, Jenkins 1980). Anoles were weighed to the nearest 0.1 g at capture, at insertion into enclosures, and at removal from enclosures; in general, anoles gained weight between the day of their capture and the day they were placed into enclosures (despite their two-day starved state at enclosure insertion).

For each experiment, anoles were size matched by snout-vent-length (SVL) so that differences across individuals of both species were usually within 1-2 mm, and never more than 3 mm. Minimum and maximum SVLs across all experiments were 56 mm and 60 mm, respectively. After their use in experiments, green anoles were returned to captive housing for feeding and later release back to their point of capture. Brown anoles were euthanized at the end of experiments.

Anoles not being used in the current experiment were used in feeding trials to verify focal arthropod edibility and, for some arthropods, to determine maximum per-capita consumption rates. As with experimental anoles, crickets were withheld from feeding-trial anoles two days prior to the trials. For maximum consumption estimates, focal prey were fed to anoles *ad libitum* for the same number of days (5) that anoles remained in enclosures.

Behavioral observations

Perch height and type data were collected for all anoles in each experiment. Observations were conducted between 0730 and 1200 h by three observers. For each observation, an observer slowly approached the enclosure and attempted to sight the anole through binoculars at a distance of approximately 10 m. If the anole could not be found, the observer slowly spiraled around and closer to the enclosure, to the extent permitted by the surrounding habitat matrix, until the anole was spotted or the enclosure reached. Perch height class (0, 0-25, 25-50, 50-75, …, 175-200, > 200 cm) and perch type (green/live leaf, green/live petiole, dead leaf, dead petiole, central unexpanded leaves, ground, or net) were recorded for each observed anole. To facilitate perch height determination, each of the four upright enclosure poles was marked at 25 cm intervals. Anoles were typically observed more than once by different observers on a given observation day.

Movement frequency and distance data were also collected between 0730 and 1100 in four of the six experiments. Enclosures were approached as described above, except that observers approached no closer than 5 m for anoles that could not be immediately sighted, and once such an anole was spotted, the observer withdrew to a distance of 10 m if possible. Sighted anoles were continuously monitored through binoculars for 10-minute or 20-minute observation sessions that were divided, respectively, into two or four 5-minute periods. For anoles that could not be found upon approach to 5 m, the clock was started while the observer continued to search for the anole at that distance; in such instances, total observation time was reduced by the amount of time it took to locate the anole. Perch height and type data were collected at the beginning and end of each period, and within each period, the number and distances of all movements were recorded. Movements were defined as changes in position of a body length (SVL) or more, which prevented simple changes in survey posture from counting as moves. A movement bout was determined to have ended when the anole remained in the same location for three seconds or longer. The distance of each movement bout along the path travelled by the anole (i.e., not Euclidean distance) was estimated to the nearest 10 cm. When a movement resulted in the anole moving out of sight, a frequent occurrence among green anoles, movement distance was estimated to the point at which sight contact was lost. Observers changed positions and approached enclosures (to within 5 m) as necessary to try and reestablish sight contact with out-of-sight anoles. Time spent out of sight was recorded for each observation period.

Five parameters of interest were extracted from behavioral observations: (1) average perch height, (2) proportional usage of different perch types, (3) average number of movements occurring per minute, (4) average distance traveled in each movement, and (5) average distance traveled per minute. Since differential utilization of natural habitat structures was the focus of this study, all data involving enclosure poles or netting (including movement to and from these structures) was omitted for calculations of the above measures. Movements and behaviors related to interactions with other anoles (e.g., when non-focal anoles climbed on the outsides of enclosures) were also excluded from analyses. Due to variation in the number and types (i.e., snapshot vs. timed session) of behavioral observation efforts among the six experiments, as well as differential visibility among individual anoles, variable amounts of data were collected for individual lizards. To weight individual lizards equally in statistical analyses, a single value for each behavioral measure (for which there were data) was calculated for each individual lizard. Data were pooled for each lizard across all observation sessions and dates prior to the calculation of a given measure. For example, for a lizard making two 20 cm movements in 5 minutes of observation time on one day and one 10 cm movement in 18 minutes of observation on another day, movement frequency = 3/23 moves per minute, average movement distance = 50/3 cm per move, and travel rate = 50/23 cm per minute. Perch height classes were converted to their midpoints (0, 12.5, 37.5, 62.5, …, 187.5 cm; all > 200 cm perch heights involved the net) prior to calculation of means. Unexpanded leaves were excluded as a perch type class for statistical analyses because they occurred in only one observation. Movement data from lizards with no observed moves were used only if the lizard was observed for a total of at least 10 minutes.

Statistical analyses

Several statistical tests were used to evaluate anole behavioral differences. Mean perch heights for each species were approximately normally distributed and were compared with an equal variance, two-sample *t*-test. For perch type comparisons, the proportional usages of individual lizards were summed across species (so that each lizard's contribution to the species totals equaled 1), and species-level usage patterns were compared with a chi-squared test of independence. Mean movement rates, movement distances, and total travel rates were not normally distributed and were compared with Wilcoxon rank sum tests and differences in medians; similar results were obtained using *t*-tests of log-transformed movement variables, but are not reported.

Differences in arthropod numbers remaining at the end of each experiment were assessed with one-way ANOVAs. For significant ANOVAs, Fisher's least significant difference (LSD) tests were used to identify significantly differing treatment groups. Model assumptions were met for all response taxa except combined orb web spider species and *Argiope aurantia* alone; Kruskal–Wallis tests followed by Wilcoxon rank sum tests were used for these responses. To estimate anole predation rates for each response, the mean number of arthropods remaining in the anole treatment group was subtracted from the mean number remaining in controls, and this difference in mean numbers was divided by the number of full days anoles were in enclosures (6 for the jumping spider experiment, 5 for all others).

Power analyses for *t*-tests were conducted to assess the magnitudes of differences in anole treatment means that were likely to be detected, given a significant ANOVA. Since Fisher's LSD tests use pooled error variance estimates, mean square error from the ANOVA of a response was used in the effect size calculation; for orb web spiders and *Argiope* alone, the control treatment was excluded from pooled error variance estimates because its variance was significantly smaller than the anole treatment variances. Power analyses were used to determine the minimum difference between estimated green anole and brown anole predation rates required to achieve power = 0.80.

All statistical tests were performed using the R statistical environment (R Development Core Team 2010) and were two-sided with a significance criterion of $\alpha = 0.05$.

RESULTS

Green anoles and brown anoles differed in their perch use and movement through cabbage palm microhabitats (Figures 3.3, 3.4). Green anoles tended to perch on green leaf blades and were, on average, perched 45 cm higher than brown anoles, which tended to perch on the petioles of dead fronds (perch height: $t = 6.77$, df = 58, $P < 0.0001$; perch type: $X^2 = 25.04$, df = 3, $P < 0.0001$). Green anoles moved 3.1 times more frequently than did brown anoles (W = 66, $n_{b,g} = 23, 21$, $P < 0.0001$) and travelled, per unit time, 2.2 times farther (W = 127, $n_{b,g} = 23, 21$, $P = 0.007$). Distances travelled in individual movement bouts, however, were 1.5 times greater for brown anoles than green anoles (W = 262.5, $n_{b,g} = 18, 21$, $P = 0.039$).

Fewer arthropods remained in anole treatment enclosures than control enclosures for most response taxa, but green anole and brown anole treatment groups did not significantly differ for any of the experiment-level responses (Figure 3.5). For grasshoppers, scaly crickets, and orb web spiders, both green and brown anole enclosures contained significantly fewer remaining arthropods than controls (respectively, $F_{2,15} = 8.39$, $P = 0.004$; $F_{2,15} = 4.03$, $P = 0.040$; H = 9.59, df = 2, $P = 0.008$); in the jumping spider experiment, only the brown anole and control groups could be significantly distinguished ($F_{2,15} = 4.60$, $P = 0.028$). Remaining numbers of planthoppers and anyphaenid spiders did not significantly differ among treatments. Significant ANOVAs corresponded to estimated anole predation rates (i.e., average daily arthropod losses, relative to controls) of at least 0.36 arthropods/day in at least one anole treatment group (Table 3.2; but note that the brown anole predation estimate of 0.37 planthoppers/day was not significant). Differences between estimated green anole and brown anole predation rates ranged 0.03–0.37 for experiment-level responses and were at most half the magnitude required for statistical tests of differential anole effects to achieve a power of 0.8 (Table 3.2).

The two species comprising the orb web spider response built their webs in different locations and were differentially impacted by green and brown anoles (Figure 3.6). *Argiope aurantia* generally constructed their webs amidst the ground vegetation or lower palm leaves, or between the two, and were equivalently impacted by green and brown anoles (H = 8.94, df = 2, $P = 0.011$). By contrast, *Nephila clavipes* constructed webs in the upper corners of the enclosure nets—a region more regularly frequented by green anoles than brown anoles—and were negatively affected only by green anoles ($F_{2,15} = 16.30$, $P = 0.0002$).

With the exception of jumping spiders, the average numbers of response arthropods lost from anole enclosures were far less than the numbers that could have been consumed by anoles. For example, in captive feeding trials green and brown anoles consumed, respectively, averages of 5.4 and 5.3 grasshoppers per day over a five day period—twice the total loss rate for anole enclosures and 3–4 times greater than estimated anole predation rates (i.e., loss rates relativized to controls). As another example, planthopper consumption rates in feeding trials averaged 11.0 and 9.9 planthoppers per day for green and brown anoles, respectively, which were 3–4 times greater than total loss rates and 27–48 times greater than estimated predation rates. Anoles frequently avoided jumping spiders in feeding trials, especially the larger spiders, and this tendency was more pronounced for green anoles. The numbers of jumping spiders remaining in enclosures therefore likely reflects differential anole attack probabilities rather than differential detection and successful capture probabilities.

Anoles tended to lose weight in most experiments, with the greatest average weight losses corresponding to the experiments with nonsignificant treatment effects and the smallest estimated predation rates (Figure 3.7). Only in the grasshopper and jumping spider experiments did anoles tend to gain weight, and these gains significantly differed from zero only for brown anoles in the grasshopper experiment ($t = 2.80$, df = 5, $P = 0.049$) and green anoles in the jumping spider experiment ($t = 3.16$, df = 5, $P = 0.025$). At least some of the brown anole weight gain in the grasshopper experiment is attributable to the consumption of non-focal arthropods, as average weight gains among experimental and feeding trial brown anoles were equivalent despite the fact that brown anoles consumed twice as many grasshoppers in feeding trials as were lost from brown anole treatment enclosures (t = 2.98, df = 5.2, P = 0.029).

DISCUSSION

Despite their differential utilization of cabbage palm microhabitats, green anoles and brown anoles had similar per-capita effects on an array of arthropods with very different autecologies. This overall similarity in effects is all the more striking when one considers that average predation rate differences of 0.4–1.3 prey per day were relatively likely to be detected (Table 3.2), and that the only significant difference in green anole versus brown anole effects was an enclosure artifact that may or may not have relevance to more natural environments. Before considering the particular mechanisms that may have enabled these unexpected results, some discussion is warranted concerning the generality and implications of the observed differences in anole behavior.

Anole perch and movement behavior

As expected and in accordance with previously observed patterns, green anoles perched on palm leaves far more frequently than did brown anoles (87% vs. 31%, Figure 3.3). Green anoles and their Caribbean analogs (i.e., species in the *carolinensis* subgroup; Burnell and Hedges 1990, Glor et al. 2005) frequently perch on leaves, and though this frequency is affected by habitat configuration, syntopic anole species, and ontogeny, it is always observed to be greater than corresponding brown anole leaf use in the same habitat (Schoener 1968, 1975, Jenssen et al.

1998, Rodríguez Schettino et al. 2010). In Louisiana, green anoles predominantly perched on leaves (72% of observations) in a habitat that, like palm enclosures, was dominated by plants with large, broad leaves (Irschick et al. 2005a), and palm leaves constituted the majority of green anole perch use in a Florida habitat dominated by small (height < 3 m) cabbage palms (Gilman and Irschick 2013).

This differential selection of perch type corresponded well to differences in anole ecomorphology. Trunk–crown anoles typically have larger toepads with more lamellae than do trunk–ground anoles (Glossip and Losos 1997; related via perch height in Macrini et al. 2003), which presumably gives them greater maneuverability and clinging ability among the thin branches and leaves that they more frequently perch on (Irschick et al. 1996, Elstrott and Irschick 2004), and this pattern holds true for green versus brown anoles (Collette 1961). Moreover, the more slender form of green anoles (i.e., lesser weight for a given SVL) should further magnify, relative to brown anoles, the clinging advantages imparted by their larger toepads. Differences in maneuverability on palm leaves were evident in the way anoles used them: green anoles perched on and moved across the whole gamut of leaf regions and orientations (see also Gilman and Irschick 2013), but brown anoles generally used only the upper surfaces and least flexible parts of the more horizontally-oriented leaves. Brown anoles predominantly perched below palm canopies on the dead petioles of attached or broken off fronds, which ranged approximately 2–8 cm in width, depending upon distance from the basal "trunk" attachment and overall frond size; perches of similar diameter are frequently and preferentially utilized by adult male brown anoles in more complex habitats (Schoener 1968, Mattingly and Jayne 2004, Rodríguez Schettino et al. 2010). Interestingly, brown anoles were only very rarely observed to perch on the ground (1% of perch use). Though brown anoles in their native and introduced ranges are typically observed to perch on the ground more frequently than they did in enclosures (Schoener 1968, Losos et al. 2006, Wright 2009), similarly low frequencies have been observed on islands lacking additional anole species (Lister 1976; but see Rodríguez Schettino et al. 2010 for a counterexample).

To some extent, differential perch type selection was likely responsible for observed differences in perch height, a major niche axis of structural habitat use among anoles. Little overlap in height above ground existed among green leaves and dead petioles, and thus differential anole preferences for these perch types should generate different perch height distributions. Although the possibility that differential perch height preferences generated the observed differences in perch type use cannot be ruled out, it seems unlikely. The *degree* to which perch type preferences affected green and brown anole perch height differences, however, is an open question. Did brown anoles select particular petioles on the basis of their height above ground or their distance from the canopy, or was some other factor involved (e.g., insolation)? Does palm height affect green anole use of dead petioles? In addition to answering these and related questions, a study examining green and brown anole perch behavior on palms of varying height could provide some insight into why green anoles (or their Caribbean analogs) in allopatry sometimes perch higher than brown anoles in similar habitats (Losos and Spiller 1999, Edwards and Lailvaux 2012, Stuart et al. 2014 [2010 study]) and other times do not (Vincent 2002, Stuart et al. 2014 [1995–1998 experiment]).

Green anole and brown anole movement behavior also differed as expected, matching previously observed differences between *carolinensis* subgroup species and brown anoles, ecomorph-associated patterns, and assumed adaptations to differing habitat visibility profiles. In previous studies permitting comparison, green anoles or their closely related analogs have, on average, moved 2.2–3.5 times more frequently and travelled 2.9 times farther per unit time than brown anoles, whereas the average distance travelled in individual movement bouts has been 1.2–1.4 times greater for brown anoles (Irschick 2000, Mattingly and Jayne 2004, Johnson et al. 2008, Rodríguez Schettino et al. 2010). Similarly, in this study green anoles on average moved 3.1 times more frequently and travelled 2.2 times farther per unit time than brown anoles, while brown anoles on average covered 1.6 times more distance in individual movements. More generally, the observed differences in green and brown anole movement behavior reflect patterns observed for trunk–crown versus trunk–ground ecomorphs, which are thought—but not yet demonstrated—to be adaptive solutions for finding prey in microhabitats presenting differing amounts of visible, accessible surface area (Moermond 1979, Cooper 2005, Johnson et al. 2008). Thus, the more active foraging style of green anoles is likely adaptive for the reduced visibility ranges and visual obstructions present in cabbage palm canopies and other foliage-dominated microhabitats, as it allows them to increase the surface area and volume of habitat surveyed per unit time. Conversely, a more sit-and-wait foraging mode would seem adaptive for brown anoles perched on dead petioles below palm canopies, as the relatively unobstructed views offered by these and similar perches allow the anoles to survey relatively large areas for prey.

Differences in movement behavior may explain why green anoles tended to lose more weight (or gain less) than brown anoles under similar rates of estimated biomass consumption (Figure 3.7b). Because a more active foraging strategy should require greater energy expenditure than a more sit-and-wait approach, foraging efficiency (energy intake / energy expenditure) for a given rate of prey consumption per unit time should be lower for green anoles than brown anoles. One of the important implications of this difference is that brown anoles may grow faster and/or devote more energy to reproduction than similarly-sized (by mass, at least) green anoles with a similar prey intake rate. Another important implication is that green and brown anoles may be asymmetrically impacted by periods of low prey availability, such as might occur towards the end of the dry season or during drought conditions. Further, if invading brown anoles lower ambient prey availability via increased anole predation pressure, as they appear to do on small Floridian islands (Chapter 2), any negative effects of exploitative competition for prey might be substantially greater—absent any behavioral modifications—for green anoles. Whether green anoles modify their foraging behavior in response to prey availability has not been studied, but male green anoles have been observed to move less frequently on islands with co-occurring brown anoles than on islands without brown anoles (Kamath and Stuart 2015), possibly in response to lower prey availabilities. In this study, however, there were no significant correlations between weight loss and perch height, movements per minute, or distance traveled per minute for either green anoles or brown anoles (all $|r| < 0.16$, all $P > 0.46$; Turnbough, unpubl. analyses), which suggests that anoles did not tailor their foraging behavior to small changes in ambient prey availability.

Per-capita effects on arthropod prey

Given the differences in green anole and brown anole use of canopy versus below-canopy palm microhabitats, why were arthropods differentially occupying these microhabitats not differentially impacted by the two species? Factors responsible for the similarity of anole effects likely varied among the different arthropod response taxa, but the possibility that anoles were satiated on non-focal arthropods and thus unmotivated to prey on focal arthropods can be largely ruled out. Anoles tended to lose weight in all but two experiments, and since anoles had empty (or nearly empty) stomachs when experiments began, this lost weight implies poorer body condition or a further emptying of the digestive tract—neither of which correspond to anoles satiating themselves on non-focal arthropods (which were regularly removed from enclosures; see Methods). The positive and nearly linear association between focal prey consumption rate (scaled by biomass; Figure 3.7b) and anole weight change provides further evidence that anoles were food-limited in all but one experiment. Only brown anoles in the grasshopper experiment had weight gains equivalent to those of feeding-trial anoles with unrestricted food access, and it can be assumed that in all other cases anoles did not consume as many arthropods, focal or otherwise, as they were physically capable of.

For planthoppers, equivalently low interaction rates with green anoles and brown anoles appear to have occurred either because the anoles did not recognize planthoppers as prey or because they were unable to capture them. The rarity of interaction is surprising, given that the planthoppers were large, abundant (as they often are in natural settings), and highly visible—at least to a human observer. Indeed, it would seem difficult for green anoles to have moved about palm canopies without actively avoiding physical contact with planthoppers, and planthoppers were common on the undersides of green petioles where they should have been within view of perched brown anoles. The palatability of *Ormenaria rufifascia* was confirmed in feeding trials: in the confines of cages, anoles consumed 10–11 planthoppers per day (compared to predation rates of 0.2–0.4 planthoppers per day in enclosures). *Ormenaria rufifascia* have a powdery, waxy coating and—when touched—an explosive jump, such that it is extremely difficult to capture them with the pinching action of human fingers. It is therefore possible that the initial lingual contact in an anole attack strike (Reilly and McBrayer 2007) causes these planthoppers to explosively jump away before the anole’s teeth and jaws are able to engage them, possibly with the aid of the planthopper’s powdery coating. *Ormenaria rufifascia* do not move about diurnally, and thus it is also possible that this motionless state prevents their recognition by anoles; if so, the small movements *O. rufifascia* make while secreting honeydew to tending *Camponotus floridanus* ants (Turnbough, pers. obs.; see also Wilson and Tsai 1984) may increase their susceptibility to anole predation. Although the interaction may be rare, green anoles do at least occasionally prey on *O. rufifascia* (Turnbough, pers. obs.).

For anyphaenid spiders, the similarity of anole treatment effects and their lack of difference from controls may reflect equivalently low interaction rates, but it is also possible that anole treatment effects were obscured by compensatory cannibalism among the spiders. The anyphaenid spider experiment was the only one in which focal arthropod recovery in controls was relatively low (64%), suggesting spider cannibalism. Stocked anyphaenid spider densities (one per frond) were approximately four times greater than the densities observed on experimental palms at the outset of the study, before non-focal arthropods were removed from enclosures; given these artificially high densities, the general absence of other arthropod prey, and the cannibalistic tendencies of cursorial spiders (Wise 2006), it seems likely that cannibalism was responsible for the low recovery rates among at least the control enclosures. Whether cannibalism was likely equally responsible for spider losses in the anole treatments is uncertain. Anole weight losses in the anyphaenid spider experiment generally matched the across-experiment trend for control-standardized, biomass-scaled consumption rates (Figure 3.7b), but these weight losses would have fit the overall trend even if the anyphaenid consumption rates were doubled for green anoles and quadrupled for brown anoles. Thus, the weight loss data do not rule out the possibility that green and/or brown anole predation on anyphaenid spiders was underestimated due to the occurrence of compensatory spider cannibalism in the other treatments. That anoles do indeed prey on *Hibana* spiders is confirmed by the stomach contents of green anoles removed from cabbage palms (Turnbough, unpubl. data), though the means by which they do so is unclear, as *Hibana* generally spend the day hidden in silken retreats that, on palms, tend to be located in the crevices of leaf pleats.

For prey taxa that were reduced in anole enclosures relative to controls, variation in arthropod and anole habitat use might be sufficient to explain the absence of differential anole effects. Some grasshoppers (but not most) moved into palm canopies, and scaly crickets, jumping spiders, and *Argiope* spiders used both canopy and below-canopy microhabitats. Green anoles sometimes made quick forays into lower microhabitats to forage or capture prey, a behavior that has been observed in natural habitats (Kamath et al. 2013), and brown anoles often slept in palm canopies where they may have consumed canopy arthropods before or after sleeping. Together, the less frequent use of non-preferred microhabitats by anoles and the variation in habitat use exhibited by prey taxa may have facilitated, in whole or in part, similarity in the per-capita effects of green anoles and brown anoles on prey. For example, a green anole consuming 7 of 8 grasshoppers in the canopy and 5 of 22 on the ground would have the same effect on total grasshopper abundance as a brown anole consuming 1 of 8 grasshoppers in the canopy and 11 of 22 on the ground.

Another possible explanation for equivalently negative anole effects is that variation in the behavior of arthropod individuals caused a certain proportion of them to be vulnerable to anole predation, and that anoles predominantly consumed those high-risk individuals. For example, it is possible that a certain proportion of scaly crickets moved about diurnally, whether to search for mates or for other reasons, and that these individuals were eventually consumed by anoles over the course of the experiment. As another example, variation in movement frequency within or between the six grasshopper morphospecies may have led to eventual anole predation of the most frequently moving individuals, especially if movement frequency influenced the likelihood of ending up on the enclosure net. Grasshoppers were often observed crawling up the net, a behavior that probably made them highly visible to anoles, and anoles were observed to capture such grasshoppers on more than one occasion. The different grasshopper morphospecies were differentially impacted by green and brown anoles (Turnbough, unpubl. analyses), and it is possible that species-specific differences in grasshopper movement behavior contributed to this result.

Although differences in green anole and brown anole effects on jumping spiders were not significant, the lack of significance probably resulted from low stocking numbers of the most vulnerable size classes. In a feeding trial experiment, brown anoles were more likely to prey on *Phidippus regius* spiders than were green anoles of equivalent SVL (Turnbough, unpubl. study), but willingness to attack even the smallest *P. regius* size class tested (~8–11 mm body length) varied among brown anole individuals. In the current study, both small- and medium-sized *P. regius* were completely absent by the end of the experiment in 33% of the brown anole enclosures (versus 0% of the green anole enclosures), and it is likely that additional small or medium-sized *P. regius*, had they been present, would have been consumed in these enclosures. Thus insufficient numbers of stocked spiders, possibly acting in concert with variation in the propensity of individual anoles to attack *P. regius*, probably obscured stronger per-capita effects of brown anoles on this species. Such a difference in per-capita effects is consistent with negative associations previously observed between brown anole abundance on small islands and both the abundance of *P. regius* in swept foliage samples (Chapter 2, Appendix S2) and the density of *P. regius* in small cabbage palm canopies (Turnbough, unpubl. study). However, differential green and brown anole interaction rates with *P. regius* appear to be driven by differences in anole boldness or capture abilities rather than differences in perch or foraging behavior.

The two anole species did have significantly different per-capita effects on *Nephila clavipes* (Figure 3.6), but this difference appears to have been an enclosure artifact. These spiders predominantly built atypically small and irregular webs (e.g. often lacking orbs) in the top corners of enclosure nets. Green anoles, but not brown anoles, were commonly observed at the top of the nets, and thus green anoles probably had greater opportunity to interact with *N. clavipes* than did brown anoles. That the interaction was an enclosure artifact is suggested more by the irregularity of the webs than their location in net corners: *N. clavipes* webs in natural habitats typically span much larger open spaces, which tends to position most of the web, and the spider residing within it, farther from environmental structures that anoles could use to launch attacks. However, to the extent that the upper nets approximated the structural configuration of some aspects of natural vegetation, the greater per-capita effects of green anoles on *N. clavipes* could be indicative of greater per-capita effects on accessible (i.e., within striking range) web spiders located at similar aboveground heights.

Implications for population-level impacts

The results of this study suggest that for a given habitat feature (e.g., small cabbage palms), green anoles and brown anoles foraging at similar heights (i.e., within ~ 0.5–1.0 m) will have similar per-capita interaction rates with most arthropod species in their nearby vicinity. If so, the impacts of brown anole invasion and green anole displacement will primarily depend on, and may be adequately modeled by, corresponding changes in the concentration of foraging anoles at different heights in the vegetation.

Thus, for habitats or habitat features in which anoles are constrained to use similar perch heights, such as the experimental palms and the open scrub habitat they were embedded in, the impacts of brown anole invasion on arthropod communities may driven primarily by increases in total *Anolis* density. To model such impacts, the effects of green anoles in the system would simply need to be scaled up (though not necessarily linearly) to the post-invasion, combined densities of green and brown anoles. Modeling efforts would of course require data on the effects of green anoles on arthropods, which are currently limited to qualitative observations for invaded Pacific islands (Makihara et al. 2004, Abe et al. 2008, Yoshimura and Okochi 2010), but a reasonable first-order approximation could probably be made using the effects of brown anoles (or another similarly-sized trunk–ground or trunk–crown anole) on arthropods in a similar habitat (e.g., Schoener and Spiller 1999, Spiller and Schoener 2001). Exceptions to the scaling-up modeling approach would need to be made for arthropod species that are likely to be differentially consumed by green and brown anoles due to differences in gape size (e.g., cicadas) or other factors (e.g., large *Phidippus* jumping spiders).

In habitats offering a greater range of vertical habitat structure, however, overlap in the foraging efforts of green anoles and brown anoles is likely to be less extensive because green anoles tend to more fully utilize the available range of vertical space. Vertical habitat use for individual green anoles is best documented for a well-studied population in Georgia, in which male territories incorporated the entire 6–8 m vertical range of the riparian habitat and encompassed volumes that were, on average, over six times greater than the 11 m^3 contained within palm enclosures (Jenssen et al. 1995, Jenssen and Nunez 1998). Comparable data for male brown anoles have not been published, but their typical rarity at heights above 2–3 m and smaller population-level perch height variation (compared to male *carolinensis* subgroup anoles in the same or similar habitats; Lister 1976, Edwards and Lailvaux 2012) provide indirect evidence that brown anoles make less extensive use of relatively tall vegetation. Although perch height differences on the order of 0.5–1.0 m in palm enclosures had little effect on the per-capita effects on prey within a 1–2 m band of habitat, perch height differences on the order of 2–5 m seem far less likely to produce such a result.

It is therefore likely that in habitats with relatively tall vegetation (e.g., heights > 3 m), substantial increases in anole predation pressure following brown anole invasion will occur only in the lower portions of the habitat. Such an expectation does not devolve from the findings of this study, but the near equivalence of anole–prey interaction rates for given perch location neighborhoods that is suggested by this study greatly simplifies efforts to quantitatively model the differences in anole predation pressures. Two approaches to modeling pre- versus post-invasion predation pressures are shown in Figure 3.8. Both approaches—one perch-height naïve and the other perch height-informed—yield qualitatively similar predictions: following brown anole invasion, the greatest changes in absolute and relative anole predation pressures occur in the lowest vegetation height classes, and reductions in predation pressure may even occur in the highest vegetation classes of open habitats. These modeling exercises are not meant to be rigorous predictions of anole foraging distributions, as vegetation profiles were merely schematic habitat representations and simplifying assumptions were made for factors that could be more realistically modeled with existing data (e.g., the uniform distribution of female home ranges within male territories). Rather, the models serve to demonstrate (1) how differential utilization of vertical habitat space could cause green anoles and brown anoles to differ in their overall per-capita effects on arthropods, despite similarity in their site-specific interaction rates with prey; (2) how post-invasion changes to anole predation pressures could, due to the combination of differential green and brown anole vertical habitat use and densities, greatly vary for different vegetation heights; and (3) how anole perch height distributions and densities—data that are relatively simple to gather—might be used to model the relative pre- and post-invasion effects of anoles on arthropod communities.

The results of this study and the inferences derived from them have bearing on several findings from a previous study of the relative population-level impacts of green versus brown anoles on the arthropod communities of small spoils islands in a nearby lagoon (Chapter 2). For instance, the greater explanatory power of brown anole abundance for ground-active arthropod communities than for foliage-inhabiting communities (sampled at 1–2 m) agrees with the qualitative predictions of the open habitat models in Figure 3.8 (a better test of these predictions, however, would be to compare explained variation fractions for foliage arthropods collected at different vegetation heights) .

One of the more puzzling results of the spoils island study was the absence of expected associations between brown anole abundance and the abundances of foliage spider size classes, foraging guilds, and families (Chapter 2, Appendix S2). The palm enclosure experiments have particular relevancy for this unexpected finding, as all of the most frequently collected foliage spiders were common on small cabbage palms (Turnbough, unpubl. data) and several may have been primarily associated with palms and palmettos (e.g., *P. regius*). For example, the enclosure experiments suggest that the lack of an association between brown anoles and the most frequently collected hunting spider, *Hibana sp.* (Anyphaenidae), may have occurred because anole predation on this nocturnal spider is relatively rare and not an important factor affecting its abundance (although spider cannibalism could have obscured higher anole–*Hibana* interaction rates in palm enclosures). For the remaining common spider families in island foliage arthropod samples, the hypothesis that stronger per-capita interactions between green anoles and foliage spiders (due to differences in anole foraging behavior) largely offset the effects of greater brown anole densities (Chapter 2, Appendix S2) was supported to some extent by the greater per-capita effects of green anoles on *Nephila* orb web spiders in enclosures. However, another possible explanation is suggested by the overall similarity of anole effects in enclosures and the models they prompted: similar pre- and post-invasion levels of anole foraging intensity at vegetation heights of 1–2 m (from which foliage arthropod samples were taken). In the open habitat models (which best characterize the structure of sampled island habitats), there is a strong contrast in the predicted post-invasion changes to anole foraging intensity at the 1–2 m and 2–3 m height classes (a 150% increase and 20% decrease, respectively, under the PH-informed model; Figure 3.8a), which suggests that model predictions at this height range are relatively sensitive to model details concerning habitat configuration, differential anole habitat use, and differential anole densities. Thus, it is possible that similar pre-and post-invasion foraging intensities at 1–2 m vegetation heights would be revealed by a better model (e.g., one that more accurately models female anole habitat use and spoils island vegetation profiles) or an actual assessment of anole densities and height-stratified habitat use on invaded and uninvaded islands.

Several important caveats apply to the inferences derived above. First, because focal ground-dwelling arthropods were limited to grasshoppers and some *Argiope* individuals, the evidence for similar per-capita anole effects was weaker for ground arthropods than for foliage-inhabiting arthropods. Few arthropods other than ants were observed to be diurnally active on the ground at the study site, and those that were observed (e.g., tiger beetles and unused grasshopper species) were not sufficiently abundant to be used in experiments; even the grasshoppers used for experiments were captured off-site in more grassy habitats. Thus, the inference that green and brown anoles foraging within 1–1.5 m of the ground have similar per-capita effects on ground arthropods should be considered particularly tentative and in need of further study. Second, results obtained for a single habitat substrate and configuration—albeit a naturally common one—may not apply to other habitat contexts. Finally, the per-capita effects of female green and brown anoles were not compared. Female brown anoles tend to perch at lower heights than males (Schoener 1968, Lister 1976, Meshaka 1999), whereas perch heights of female green anoles (and their Caribbean analogs) tend to be similar to those of males (Schoener 1968, Irschick et al. 2005a,b), or even slightly higher (Jenssen and Nunez 1998). It therefore appears likely that the foraging efforts of green and brown anole females overlap less extensively than do those of males, but whether those differences translate to differential per-capita interaction rates with prey when perch height availabilities are constrained (as on small palms) will have to be experimentally determined.

Summary and conclusions

Contrary to my initial hypothesis, differential microhabitat use by green anoles and brown anoles did not lead to substantially different per-capita effects on arthropod prey that differentially occupied those microhabitats. Only a single prey species—the orb weaver *N. clavipes*—was differentially affected by the two anoles, and even this difference did not, due to its appearance as an enclosure artifact, provide good evidence that differences in anole foraging behavior generate differential impacts on prey. These results suggest that green anoles and brown anoles have similar per-capita interaction rates with prey when they forage in spatially proximate locations, and thus have similar per-capita effects on prey assemblages in habitat contexts that constrain the two anoles to relatively similar perch height distributions. The results should not, however, be taken to imply that green and brown anoles are functionally equivalent predators, not only because of the limitations of the study (e.g., the absence of female anole comparisons) but also because (1) in most habitats their per-capita foraging efforts are likely to be differentially allocated along the vertical axis of habitat space, and (2) the larger gape size and perhaps greater boldness of brown anoles probably allows them to consume larger prey and more frequently attack potentially dangerous prey (e.g., large spiders).

This study supports the hypothesis that by partitioning habitat space, anoles partition prey resources (Losos 2009 and references therein). The similarity of per-capita effects in enclosures suggests that similarly-sized green and brown anoles foraging in the same habitat space will overlap greatly in the species-level composition of their diets; if arthropod prey are a limiting resource, as they commonly appear to be (Andrews 1979, Losos 2009), such overlap should result in strong interspecific competition for prey that could be minimized by partitioning habitat space. Following this line of reasoning, dietary differences observed between brown anoles and syntopic *carolinensis* group anoles (e.g., greater proportional consumption of flying insects by green anoles; Schoener 1968, Campbell 2000) may simply reflect different prey availabilities at different heights of the vertically-partitioned habitat rather than differences in the relative effectiveness of differing anole foraging behavior for various prey types.

Although the absence of differential anole effects on a suite of potential prey species was unexpected, similar results have been obtained for vertebrate predators in aquatic environments. In a comparison of three ecologically and morphologically similar species of *Enneacanthus* sunfish, Resetarits and Chalcraft (2007) found two species to be functionally equivalent in their per-capita effects on an assemblage of three larval anuran prey species. Two cautionary points regarding functional equivalence emerge from this study and others, however. First, the functional differences of the third sunfish suggest that it may be difficult to make accurate *a priori* predictions of functional equivalence even among ecologically similar congeners. Second, because the effects of the third sunfish were statistically indistinguishable from the effects of one or both members of the functionally equivalent pair for seven out of nine anuran response variables, conclusions about functional equivalence or similarity are likely to depend on the extent and identity of the response variables considered. Indeed, comparisons of predatory fish and/or aquatic salamander species in experimental ponds amply demonstrate (at least for pond environments) that the per-capita functional similarity of trophically-similar predators is very much dependent upon the response under consideration (Harris 1995, Morin 1995, Kurzava and Morin 1998, Chalcraft and Resetarits 2003b, Baber and Babbitt 2003). Thus the similarity in anole per-capita effects in enclosures may have been strongly affected by the identities of the arthropod species selected for study. Although the relative functional similarity of different predators for a given response should be predictable if the hierarchical importance of the relevant predator traits is known or correctly assumed (Chalcraft and Resetarits 2003a), the current study exemplifies the difficulty ecologists might face in judging *a priori* the importance of a given trait difference.

This study represents a small contribution to a large gap in knowledge: how similar are the effects of closely-related, ecologically similar predators on their prey? This question is particularly important for understanding and predicting the impacts of invasive species that displace their native counterparts. Recent meta-analyses suggest that introduced predators have greater impacts on prey than do native predators (Salo et al. 2007, Paolucci et al. 2013), but this finding may not hold for closely-related ecological “equivalents”. Furthermore these analyses do not address the important question of whether (or the extent to which) introduced predators are functioning differently in their invaded environments or whether they simply tend to be more abundant than native predators. The results of the current study suggest that for one particular group of terrestrial vertebrate predators, arboreal lizards, ecologically similar congeners may have similar per-capita effects on local prey even when the lizards differ in foraging-related behavior, and thus that the impacts of lizard invasion and native species displacement may be driven largely by differences in the density and distribution throughout the habitat of the lizard species involved. The generality of this finding with respect to other habitat contexts and other lizard species awaits further study.

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APPENDIX 3:

TABLES AND FIGURES

Table 3.1 Focal arthropods used in experiments.

Arthropod response	Numbers stocked [sizes[1]]	Body length (mm)	Diurnal behavior	Diurnal microhabitat	Experiment dates (2008)
Planthoppers Flatidae: *Ormenaria rufifascia*	36	6–8	Motionless, exposed	Live leaves and live petioles (mostly lower surfaces)	16-June to 22-June
Grasshoppers Acrididae: 6 morphospecies	30 (5 each species)	9–20	Variably active, exposed	Mostly ground vegetation	25-June to 1-July
Scaly crickets Gryllidae: *Cycloptilum sp*.	20	8–12	Usually hidden in crevices	Live leaves, dead leaves, unexpanded leaves, trunk bole	8-July to 14-July
Ghost spiders Anyphaenidae: *Hibana sp*.	12 [Sx4 Mx4 Lx4]	6–12	Hidden in silken retreats in crevices	Live leaves, dead leaves, unexpanded leaves	16-July to 22-July
Regal jumping spiders Salticidae: *Phidippus regius*	5 [S M M M L]	8–17	Active foraging, exposed	All palm microhabitats	23-July to 30-July
Orb web spiders Araneidae: *Argiope aurantia* Nephilidae: *Nephila clavipes*	12 (6 each species: [S S M M L L])	6–14	In web, exposed	*Argiope*: live fronds, dead fronds, ground vegetation *Nephila*: live fronds, dead fronds, net	4-Aug. to 10-Aug.

[1] Small (S), medium (M), or large (L)

Table 3.2 Predation rate estimates (arthropods per lizard per day) for anole treatment groups. Estimates represent the average daily loss of arthropods from enclosures, relative to controls. Lower confidence interval bounds are truncated at zero. Rates corresponding to significant differences between anole and control groups are indicated in bold, as are rate differences corresponding to significant differences between anole treatments. Estimated minimum differences required for 80% power levels are indicated.

	Predation rate [95% CI]				Anole treatment differences	Minimum difference for power = 0.8
Prey taxon	Brown anoles		Green anoles			
Planthoppers	0.37	[0–0.91]	0.23	[0–0.59]	0.13	0.73
Grasshoppers	**1.57**	[0.75–2.38]	**1.33**	[0.66–2.00]	0.23	1.28
Scaly crickets	**0.60**	[0.15–1.05]	**0.57**	[0.08–1.05]	0.03	0.74
Anyphaenid spiders	0.17	[0–0.50]	0.27	[0–0.55]	0.10	0.65
Jumping spiders	**0.36**	[0.10–0.62]	0.19	[0–0.43]	0.17	0.37
Orb web spiders	**0.60**	[0.05–1.15]	**0.97**	[0.53–1.40]	0.37	0.85
Argiope	**0.60**	[0.11–1.09]	**0.47**	[0.18–0.76]	0.13	0.68
Nephila	0.00	[0–0.11]	**0.50**	[0.25–0.75]	**0.50**	0.31

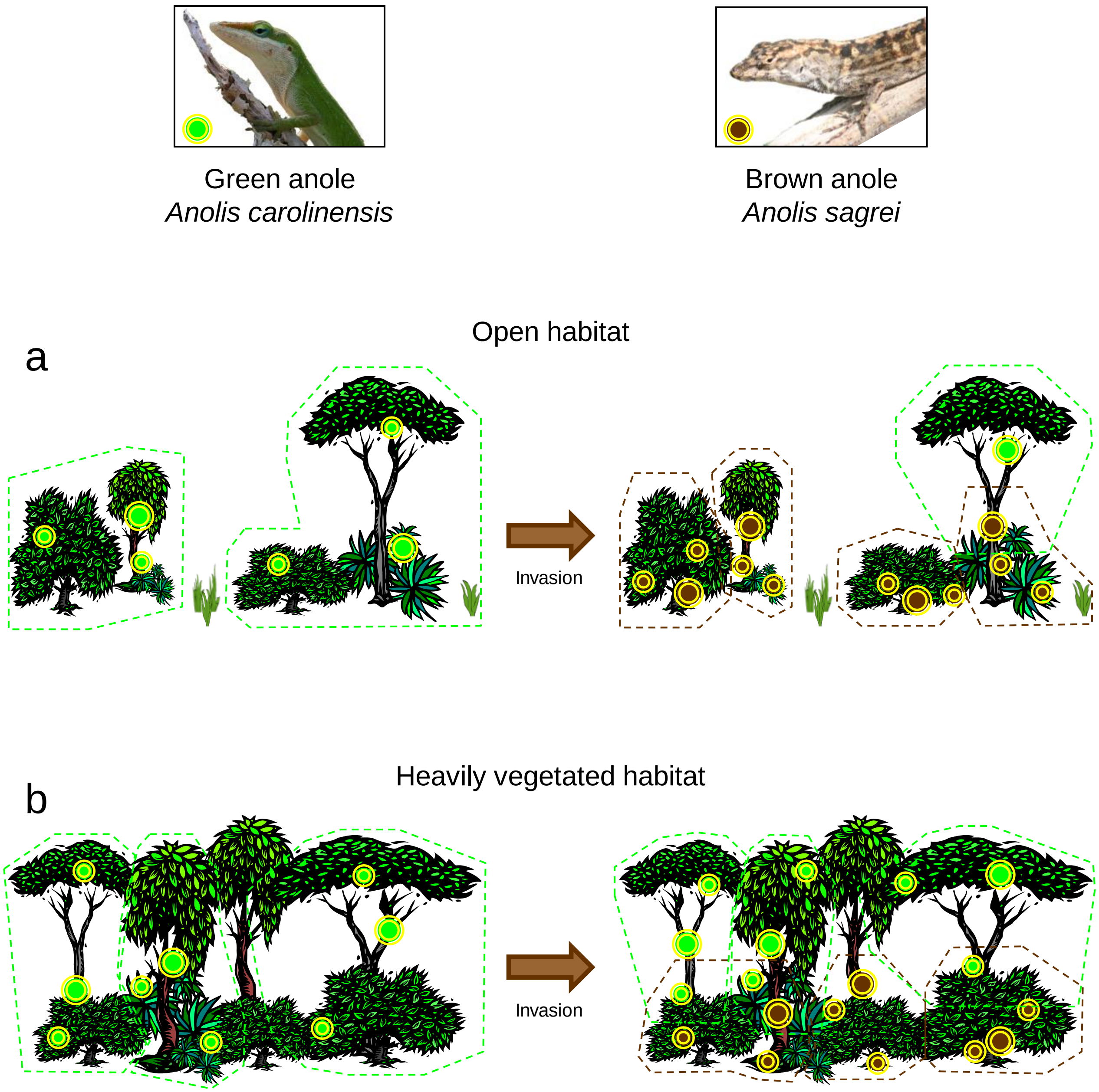


Figure 3.1 Schematic diagram showing the expected effects of brown anole invasion on the spatial configuration of anole territories in (a) open and (b) heavily vegetated habitats. Males are represented by a slightly larger symbol. For simplicity and ease of interpretation, only male territories are shown, and with the exception of invaded open habitat, the home ranges of two conspecific females are embedded in each male territory; female green anoles are absent in the invaded open habitat because the green anole population has been almost entirely displaced.

Figure 3.2 Example palm enclosure. Arrow denotes 2 m in height.

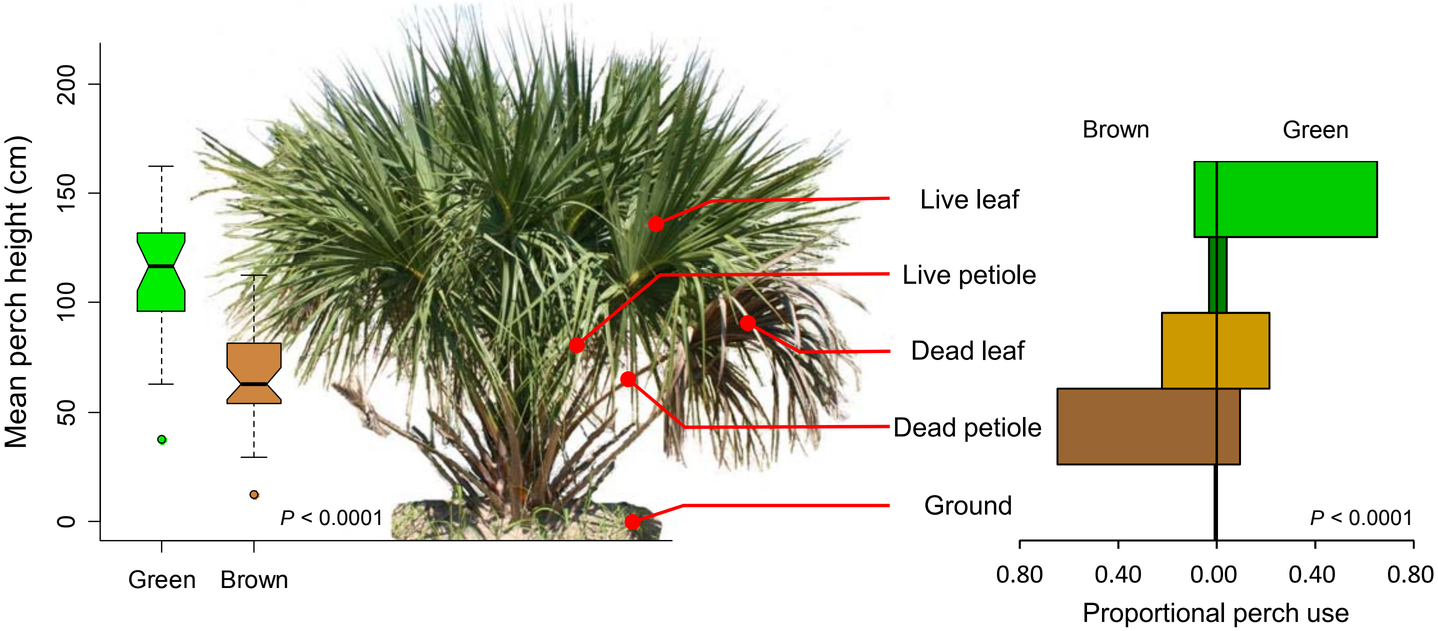


Figure 3.3 Mean perch height and proportional perch type use for green anoles and brown anoles. Data for notched boxplots are the mean perch heights of individual lizards, and the pictured palm is approximately to scale with the perch height axis. Lizards were weighted equally for proportional perch use calculations. $n_{\mathrm{Brown}} = 33$, $n_{\mathrm{Green}} = 27$.

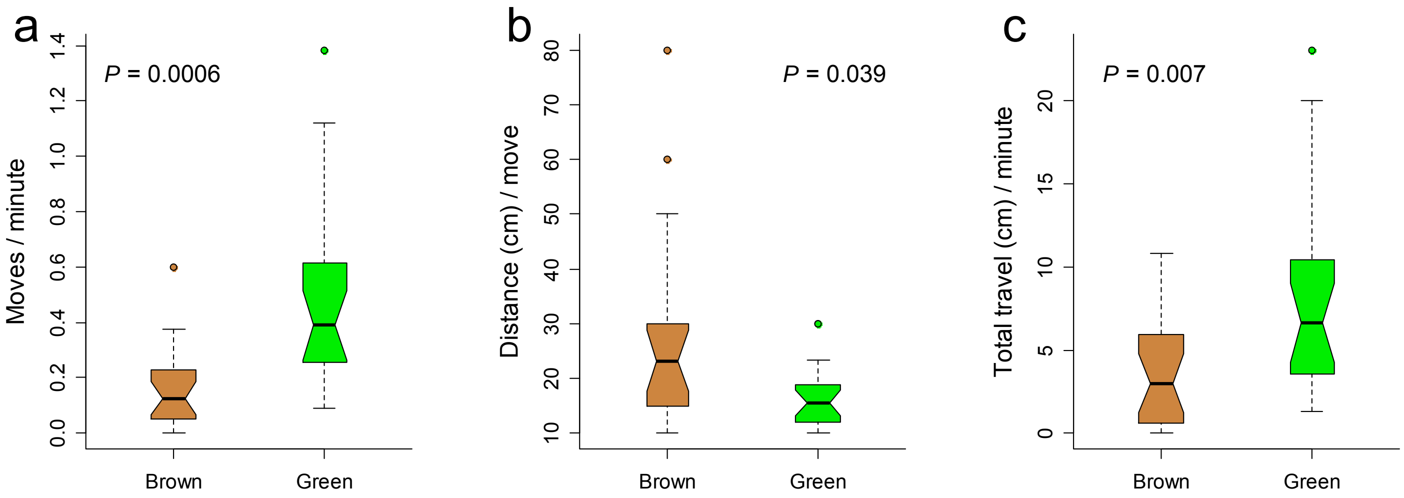


Figure 3.4 Notched boxplots for green and brown anole (a) movement frequencies, (b) average movement distances, and (c) total travel rates. Data are mean values from individual lizards; n_{Brown} = 23 (a, c) or 18 (b), n_{Green} = 21. *P* values for Wilcoxon rank sum tests for location are displayed.

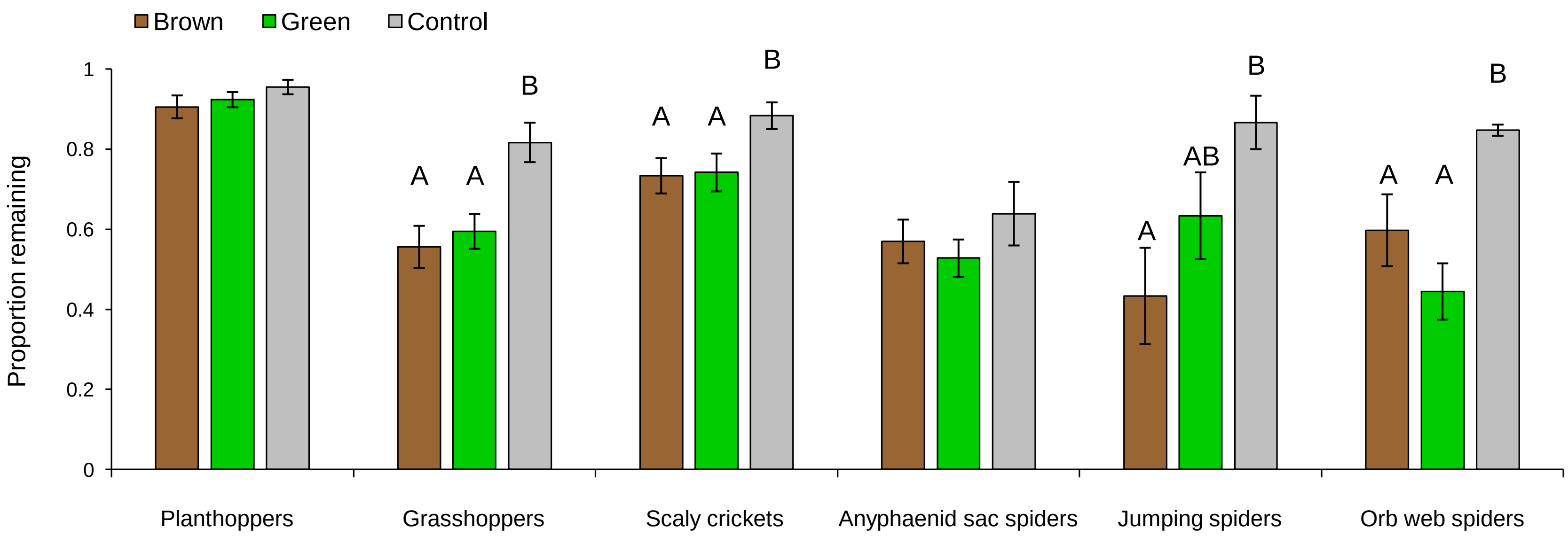


Figure 3.5 Proportion of arthropods added to enclosures remaining at the end of experiments (± 1 SE). Within each experiment, different letters indicate a significant difference in treatment medians (orb web spiders) or means (all other taxa).

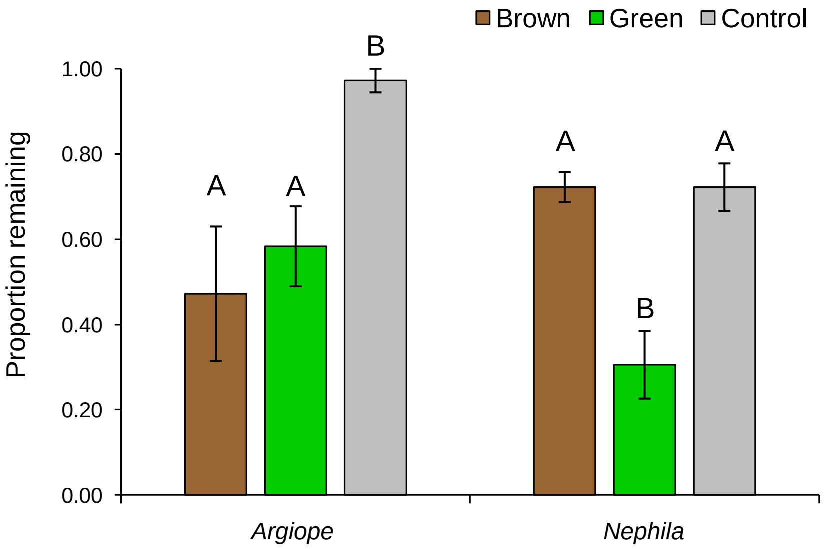


Figure 3.6 Proportion of *Argiope aurantia* and *Nephila clavipes* individuals remaining at the end of the orb web spider experiment (± 1 SE). For each species, different letters indicate significantly different treatment medians (*Argiope*) or means (*Nephila*).

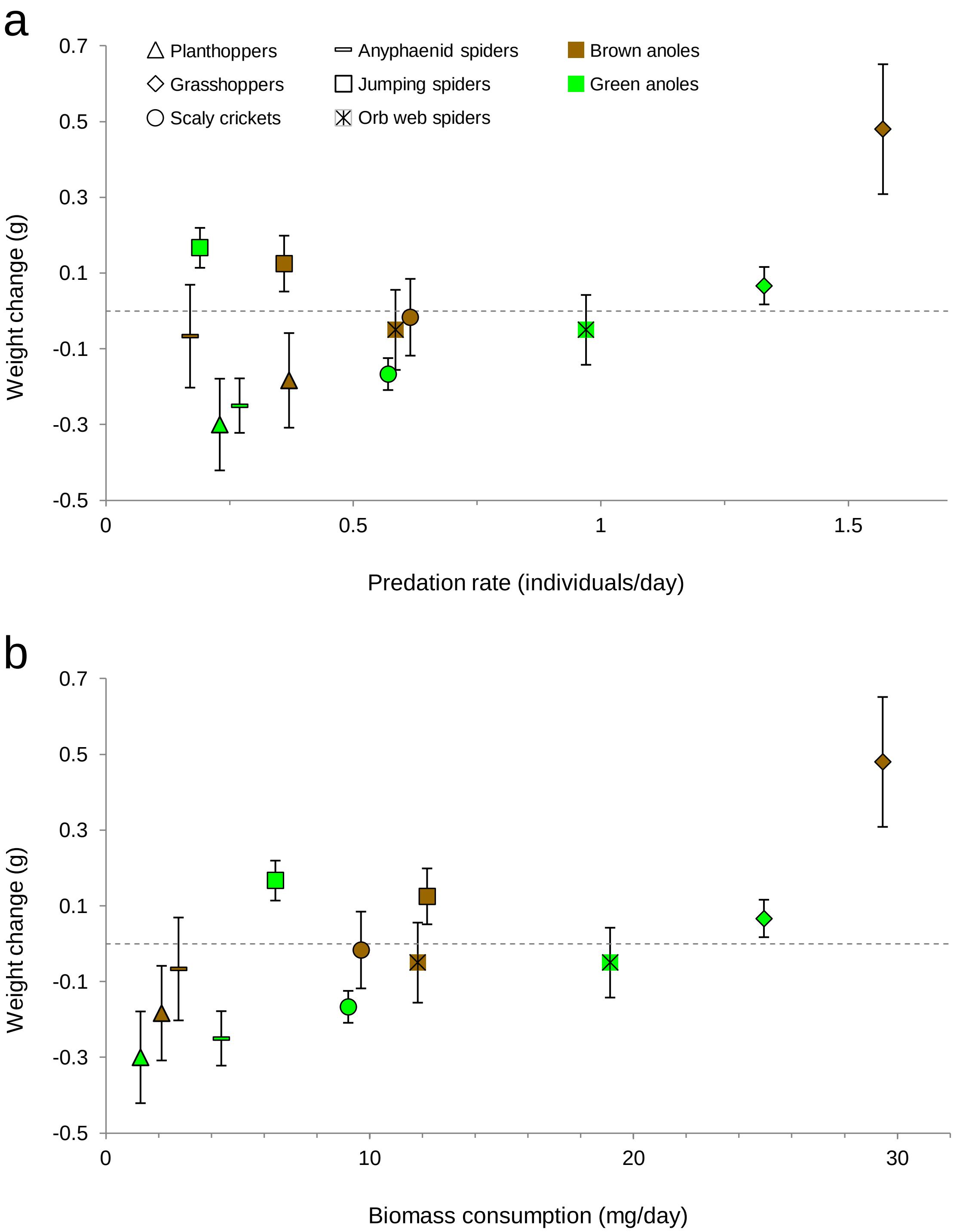
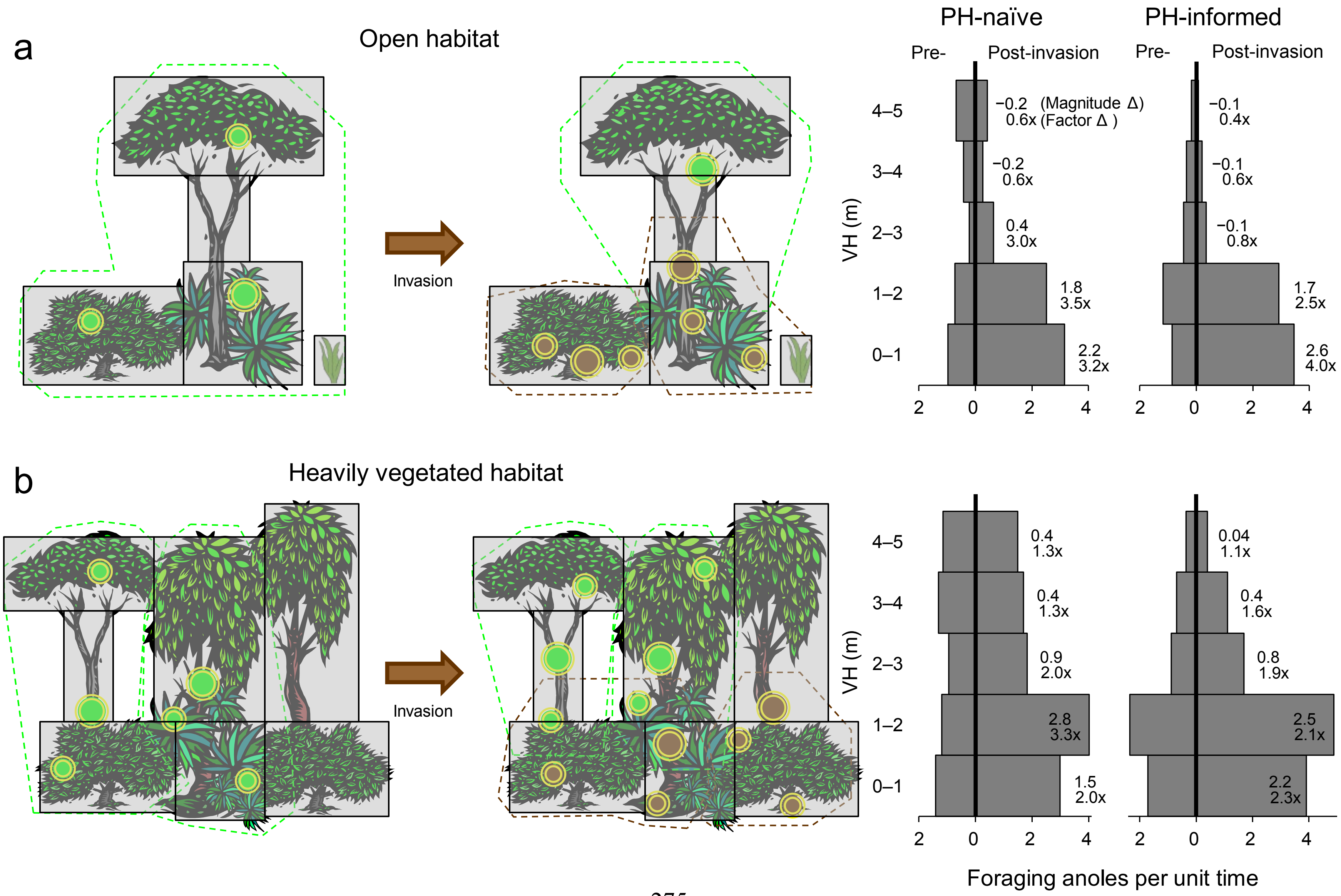


Figure 3.7 Mean anole weight change versus (a) predation rate and (b) biomass consumption rate, by experiment. Error bars represent ± 1 SE. Biomass consumption is the predation rate multiplied by the biomass of an average-sized focal arthropod.

Figure 3.8 Modeled pre- and post-invasion distributions of anole predation pressure by vegetation height (VH) class for (a) open and (b) heavily vegetated habitats. Vegetation profiles are assumed to be representative of their respective habitat type, and gray boxes are proportional to the contribution of each habitat feature to vegetation totals; a scale of 10 mm figure space to 1 m habitat space was used for calculations. Female home ranges were assumed to be evenly and identically distributed within encompassing male home ranges. For perch height (PH)-naïve models, anole habitat use was assumed to be uniformly distributed over the vegetation within a territory. For PH-informed models, allopatric green anole PH distributions (both sexes) were assumed to follow the PH distribution of male green anoles in Jenssen et al. (1995), truncated and recalculated as necessary to fit available vegetation heights in a territory; PH distributions for brown anoles (both sexes) and syntopic green anoles (both sexes) were assumed to follow the species-specific, male PH distributions (truncated and recalculated as necessary) given by Lister (1976) for Exuma in the Bahamas. Anole foraging efforts were assumed to be proportional to their occupancy of VH classes. Changes (Δ) in magnitude listed for each VH class are the differences between post-invasion and pre-invasion anole foraging effort (i.e., occupancy); factor changes are the ratio of post-invasion to pre-invasion anole foraging effort. Symbols and anole territory representations are as in Figure 3.1.


a
Open habitat
Invasion
PH-naïve
PH-informed
Pre-
Post-invasion
Pre-
Post-invasion
VH (m)
4–5
3–4
2–3
1–2
0–1
−0.2 (Magnitude Δ)
0.6x (Factor Δ)
−0.2
0.6x
0.4
3.0x
1.8
3.5x
2.2
3.2x
−0.1
0.4x
−0.1
0.6x
−0.1
0.8x
1.7
2.5x
2.6
4.0x
2
0
2
4
2
0
2
4
b
Heavily vegetated habitat
Invasion
VH (m)
4–5
3–4
2–3
1–2
0–1
0.4
1.3x
0.4
1.3x
0.9
2.0x
2.8
3.3x
1.5
2.0x
0.04
1.1x
0.4
1.6x
0.8
1.9x
2.5
2.1x
2.2
2.3x
2
0
2
4
2
0
2
4
Foraging anoles per unit time

CHAPTER 4:

DIFFERENCES IN THE WINTER ABUNDANCES OF ARTHROPOD-CONSUMING BIRDS ON ISLANDS WITH AND WITHOUT THE INTRODUCED LIZARD *ANOLIS SAGREI*

ABSTRACT

Exploitation competition for prey is one of several mechanisms by which introduced predators may impact resident species in invaded communities. Such a mechanism could result in interclass competition between insectivorous birds and introduced *Anolis* lizards, as *Anolis* are known to reduce arthropod abundance in a variety of systems. To investigate whether brown anole (*Anolis sagrei*) invasions in Florida negatively impact arthropod-consuming birds (both insectivores and omnivores), I censused winter bird communities on a series of small islands that varied with respect to brown anole presence and abundance. Although community-level patterns in arthropod-consuming bird abundances were not well resolved by brown anole abundance, within-community abundances of arthropod-consuming response groups and species tended to be negatively associated with brown anole abundance. Negative abundance associations were observed in at least one habitat type (open/xeric or forested) for gray catbirds (*Dumetella carolinensis*), non-dominant (i.e., non-yellow-rumped warbler) insectivorous birds, omnivorous birds, and all arthropod-consuming birds; marginally significant negative associations were observed for yellow-rumped warbler (*Setophaga coronata*) and northern cardinal (*Cardinalis cardinalis*) abundances. Estimated anole effects were stronger for species of greater size and more insectivorous diet, but these differences in estimated effect size were not significant. Species densities of arthropod-consuming birds were also negatively associated with brown anole abundance. Although the observed associations were consistent with the expected effects of exploitative competition for prey, evidence that brown anole invasions were causally responsible for these response patterns was relatively weak. Invaded islands tended to be relatively scrubby, and the explanatory power of brown anole abundance for island avifauna

overlapped strongly with that of environmental covariables. A positive association between brown anole abundance and dove abundance further weakened the evidence for anole–bird competition, as it would seem unlikely that brown anoles mechanistically affected doves. The patterns documented in this study provide a baseline for strengthening the inferences of future studies in this progressively invaded system, in which it should become increasingly possible to differentiate the explanatory powers of brown anoles and environmental variation for island avifaunal communities.

INTRODUCTION

The impacts of invasive species often extend beyond the species with which they directly interact (White et al. 2006). For invasive predators, indirect effects on resident species can include exploitative competition for shared prey resources (e.g., Hrabik et al. 1998, Freed and Cann 2009, Cole and Harris 2011, Ligon et al. 2011, Howe et al. 2016), but the relative importance of such interactions remains largely unknown. Although invasive predators are frequently observed to negatively impact resident species with overlapping diets, studies of these impacts are rarely able to disentangle the potential effects of exploitation competition from those of other mechanisms (e.g., interference competition or intraguild predation) that may also negatively affect resident predators (Reitz and Trumble 2002, Snyder and Evans 2006, Kenis et al. 2009, Medina et al. 2014). For many potentially competing species or taxa, carefully designed experiments will be necessary to elucidate the role of exploitation competition in generating invasion impacts (e.g., Petren and Case 1996). For others, like some groups of insectivorous birds and lizards, a paucity of alternative impact mechanisms may lessen the difficulty of inferring competition for prey.

Introductions of *Anolis* lizards have the potential to indirectly affect resident insectivores, including insectivorous birds, by altering ambient prey densities. Anoles are known to reduce arthropod abundances—particularly larger arthropods and spiders—in a variety of systems ranging from xeric coastal scrub to tropical rainforest canopies (Pacala and Roughgarden 1984, Spiller and Schoener 1988, Dial and Roughgarden 1995, Schoener and Spiller 1996, Schoener et al. 2002), and arthropod prey availability can affect insectivorous birds in a variety of ways. For example, arthropod abundance levels may affect bird foraging dynamics (Krebs et al. 1974, Smith and Sweatman 1974, Holmes and Schultz 1988), habitat use and densities (Root 1967, Hutto 1985, Blake and Hoppes 1986, Johnson and Sherry 2001, Venier and Holmes 2010; but see Champlin et al. 2009), body condition and survival (Gibb 1960, Strong and Sherry 2000, Studds and Marra 2005), and reproductive success (Seagle and Sturtevant 2005, Ligon et al. 2011).

Exploitation competition between anoles and birds may be an important interaction that helped to shape avifaunal composition patterns on Caribbean islands, where *Anolis* lizards are generally a conspicuously abundant component of predator communities and avian insectivore assemblages appear to be relatively depauperate (Terborgh and Faaborg 1980). Although competition between syntopic anoles and avian insectivores does not appear to be an interaction of current importance in the Caribbean (Schoener and Schoener 1982, Adolph and Roughgarden 1983, Bullock and Evans 1990), this unimportance may reflect the outcome of past competitive exclusions or the current prevention, through depressed prey availability (i.e., the R^* mechanism; Tilman 1990), of habitat colonization by insectivorous bird species (Wright 1979, 1981, Moermond 1983, Wright et al. 1984; but see Waide and Reagan 1983). Current anole invasions may provide insight into the historical importance of anole–bird competition in the Caribbean.

Populations of the widely introduced brown anole (*Anolis sagrei*, Polychrotidae) may be particularly likely to negatively impact birds. This small insectivorous lizard, native to several Caribbean islands, has been introduced around the world to locations that include the southeastern United States, Mexico, California, the Hawaiian Islands, Taiwan, and Singapore (Oliver 1950, McKeown 1996, Norval et al. 2002, Calderon et al. 2003, Tan and Lim 2012, Mahrdt et al. 2014). Brown anoles typically attain high densities in both their native and introduced ranges, and in some habitats reach near or above 1 adult lizard per m^2 (Schoener and Schoener 1980, Campbell and Echternacht 2003), a feat matched by few terrestrial vertebrates (Rodda et al. 2001). Since even relatively low densities (for the species) of brown anoles can competitively affect web spiders by reducing the abundances of large aerially-active insects (Spiller and Schoener 1990, Schoener and Spiller 1999), it seems plausible that dense brown anole populations could competitively affect resident insectivores in invaded lands.

Although the impacts of brown anole invasions in the southeastern U.S. are probably offset to some degree by brown anole displacement of the native and ecologically similar green anole (*Anolis carolinensis*), increases in total *Anolis* density are sufficiently great in many invaded habitats that it is reasonable to expect direct and indirect effects to result from increased anole predation pressure on arthropods. In a brown anole introduction study conducted on islands with relatively open, anole-favorable habitats, post-invasion total anole densities were on average about three times greater than green anole densities on uninvaded islands, corresponding to an average difference in total anole density of 2,790 anoles/ha (Campbell 2000). For comparison, differences in brown anole abundance of only 960 anoles/ha were sufficient to directly and indirectly affect several arthropod response groups in experimental enclosures (Spiller and Schoener 1988, 1990, Schoener and Spiller 1999). Moreover, because brown anoles in Campbell's (2000) introduction study tended to be about 1.5 times more massive than green anoles of the same sex and snout–vent length (SVL; adults of both species are similar in SVL), total anole biomass was about 4–5 times greater on invaded than uninvaded islands. Such changes are almost certain to affect the food web dynamics of invaded communities.

Indeed, observational evidence from invaded and uninvaded islands in Florida suggests that brown anole invasion may generate a 25% reduction in foliage-dwelling arthropod abundance and a corresponding 50% reduction in biomass (Chapter 2). As lesser differences in foliage arthropod biomass (averaging 34%) have been associated with reduced foraging activity in avian insectivores (Haemig 1994), it seems likely that invaded islands offer poorer-quality habitats to foliage-gleaning birds than do uninvaded islands—at least for birds foraging in the lowest 2 m of vegetation, where foliage arthropod abundances were estimated. Depleted prey resources could negatively impact the abundances of non-breeding insectivorous birds in several ways. Birds that maintain winter territories may require larger territory sizes on invaded than uninvaded islands, thus reducing bird densities on invaded islands. Birds that move through the landscape may not settle on invaded islands, or they may forage on them for shorter durations of time before moving on. Of course it is also possible that reduced prey resources could reduce the body condition of avian insectivores rather than their abundance, potentially affecting their survival or reproductive success.

I censused winter bird communities on a series of invaded and uninvaded islands in Florida to assess whether the abundances of arthropod-consuming birds varied in concert with brown anole abundance. I expected the abundances of these birds to be negatively associated with brown anole abundance and, further, that the strength of these associations would be stronger for (1) birds that incorporate greater proportions of arthropods into their winter diets, and (2) birds of larger body size, which may depend more heavily on larger arthropod prey (see Janes 1994). Additionally, I expected the abundances of granivorous birds to be unassociated with brown anole abundance.

METHODS

Study system

This study was conducted on a series of 33 dredge-spoils islands in Mosquito Lagoon, Volusia and Brevard Counties, Florida. These islands are part of a linear chain of over 60 islands that were created in the lagoon in the 1940's as a byproduct of dredging operations for the Intracoastal Waterway (ICW), a shipping canal (Campbell 2000). Details regarding the selection and characteristics of study islands have been given elsewhere (Chapter 2); briefly, I selected all the large islands west of the ICW that had open, xeric interiors with surrounding bands of forest and marsh vegetation. Study islands were similar in size (mean = 1.6 ha, SD = 0.6 ha), shape, and distance from the mainland (mean = 240 m, SD = 76 m). Xeric interior and forest habitat vegetation was dominated by southern red cedar (*Juniperus virginiana*) and cabbage palms (*Sabal palmetto*); other vegetation was comprised primarily of wax myrtle (*Morella cerifera*), Brazilian pepper (*Schinus terebinthifolia*), Simpson's stopper (*Myrcianthes fragrans*), and saw palmetto (*Serenoa repens*). Differences in the relative abundances of these species existed across islands, as did differences in the overall extent and stature of the vegetation: islands in the northern half of the lagoon tended to be scrubbier, with shorter and less extensive vegetation cover. Many study islands were connected by marsh habitat to one or two adjacent islands. I considered marsh-connected islands to be independent sampling units under the assumption that relative to similar island pairs with closely-approaching but physically disjunct marshes, the effects of marsh connections on island bird communities would be negligible. Study islands were protected within the combined boundaries of Canaveral National Seashore and Merritt Island National Wildlife Refuge.

Brown anoles probably began invading islands in this system in the late 1980's, when their presence was first reported in Brevard and Volusia Counties (Cochran 1990, Campbell 1996). The available evidence strongly suggests that human recreational use is the primary vector of brown anole propagules onto the islands (Campbell 2000, Chapter 2), and as a result, the spatial configuration and habitat characteristics of invaded islands were highly nonrandom at the time of this study. Invaded islands, particularly those with the highest brown anole abundances (presumably reflecting older invasions), tended to be near boat launches and to have relatively scrubby vegetation (both of these characteristics contribute to greater human recreational use; see Chapter 2). Although successful experimental introductions and unaided invasions of brown anoles on a variety of island types in Mosquito Lagoon demonstrate that the observed invasion patterns predominantly reflect invasion contingencies rather than ecological sorting (Campbell and Echternacht 2003, Stuart et al. 2014, Chapter 2), the correlation of brown anole occurrence and abundance with island spatial configuration, habitat structure, and (to a lesser extent) vegetational composition necessitated the use of analysis strategies and techniques that characterized the degree to which potential brown anole invasion effects ("anole effects") could be co-explained by spatial or environmental covariables.

These islands serve well as a study system for brown anole displacement of green anoles in open, disturbed, or structurally-simple habitats. Brown anole invasion and population expansion has been shown to cause sharp declines in green anole populations on spoils islands in this system (Campbell 2000, Stuart et al. 2014), providing experimental support for anecdotal observations of this phenomenon elsewhere in Florida (e.g., Crews 1980, Christman 1980). On islands of the type used in the current study, remaining green anoles on heavily invaded islands primarily occupy the marsh and adjacent forest–marsh edge habitats of island margins (Campbell 2000), and thus brown anoles effectively replace green anoles in the food webs of interior xeric and forest habitats.

I estimated brown anole abundance on study islands in June 2006 by summing the results of four within-island, 10-minute standardized counts conducted along different segments of the xeric–forest habitat edge (Chapter 2). Mark–resight population density estimates from two study islands were used to convert brown anole count totals into density estimates, and these density estimates were used in conjunction with data from Campbell's (2000) introduction experiment to infer the extent of green anole displacement (see Chapter 2 for details). For heuristic purposes, I divided the study islands into two groups according to the presumed identity of their dominant anole: 20 "green anole islands", of which 14 were uninvaded and 6 were sparsely populated by brown anoles, and 13 "brown anole islands" (Table 4.1). For statistical analyses, however, the $\log_{10}(\text{count} + 1)$ transformation of brown anole total counts—"BA_{Abund}"—was used to model the effects of brown anole invasion on response variables.

Bird activity and species density estimates

I used timed transect counts and point counts to estimate the number of bird individuals and species active in standardized areas on study islands in the winters of 2006, 2007, and 2008 (January 5–13, 4–16, and 1-12, respectively). Because time available for bird censuses was relatively limited, censuses were conducted between 0700 and 1120 h on all available non-rainy days. As a result, time and weather conditions varied substantially among censuses (Table 4.2). I attempted to minimize the effects of this variation on the analyses of interest by (1) varying the order of island visitation in successive censuses within and across years, and (2) statistically controlling for the effects of time and weather on bird activity patterns (see below). Different censusing methods were used in 2006 and 2007–2008.

In 2006, I used two-minute transect counts to estimate bird activity densities and species densities in the xeric habitat of island interiors. Xeric habitats were visually subdivided into four quadrants, with the longitudinal axis of division parallel to the ICW (Chapter 2), and transect count starting points were sited approximately 15 m from the xeric–forest edge in both the northeastern and southwestern quadrants (Figure 4.1a). In each two-minute count, I walked parallel to the xeric–forest edge at slow, standardized pace (~ 10 m/min) and counted all birds heard or seen within 20 m of the transect route. Each transect count was preceded by (1) a two-minute waiting period to allow birds to settle back into their activity patterns following my movement to the transect starting point, and (2) a two-minute point count of all birds heard or seen anywhere on the island (not analyzed here). Each island was censused twice in 2006. Islands were divided into four blocks containing eight or nine consecutive islands that would be censused on the same day, and the order of block censusing was randomized (Table 4.2). Islands within a block were visited from north to south in the first set of censuses and from south to north in the second set of censuses.

In 2007 and 2008, I used two-minute point counts to estimate activity densities and species densities in both xeric and forest habitats. Point counts were sited near the outer "corners" of each quadrant, with xeric count sites located approximately 15 m from the xeric–forest edge and forest count sites located approximately 5 m into the forest (Figure 4.1b). I counted all bird individuals heard or seen within a fixed radius of 20 m in each two-minute count, and all counts were preceded by a two-minute waiting period to allow to birds to settle back to their activity patterns following my movement to the count site. Each forest count immediately followed the xeric count for that quadrant. After each forest count, I briefly made several relatively soft "psshhhh" calls to flush out birds in the immediate area; unless it was apparent otherwise, additional birds detected with these calls were assumed to have been present in the surveyed area during the count and were added to the forest count total. Because the censusing methods used in 2007 and 2008 required more time than those used in 2006, in the latter two years only three or four islands were censused per day and most islands were censused only once in each year. In general, on a given day I censused islands that were two positions apart (e.g., 1, 3, 5, 7) to lessen the potential for confounding between weather conditions and island characteristics, as adjacent islands tended to be more similar in habitat structure and brown anole invasion status than islands farther apart. As in 2006, the order of block censusing was randomized. Insufficient time was available for censusing in 2008, and as a result eight islands were not censused in that year (Table 4.1); these uncensused islands were similar in location, habitat characteristics, and invasion status to islands that *were* censused in 2008.

On two occasions the presence of a *Buteo* hawk caused birds to be unusually quiet and inactive during a census; these two censuses were omitted from analyses (Table 4.1).

Point and transect count totals represent the minimum number of individuals or species active in the count area over the two-minute count period. Care was taken to avoid counting individual birds more than once in a given count, and I erred on the side of caution when uncertain about the number of unique individuals. Flocks of dozens or even hundreds of yellow-rumped warblers (YRWA; *Setophaga coronata*) were active on the islands in 2007 and 2008, and because it was impossible to simultaneously keep track of dozens of YRWA as they flitted about, counts for this species in several instances greatly underestimated true activity densities. When it was apparent that far more YRWA were active in the count area than I could keep track of, I added 20% to the YRWA count total, and I am reasonably certain that these adjusted counts still underestimated the true activity densities.

Although the degree to which activity density estimates accurately reflected habitat use intensity may have been influenced by the horizontal movement patterns of the particular birds in question, the short duration of the counts suggests that they provided a relatively good, approximately scale-independent measure of habitat use, and thus bird abundance (I will refer to activity densities interchangeably as abundances). Species density estimates, however, were no doubt influenced nonlinearly by the total area surveyed, and thus the results of species density analyses must be interpreted within the context of survey area size.

Counted birds were classed into three dietary groups for analyses: insectivores, omnivores, and granivores (i.e., doves). With the exception of YRWA, insectivores were species that maintained primarily insectivorous diets in winter, including multiple wren and warbler species, blue-gray gnatcatchers (*Polioptila caerulea*), and white-eyed vireos (*Vireo griseus*).

Although quantitative data are limited (reviewed in Hunt and Flaspohler 1998), YRWA winter diets are frequently comprised largely of fruits (including the fleshy cones of red cedar), especially in habitats containing wax myrtle (Yarbrough and Johnston 1965, Lowe 2005); for this reason and because YRWA were by far the dominant component of censused bird communities, I analyzed YRWA and non-YRWA insectivores separately. Omnivores were species for which arthropods comprise a minor but nontrivial fraction (around 5–25%) of an otherwise plant-based (fruits and seeds) winter diet; this group consisted of northern cardinals (*Cardinalis cardinalis*), gray catbirds (*Dumetella carolinensis*), red-winged blackbirds (*Agelaius phoeniceus*; diets reviewed in Halkin and Linville 1999, Smith et al. 2001, and Yasukawa and Searcy 1995, respectively). Granivores were species with seed-based diets that rarely consume arthropods in winter; because this group was comprised solely of common ground doves (*Columbina passerina*) and mourning doves (*Zenaida macroura*; diets reviewed in Bowman 2002 and Otis et al. 2008, respectively), I refer to it simply as “doves”. All counted birds were assigned to one of the above groups for analyses, except for single instances of a probable vulture or heron heard flying away, a pileated woodpecker (*Dryocopus pileatus*), and a tree swallow (*Tachycineta bicolor*). The latter two of these birds were excluded from analyses under the assumption that they consumed insects unlikely to be affected by anoles. Birds heard during counts that could not be identified to species were assumed to be insectivores because (1) most of the sounds in question were warbler calls that I could not identify with certainty, and (2) the non-insectivores (doves, herons, egrets, raptors, and vultures) and omnivores known to be present on the islands in winter could be ruled out.

In several analyses, insectivorous and omnivorous birds were pooled together as “all arthropod-consuming birds”.

Explanatory covariables

I used sets of environmental and spatial covariables to characterize the extent to which the explanatory power of BA_{Abund} for avian response patterns overlapped with that of island habitat characteristics and spatial position attributes. Separate covariable sets were assembled for xeric habitat and forest habitat responses.

Environmental covariable sets included variables related to the structure and vegetational composition of xeric and forest habitats. Because many aspects of these habitats were correlated (e.g., the size and proportional vegetation cover of xeric habitats), I used principle component analyses (PCAs) to extract the main axes of multivariate variation in habitat structure and vegetational composition. The first two principle components were retained in each PCA, and together these captured 74–85% of the variation in habitat structure variables and 73–74% of the variation in vegetation composition (Table 4.3). With the exception of mean point count visibility, details concerning the habitat structure variables used in PCAs are given in Chapter 2. The average distance of unobstructed radial visibility was visually estimated for each xeric point count site in 2007, and the grand average of these visibility distances for each island—mean point count visibility—was incorporated into the PCA of xeric habitat structure. Vegetation composition PCAs incorporated the cover class estimates of the common plant species (see Chapter 2 for cover estimation details). Since some forest habitat was surveyed in xeric counts and vice versa (see Figure 4.1), xeric and forest vegetation cover estimates were combined prior to PCA with a 2:1 weighted averaging scheme that gave greater weight to the cover estimates of the habitat being analyzed. In contrast to habitat structure PCAs, vegetation composition PCAs were performed on covariance matrices. Simpson's diversity estimates for plant cover (as described in Chapter 2) were also included in environmental covariable sets. Xeric and forest diversity estimates were averaged for each island using, again, a 2:1 weighting scheme giving greater weight to the habitat under analysis.

Spatial covariable sets included (1) spatial variables potentially affecting the use of islands by birds, and (2) factors related to the spatial configuration of islands. Variables potentially affecting bird use of islands included minimum distance from the mainland and an index of island isolation. Island isolation was calculated as the weighted average of the minimum distances to the island's nearest northern and nearest southern neighbors (islands with areas less than 1,000 m^2 were not counted as neighbors), with a weighting ratio of 2:1 in favor of the closest neighboring island. Spatial configuration was captured by the linear position of islands along the ICW (Table 4.1) and a best-fitting set of Moran's eigenvector maps (MEM). The MEM approach (Dray et al. 2006) uses the eigenvalue decomposition of a matrix of geographical distances among sampling units to generate spatial variables that are suitable for use in regression analyses. The incorporation of a spatial weighting matrix gives the MEM approach great flexibility in modeling distance–similarity relationships among sampling units, and the selection of this weighting matrix is the most critical MEM step; when the appropriate or expected spatial weighting matrix is unknown, Dray et al. (2006) recommend the selection of a best-fitting weighting matrix. I generated 126 unique spatial weighting matrices (using two different connectivity algorithms and a two-parameter distance–similarity function; see Chapter 2) and selected, for each habitat, the weighting matrix that produced MEM with the greatest explanatory power for community-level patterns in the activity densities of arthropod-consuming birds. MEM devolved from these weighting matrices that significantly explained both spatial autocorrelation structure and community-level variation in bird activity densities were retained for spatial covariable sets (see Chapter 2 for details concerning MEM generation, selection, and retention). No MEM were retained for xeric bird analyses (i.e., under the selection criteria, no MEM offered a significant explanatory improvement over position along the ICW), and one MEM was retained for forest bird analyses.

Statistical analyses

I used a multi-pronged modeling strategy to assess the explanatory power of BA_{Abund} for bird assemblage response patterns and characterize the extent to which it overlapped with the competing explanatory power of environmental and spatial covariables. Each response was analyzed under the “anole”, “best”, and “full” models. The anole model was the least conservative of the three models, as BA_{Abund} served as its sole explanatory variable (ignoring time and weather-related variables, which were incorporated, when significant, into all models for a given response). In most cases, the anole model yielded the maximum amount of response variation and greatest effect size attributable to BA_{Abund}, but for some responses the magnitude of these measures increased when other explanatory covariables were added to the model. A best model was selected for each response that maximized parsimony (under the model selection criteria) and provided a more conservative estimate of BA_{Abund} explanatory power. The full model incorporated all relevant covariables—environmental for univariate responses and both spatial and environmental for multivariate dissimilarity analyses (see below)—irrespective of their significance, and thus served as the most conservative estimate of BA_{Abund} explanatory power that yielded, in most cases, the minimum amount of response variation and smallest effect size attributable to BA_{Abund}. Together, the anole, best, and full models provided a strength-of-evidence hierarchy for the effects of brown anoles on avifaunal responses. The attributes of this analysis strategy and its advantages for the spoils islands study system are discussed more fully in Chapter 2.

For univariate responses, I complemented the above strategy with a fourth approach: model-averaged estimates of BA_{Abund} effects. In this information-theoretic, “average” model approach, AICc-based Akaike weights from all possible explanatory variable models were used to derive a multimodel-averaged estimate of the BA_{Abund} regression coefficient (Burnham and Anderson 2002), and this averaged coefficient was in turn converted into an estimate of expected invasion effect. Additionally, the sum of these weights across all models incorporating BA_{Abund} measured the weight of evidence (scaled 0–1) that BA_{Abund} belonged in the best Kullback–Leibler (K–L) model for the response (i.e., the model estimated to best approximate the unknown truth, given the set of considered models; Burnham and Anderson 2002).

Time and weather-related variables were given priority over all other explanatory variables for entry into models. In general, I backward selected a best time/weather model from a starting model that included time, temperature, cloud cover, wind strength, and the time*temperature interaction. Time and weather variables that significantly ($\alpha = 0.10$) explained variation in a given response were incorporated into all subsequent models for that response.

All statistical analyses were performed in the R statistical programming environment (version 3.2.3; R Core Team 2015), and unless noted otherwise (e.g., time/weather model selection), $\alpha = 0.05$ was used to establish significance in all statistical tests.

To characterize the nature of BA_{Abund} explanatory power for community-level patterns in the activity densities of arthropod-consuming birds, I used distance-based redundancy analysis (db-RDA; Legendre and Anderson 1999) to partition the community-level variation explained by BA_{Abund} and explanatory covariable sets into jointly-explained and uniquely-explained fractions. Db-RDA is a form of constrained ordination that allows Bray-Curtis dissimilarities (used in this study) or other ecologically relevant dissimilarity measures to serve as the basis for sample unit distance or dissimilarity matrices. As described in greater detail in Chapter 2, I performed separate db-RDAs for each explanatory variable set ($\mathrm{BA}_{\mathrm{Abund}}$, environmental, and spatial) and all combinations thereof. The resulting R^2 values were adjusted to correct the bias introduced by small sample sizes (Peres-Neto et al. 2006), and these adjusted values (R^2_{adj}) served as inputs in a variation partitioning algorithm that divided the dissimilarity explained across all three explanatory variable sets into seven fractions of uniquely or jointly explained variation (Borcard et al. 1992, Økland 2003). I also performed stepwise selection (using α = 0.05 for variable entry and retention in the model and a maximum R^2_{adj} stopping rule set by the full model; see Blanchet et al. 2008) to select a best db-RDA model. The significance of R^2_{adj} fractions explained uniquely by $\mathrm{BA}_{\mathrm{Abund}}$ in the anole, best, and full models ($R^{2,\,\mathrm{BA}}_{\mathrm{adj}}$, $R^{2,\,\mathrm{BA-Best+S}}_{\mathrm{adj}}$, and $R^{2,\,\mathrm{BA-Full+S}}_{\mathrm{adj}}$, respectively; following Chapter 2, the “+S” superscript denotes the use of spatial covariables in the partitioning analyses) was determined by permuting db-RDA residuals (9,999 permutations) under the reduced model (ter Braak and Šmilauer 2002). Db-RDAs and tests of R^2_{adj} significance were performed using the R package ‘vegan’ (Oksanen et al. 2016). Because permutational tests of multivariate location (like db-RDA) can be affected by differences in the multivariate dispersion of the populations of interest, I also used the vegan function “betadisper” to test (with 9,999 permutations) whether community dissimilarities among green anole islands differed in dispersion from those of brown anole islands.

Species-level activity densities were averaged across years for xeric and forest habitat db-RDAs. Within-year count totals for each species were averaged by island and then divided by count survey area (0.206 ha in 2006 and 0.126 ha in 2007–2008) to yield yearly mean activity densities for each island, and these yearly means were averaged to derive the across-year island means. Bird species occurring on only one or two islands (≤ 6.1% of islands) in the across-year means for a given habitat were considered poorly sampled and were excluded from corresponding db-RDAs (see McCune and Grace 2002). Across-year island means were square-root transformed prior to db-RDA in order to reduce the influence of the numerically dominant species (YRWA) in Bray-Curtis dissimilarity measures.

Prior to the averaging described above, within-year time and weather adjustments were applied to the count totals of species that were detected on a majority of the islands in that year (data were too sparse to allow such adjustments for less frequently detected species). Generalized linear mixed-effects models (GLMMs) with a Poisson error distribution and log link were implemented in the R package 'lme4' (Bates et al. 2015) for backward selection of time/weather models; island and census-level (nested within island) random intercept effects were incorporated into these models, and centered time and weather variables served as fixed effects. The significance of fixed effect variables was evaluated with parametric bootstrap tests in the R package 'pbkrtest' (Halekoh and Højsgaard 2014). A minimum of 499 bootstrap samples were generated in each test, and additional samples were generated when estimated *P* values were near the significance cutoff ($\alpha = 0.10$). As a hedge against the possibility that backward selection led to a suboptimal time/weather model, I also compared the backward-selected model's AICc score (Hurvich and Tsai 1989; calculated using the number of censuses as the number of samples) to the AICc scores of all possible time/weather models (generated with the restriction that individual time and temperature terms must occur in any model that included their interaction). In most cases the backward-selected model also had the lowest AICc score, but in cases where it did not I used a lower-AICc model for count adjustments if (1) all terms in that model were significant at $\alpha = 0.10$ and (2) parametric bootstrap tests indicated that the backward selection model did not offer a significant improvement ($\alpha = 0.10$) over the lower-AICc model (note that this second requirement applied only to nested models). Once a time/weather model was selected for a given bird species in a given habitat, I used it to statistically remove time and weather effects by subtracting from count totals the difference between their fitted values and their model-predicted values under average time and weather conditions. Count adjustments occasionally led to negative census-level average activity densities, and in these cases the negative averages were replaced with zeroes.

To visualize patterns in island bird communities, I plotted the best two-dimensional nonmetric multidimensional scaling (NMDS) solutions obtained from the data used in db-RDAs (i.e., from the Bray-Curtis dissimilarities of the across-year averaged, rare species-dropped, square-root transformed activity densities of arthropod-consuming bird species). Best solutions were obtained using the vegan function “metaMDS” and three successive runs of up to 50 random-start iterations; runs terminated when the stress of an iteration’s solution was equivalent to the stress of the running set-best solution, and successive runs retained the best solution of the prior run. To aid the visual interpretation of NMDS results, in NMDS plots I distinguished three groups of islands by their invasion status: (1) uninvaded islands, (2) invaded islands on which brown anoles were relatively rare and green anoles were presumably still the dominant anole, and (3) heavily invaded islands.

I analyzed the activity densities of individual species and response groups with Poisson (log-link) GLMMs. Counts were not averaged in these analyses but were modeled directly (Bolker et al. 2009, O'Hare and Kotze 2010), with year, island, and census (nested within both island and year) serving as random intercept effects. Fixed effects included BA_{Abund} and environmental covariables; spatial covariables were not used in these analyses because db-RDAs indicated that environmental covariables also captured the variation in bird communities that was co-explained by both BA_{Abund} and spatial covariables (see also Chapter 2). Explanatory variables were centered in all GLMMs. For each response, I tested for overdispersion in the full model by comparing the sum of its squared Pearson residuals and residual degrees of freedom to a X^2 distribution with the appropriate degrees of freedom (Venables and Ripley 2002, Bolker et al. 2009). This estimate of overdispersion was only approximate, however, because the number of parameters involved in GLMM is not well-defined (Bolker et al. 2009) and expected mean counts were less than five in all models (see Venables and Ripley 2002, p. 209); I counted each variance or covariance parameter as one degree of model freedom in determining the residual degrees of freedom. When the full model was estimated to be overdispersed, I added a sample-level random effect to all models for that response to eliminate the overdispersion (Harrison 2014; note that excess zeroes were not the cause of overdispersion in the relevant activity density models). Because counts were modeled directly and were not divided by survey area to yield true activity density estimates, xeric habitat GLMMs were not technically activity density models, as survey areas were greater in 2007 than in 2008–2009. This difference in survey area probably served to lessen the magnitude of the negative random year effect for 2007 (fewer birds were detected on all islands in this year despite greater surveyed areas), but it is unlikely that the fixed effects of interest were qualitatively affected.

Species densities—the number of species active in the survey area during the counts—were also analyzed with Poisson GLMMs, as described above for activity densities.

Anole, best, and full GLMMs were constructed for each response after the best-fitting time and weather model was determined. Time/weather models were selected as described above for db-RDA, but counts were not adjusted to mean time/weather conditions; instead, selected time and/or weather variables were incorporated as explanatory variables into all models for the corresponding response. Best models were selected on the basis of lowest AICc score among all possible BA_{Abund} and environmental covariable models; I used the number of islands (33) as a conservative estimate of sample size for AICc calculations (see Whittaker and Furlow 2009). As a preliminary assessment of the significance of BA_{Abund} in the anole, best, and full GLMMs, I used likelihood ratio tests to compare each model to the without-BA_{Abund} version of the same model. When likelihood ratio test *P*-values were less than 0.20, I determined significance with computationally-intensive parametric bootstrap tests (using a minimum of 999 samples).

To illuminate the association between BA_{Abund} and activity density or species density responses, I used BA_{Abund} regression coefficients to derive the model-predicted effect of brown anole replacement of green anoles in island food webs (hereafter “replacement effect”, “RE”). BA_{Abund} regression coefficients (β_{BA}) were multiplied by 1.308—the increase in BA_{Abund} corresponding to the average untransformed difference in brown anole abundance between brown anole and green anole islands (Chapter 2)—to generate the natural log of the predicted multiplicative effect on the response, and a value of 1 was subtracted from the predicted multiplicative effect to yield the predicted proportional change in the response (i.e., the RE). For example, β_{BA} of -1.23, 0.0, and 0.310 corresponded to, respectively, predicted multiplicative effects of 0.2, 1.0, and 1.5 and REs of −0.8, 0.0, and 0.5. The above calculations were also applied to the ± 1.96*SE confidence interval bounds of β_{BA} estimates to generate 95% confidence intervals around the corresponding REs. Replacement effect estimates were calculated for each of the anole, best, and full models ($\mathrm{RE}_{\mathrm{Anole}}$, $\mathrm{RE}_{\mathrm{Best}}$, and $\mathrm{RE}_{\mathrm{Full}}$, respectively); $\mathrm{RE}_{\mathrm{Best}}$ was defined as zero for best models that did not incorporate $\mathrm{BA}_{\mathrm{Abund}}$. Additionally, $\mathrm{RE}_{\mathrm{Avg}}$ values were calculated from model-averaged estimates of β_{BA} and their unconditional standard error confidence intervals using the R package 'AICcmodavg' (Mazerolle 2015). All possible $\mathrm{BA}_{\mathrm{Abund}}$ and environmental covariable models were used for $\mathrm{RE}_{\mathrm{Avgs}}$, and model-averaged β_{BA} estimates were computed with the "zero method", in which β_{BA} and its error variance were defined as zero for models lacking $\mathrm{BA}_{\mathrm{Abund}}$ as a predictor (Burnham and Anderson 2002, Lukacs et al. 2010, Grueber et al. 2011). In a few instances, problems with model convergence caused β_{BA} standard error estimates to be excessively small in one or more models for a given response; such models were excluded from calculations of model-averaged β_{BA} standard error. In the single instance in which the β_{BA} standard error estimate was excessively small for a model of primary interest—the anole model for forest-counted non-YRWA small insectivores—, β_{BA} was averaged over those models (among all possible) that contained $\mathrm{BA}_{\mathrm{Abund}}$ (i.e., the "natural average"; Burnham and Anderson 2002, Grueber et al. 2011) and the unconditional standard error of this estimate was used to generate the corresponding $\mathrm{RE}_{\mathrm{Anole}}$ confidence interval.

Several aspects of REs are worth noting. First, due to their multiplicative effect derivation, positive REs were unbounded and negative REs were bounded by −1. Second, because REs were calculated through the back-transformation of log–linear models, relative differences in RE magnitude were not proportional to relative differences in the corresponding β_{BA} estimates. Third, $\mathrm{RE}_{\mathrm{Avgs}}$ were not evaluated for statistical significance, though they could perhaps be considered the equivalent of statistically significant where their 95% confidence intervals did not overlap zero (see Burnham and Anderson [2002] for arguments against the use of significance terminology in information-theoretic approaches). Finally, the value of $\mathrm{RE}_{\mathrm{Avgs}}$ for statistical inference was secondary to that provided by the combination of $\mathrm{RE}_{\mathrm{Anole}}$, $\mathrm{RE}_{\mathrm{Best}}$, and $\mathrm{RE}_{\mathrm{Full}}$ because (1) $\mathrm{RE}_{\mathrm{Avgs}}$ were not evaluated with parametric bootstrap tests, which reduce the chances that influential observations or departures from model assumptions will lead to type I errors, and (2) the model redundancy inherent to the all-explanatory-models averaging approach can affect the quality of the resulting model-averaged parameter estimates (see Grueber et al. 2011). The primary heuristic value of the $\mathrm{RE}_{\mathrm{Avg}}$ approach was its comparison to the other REs: because $\mathrm{RE}_{\mathrm{Avg}}$ (but not $\mathrm{RE}_{\mathrm{Anole}}$, $\mathrm{RE}_{\mathrm{Best}}$, or $\mathrm{RE}_{\mathrm{Full}}$) magnitudes were necessarily lessened by the degree of explanatory overlap between $\mathrm{BA}_{\mathrm{Abund}}$ and environmental covariables, the extent of $\mathrm{RE}_{\mathrm{Avg}}$ "shrinkage" towards zero (relative to the other REs) provided a measure of the degree to which $\mathrm{BA}_{\mathrm{Abund}}$ uniquely explained response variation.

RESULTS

Yellow-rumped warblers comprised the vast majority of counted birds in both habitats in all years (Table 4.4), and were thus the most important contributor to community-level patterns in the activity densities of arthropod-consuming birds. In the absence of other covariables, $\mathrm{BA}_{\mathrm{Abund}}$ explained 4.3% and 3.0% of the community-level variation in these activity densities for xeric-counted and forest-counted birds, respectively ($R^{2,\,\mathrm{BA}}_{\mathrm{adj}}$, Figure 4.2). Although $R^{2,\,\mathrm{BA}}_{\mathrm{adj}}$ was significant ($P = 0.043$) for xeric-counted birds, this significance was at least partly due to lower levels of dispersion among brown anole islands than among green anole islands (pseudo-F =

10.12, $P = 0.003$). By contrast, the marginal significance ($P = 0.078$) of $R_{\mathrm{adj}}^{2,\mathrm{BA}}$ for forest-counted birds was not influenced by differences in dispersion (pseudo-$F = 0.09$, $P = 0.76$). In both habitats, $\mathrm{BA}_{\mathrm{Abund}}$ explanatory power for community-level variation in the activity densities of arthropod-consuming birds overlapped completely with the explanatory power of environmental covariables (Figure 4.2), and $\mathrm{BA}_{\mathrm{Abund}}$ did not occur in the stepwise-selected best db-RDA model for either habitat.

Within communities, $\mathrm{BA}_{\mathrm{Abund}}$ was negatively associated with the activity densities of several arthropod-consuming species and groups (Figure 4.3). These associations were significant in at least one model for xeric and forest non-YRWA insectivores ($\mathrm{RE}_{\mathrm{Best}} = -0.64$ and -0.41, $P = 0.024$ and 0.026, respectively), xeric omnivores ($\mathrm{RE}_{\mathrm{Best}} = -0.53$, $P = 0.046$), forest arthropod-consuming birds ($\mathrm{RE}_{\mathrm{Anole}} = -0.26$, $P = 0.028$), and forest gray catbirds ($\mathrm{RE}_{\mathrm{Best}} = -0.62$, $P = 0.021$). Negative associations were marginally significant in a single model for xeric arthropod-consuming birds ($\mathrm{RE}_{\mathrm{Anole}} = -0.28$, $P = 0.090$), xeric northern cardinals ($\mathrm{RE}_{\mathrm{Full}} = -0.55$, $P = 0.064$), and forest YRWA ($\mathrm{RE}_{\mathrm{Anole}} = -0.24$, $P = 0.080$). In general, RE patterns were similar for responses analyzed in both habitats.

Species densities of arthropod-consuming birds were also negatively associated with $\mathrm{BA}_{\mathrm{Abund}}$ (Figure 4.4). Total species densities for arthropod consumers were significantly associated with $\mathrm{BA}_{\mathrm{Abund}}$ in both xeric ($\mathrm{RE}_{\mathrm{Anole}} = -0.22$, $P = 0.011$) and forest habitats ($\mathrm{RE}_{\mathrm{Best}} = -0.19$, $P = 0.025$), and marginally significant negative associations were observed for the species densities of xeric omnivores ($\mathrm{RE}_{\mathrm{Full}} = -0.63$, $P = 0.081$) and forest insectivores ($\mathrm{RE}_{\mathrm{Anole}} = -0.16$, $P = 0.082$). The species density RE patterns of most response groups largely reflected the activity density RE pattern of their numerically dominant member: yellow-rumped warblers for insectivores and all arthropod-consumers in both habitats, and northern cardinals for xeric omnivores. On average and across years (calculated as in Table 4.4), 0.8 insectivore species and 0.2 omnivore species were detected per count in xeric habitat censuses, and 1.2 insectivore species and 0.3 omnivore species were detected per count in forest censuses.

In contrast to insectivorous and omnivorous birds, dove activity densities were positively associated with BA_{Abund} in xeric habitats ($RE_{Best} = 3.00$, $P = 0.001$; Figure 4.3a). Dove REs were much larger in magnitude than insectivore and omnivore REs because positive REs scaled from 0 to infinity, whereas negative REs scaled from 0 to −1 (reversing the sign of the BA_{Abund} regression coefficient in the best dove model would yield a RE_{Best} of −0.75).

BA_{Abund} did not significantly explain response variation independently of all environmental covariables for any analyzed response. However, RE_{Full} estimates approached significance for the activity densities of xeric northern cardinals and xeric doves (doves: $RE_{Full} = 2.3$, $P = 0.051$) and the species densities of forest omnivores.

DISCUSSION

Arthropod-consuming bird abundances were negatively associated with brown anole abundance on spoils islands, but evidence that these associations represented indirect effects of anole-induced arthropod declines was relatively weak. BA_{Abund} explanatory power for avifaunal response patterns overlapped extensively with the explanatory power of environmental covariables, such that (1) BA_{Abund}-explained dissimilarity in the composition of arthropod-consuming bird communities was completely nested within the dissimilarity explained by environmental covariables (Figure 4.2); (2) BA_{Abund} was not significant in the full model for any arthropod-consuming response group (Figures 4.3, 4.4); and (3) summed all-models Akaike weights for most responses either did not support or provided ambivalent support for the occurrence of BA_{Abund} in the best approximating (i.e., K–L) model. Due to this extensive explanatory overlap, evidence for anole effects on birds was restricted to BA_{Abund} significance in parsimony-based best models and consistency between observed and mechanistically-expected response patterns.

Although BA_{Abund} inclusion in the most parsimonious abundance models of several arthropod-consuming bird responses was certainly consistent with anole effects, it did not provide strong statistical evidence for them (see Chapter 2), especially in the absence of full-model BA_{Abund} significance. Such best-model evidence for anole effects was strongest for forest-counted, non-YRWA insectivore abundances—the only insectivore or omnivore response for which summed Akaike weights provided moderate support for the occurrence of BA_{Abund} in the best K–L model. However, the even greater Akaike weight support for BA_{Abund} in the best abundance model for xeric-counted doves illustrates the danger, in this system, of using parsimony as the primary basis for inference. Since it seems highly unlikely that brown anoles mechanistically affected dove abundances, the observed positive association between brown anoles and doves was almost certainly driven by an unmodeled environmental or spatial factor that was correlated with BA_{Abund}. As with the doves, best-model evidence for anole effects on arthropod-consuming birds must be evaluated with respect to likely ecological mechanisms.

Beyond the negative direction of associations between brown anoles and arthropod-consuming birds, two other mechanistically-expected response patterns provide additional—albeit weak—evidential support for competitive anole–bird interactions.

First, for similarly-sized bird species, modeled anole effects were stronger for birds with more insectivorous diets. In both xeric and forest habitats, RE magnitudes were much larger for non-YRWA insectivore abundances than for yellow-rumped warbler abundances (Figure 4.3). Species comprising the non-YRWA insectivore group were warbler-sized and strongly or entirely insectivorous in winter (for the four most abundant species, see reviews in Guzy and Ritchison 1999, Wilson 2013, Haggerty and Morton 2014, and Johnson 2014), whereas yellow-rumped warblers in coastal habitats incorporate large amounts of fruit into their winter diets (reviewed in Hunt and Flaspohler 1998). Among the two most abundant omnivore species, northern cardinals and gray catbirds, within-habitat RE magnitudes were greater for the more strongly insectivorous gray catbirds (Figure 4.3b; diets reviewed in Halkin and Linville 1999, Smith et al. 2011). The possibility exists, however, that differences in fruit abundance rather than arthropod abundance were responsible for these expected RE patterns. Wax myrtle fruit availability may have been the primary driver of yellow-rumped warbler abundance patterns (Borgmann et al. 2004, Kwit et al. 2004, Lowe 2005), and thus the relative weakness of BA_{Abund}–YRWA associations may have reflected the lack of correlation between BA_{Abund} and wax myrtle relative cover estimates (xeric: $r = -0.08$, $P = 0.68$; forest: $r = -0.23$, $P = 0.19$; note that relative cover estimates do not necessarily reflect fruit abundance). *Total* fruit availability, on the other hand, may have been lower on invaded islands, as the summed relative cover estimates of plant species bearing winter fruits or fleshy cones (wax myrtle, Brazilian pepper, and red cedar) were negatively correlated with BA_{Abund} (xeric: $r = -0.37$, $P = 0.033$; forest: $r = -0.32$, $P = 0.068$). If seed consumption causes northern cardinals to be less reliant than gray catbirds on the availability of fruit in the environment, then the possibility exists that lower fruit abundance on invaded islands was responsible for the difference in RE magnitudes observed for these two species.

Second, modeled anole effects were greater for larger birds than for similarly-insectivorous birds of smaller size. Such a pattern was expected on the basis that negative associations between BA_{Abund} and foliage arthropod abundance and biomass were driven by lower abundances of the largest arthropods (Chapter 2), and larger-bodied arthropod-consuming birds are presumably more dependent upon larger-bodied arthropod prey than are smaller birds (see Janes 1994). Given the set of frequently observed bird species, the only available test of this expectation is a comparison between the response patterns of yellow-rumped warblers and gray catbirds, as both of these species tend to consume more fruit than arthropods in the winter (Hunt and Flaspohler 1998, Smith et al. 2011) and neither species is likely to frequently consume seeds. Gray catbird RE estimates were larger in magnitude and stronger in statistical significance than were yellow-rumped warbler REs (Figure 4.3), matching the expected pattern. However, if arthropod abundances did indeed causally contribute to these RE differences, it is possible that bird foraging location rather than large arthropod abundance *per se* was responsible: gray catbirds were usually observed in the lowest 2 m of vegetation, where foliage arthropod sweep samples were collected and the impacts of brown anole invasion on arthropods are presumably greatest (see Chapter 3), whereas yellow-rumped warblers were generally observed at vegetation heights above 2 m, where invasion impacts on arthropods are probably weaker. For all of the above comparisons (less insectivorous vs. more insectivorous, small-bodied vs. large-bodied), it is important to note that compared REs had overlapping confidence intervals and were thus statistically indistinguishable (with the exception of RE_{Best} comparisons between best models with and without BA_{Abund}).

Although exploitative competition appears to be the most plausible form of ecological interaction between anoles and the winter avifauna of spoils islands, other interaction types may also have affected the abundance patterns of arthropod-consuming birds. Apparent competition is one such possibility, whereby brown anoles could negatively impact birds by increasing the abundance or foraging intensity of their shared predators (Holt 1977). Two non-avian anole predators are common in this study system: black racers (*Coluber constrictor*) and raccoons (*Procyon lotor*). Although observational evidence suggests that black racers are more abundant on invaded spoils islands (Turnbough 2010), they do not appear to be an important predator of adult birds (Hamilton and Pollack 1956, Klimstra 1959, Halstead et al. 2008) and, in any case, they probably remain relatively inactive during the cooler winter months. Nevertheless, black racers on spoils islands do at least emerge to bask on warm winter days (Turnbough, pers. obs.), and their mere presence may reduce perceived habitat quality for some birds; racers could also negatively impact the winter abundances of resident bird species (northern cardinals and Carolina wrens) via the carry-over effects of nestling predation pressure during the breeding season. No island abundance data are available for raccoons, but a potential index of their summer activity levels—disturbed pitfall traps—was not significantly associated with brown anole invasion status (Turnbough, unpubl. analyses; see also Chapter 2: Appendix S2). Raccoons are important nest predators (e.g., see Schmidt 2003 and references therein), and if their abundances affect the winter avifauna of spoils islands, it is likely through the carry-over effects of breeding season nest predation. Bird predation on anoles is a second interaction that could potentially affect avian abundance patterns. A wide variety of arthropod-consuming birds, including those of small body size, are known to prey on anoles (Poulin et al. 2001, Sykes et al. 2007, Powell and Henderson 2008, Pipher and Cox 2011). Among the species observed in the current study, anole predation is known for northern cardinals (Turnbough, pers. obs.), Carolina wrens (Birkhead and Benny 2014), and white-eyed vireos (Chapin 1925), and it should probably be expected for house wrens (which are known to prey on other small lizards; Barquero and Hilje 2005) and gray catbirds. However, since birds would presumably only benefit from anole consumption, this interaction cannot explain the observed negative associations between brown anoles and arthropod-consuming birds.

The positive association between BA_{Abund} and dove abundance constituted the only unmet expectation in this study. That this association occurred is not surprising: invaded islands tended to be relatively scrubby, and both mourning doves and common ground doves prefer more open habitats (Bowman 2002, Currie et al. 2005, Otis et al. 2008). The near significance of the dove RE_{Full} estimate warrants concern, however, because it suggests that an important BA_{Abund}-correlated covariable was not incorporated into the analyses. I offer three possible explanations for this pattern. First, the unique explanatory power of BA_{Abund} for dove abundance may have simply resulted from sampling error. Doves were detected in only 7.6% of the counts, fewer than any other analyzed response, and just a few more dove detections on uninvaded islands may have substantially increased the explanatory overlap of BA_{Abund} and environmental covariables. Second, the association may reflect landscape patterns that were not well captured by environmental covariables. In a study of citrus grove avifauna on nearby Merritt Island (Mitchell et al. 1995), mourning dove abundance was unassociated with grove characteristics but was negatively associated with deciduous woodland representation along grove edges (all other edge habitat types were more open). In a similar manner, dove abundances on spoils islands may have been influenced more by proximity to open habitats on the mainland (e.g., boat launches and rural development) than by island habitat characteristics, and thus the strong brown anole–

dove association may have reflected the strong link between invasion status and boat launch proximity (Chapter 2). Finally, the anole–dove association may have been driven by one or more unmeasured, BA_{Abund}-correlated habitat characteristics. Unmeasured characteristics of the typically scant herbaceous vegetation in xeric habitats, for example, may have affected the seed resources available to doves.

The lack of unique BA_{Abund} explanatory power for arthropod-consuming bird abundances may have resulted from insufficient sampling. Most islands were censused only once in most years (Table 4.1), under varying weather conditions (Table 4.2). Given the variability in the resulting count data, this level of sampling did not provide adequate statistical power for differentiating the explanatory power of correlated variables. Within-island count variation was relatively high (1) within censuses, (2) between censuses in a given year, and (3) between years. For example, xeric yellow-rumped warbler counts on island "D9" were [2, 1, 1, 0] in the first 2007 census, [14, 14, 7, 2] in a second 2007 census, and [3, 2, 4, 0] in the single 2008 census. Such levels of variation were not uncommon. Although differences in census conditions (time and weather) were controlled for statistically and the random effects of census and year were incorporated into models, too few data were collected to permit the estimation of relatively tight confidence intervals around model regression coefficients, and consequently the modeled effects of BA_{Abund} were statistically confounded with those of environmental covariables.

The actual, unknown patterns of winter arthropod abundance on spoils islands might also have contributed to the lack of resolution between competing BA_{Abund} and environmental covariable explanations for avifaunal response patterns. Expectations of competitive anole effects on winter bird communities were based on early-summer foliage arthropod samples, and though it is reasonable to expect anole effects on arthropod abundances to persist into winter, the sizes of those effects may be smaller during the winter dry season. In the Bahamas, Spiller and Schoener (1995) found the yearly effect size of lizards (predominantly brown anoles) on web spiders to be negatively correlated with drier climactic conditions, and a similar phenomenon could occur on a seasonal basis on spoils islands. If, for example, large foliage-dwelling arthropods are rare on all spoils islands in winter, then winter foliage arthropod communities, as well as the avifauna that interact with them, may differ little on invaded versus uninvaded islands. Moreover, year-to-year variation in winter arthropod abundance, to the extent that it existed, could have reduced signal-to-noise ratios in the data and acted to further cloud explanatory resolution among BA_{Abund} and environmental covariables.

The weak evidence obtained in this study for anole effects on birds may help to strengthen future inferences concerning these effects in at least two ways. First, the observed patterns serve as a baseline comparison for future avifaunal patterns in this system. The axis of correlation between invasion and island scrubbiness should begin to break down as additional islands become colonized by brown anoles, and as it does, the degree to which avian abundance patterns track brown anole abundances (rather than remaining static) will serve as a relatively strong measure of brown anole impacts on birds. Absent the current study, inferences derived from future avifaunal patterns would be weakened by greater uncertainty about the probability of unmeasured causal factors. Second, the observed patterns may help to elucidate the landscape-level relevance of anole effects detected in small-scale manipulative experiments. Although manipulative experiments (e.g., enclosure/exclosure experiments) may permit the unambiguous detection and measurement of some types of anole effects on birds (e.g., foraging rates), because it is seldom feasible for such experiments to be large enough in scale to encompass the daily activity patterns of individual birds, the ecological importance of any anole effects they reveal may be uncertain. Large-scale observational studies can help to validate the ecological relevance of such effects. For example, if an enclosure experiment revealed that small insectivorous birds forage for shorter durations of time in enclosures containing brown anoles (and consequently fewer arthropods), then the current study would provide evidence that this effect could scale up to affect the habitat-level abundances of such birds.

In summary, this study documented negative associations between the abundances of brown anoles and arthropod-consuming birds that were consistent in pattern with a mechanism of anole-induced reductions in large arthropod abundance, but environmental covariables offered alternative explanations for these associations that could not be ruled out. Additional study to resolve these competing explanations is warranted. Brown anoles are one of the most abundant and widely-introduced members of one of the most widely-introduced lizard genera (Kraus 2009); if brown anoles or other introduced *Anolis* negatively impact arthropod-consuming birds, the sum of these impacts across the globe could be substantial. Beyond elucidating invasion impacts, studies of *Anolis*–avifauna interactions in ongoing anole invasions may shed light on the past importance of these interactions for existing patterns in the Caribbean avifauna. Unfortunately, opportunities for such studies are likely to abound as *Anolis* lizards continue to be transported into favorable environments around the world.

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APPENDIX 4:

TABLES AND FIGURES

Table 4.1 Study island names, location along the Intracoastal Waterway (ICW), invasion status, and census dates.

Island[1]	Name[2]	ICW position (km)	Latitude Longitude	Dominant anole	Invasion status	Total brown anole count[3]	Census dates (January) 2007	2008	2009
1[A]	North Lost	0.00	28.8571° N 80.8268° W	Green	Rare	2	6, 13	12	8
2[A]	South Lost	0.24	28.8554° N 80.8255° W	Green	Rare	2	6, 13	6	6
3	Line O' Cedars*	0.72	28.8516° N 80.8227° W	Brown	Abundant	15	6, 13	6	8
4	Lizard*	1.13	28.8483° N 80.8211° W	Brown	Abundant	26	8, 13	16	6
5	Hook*	1.63	28.8445° N 80.8184° W	Brown	Abundant	67	6, 13	11	8
6	Yin*	1.92	28.8422° N 80.8169° W	Brown	Abundant	43	6, 13	6	6
7	Yang*	2.12	28.8407° N 80.8160° W	Brown	Abundant	55	6, 13	12	1, 2, 6
8	Hornet*	3.00	28.8336° N 80.8120° W	Brown	Absent	0	6, 13	6	1, 2
9[4]	Raw Bar*	3.29	28.8303° N 80.8103° W	None	Absent	0	5, 11	12	5
10	Pine*, Ditto	5.62	28.8123° N 80.7981° W	Green	Absent	0	5, 11	11	12
11	North Twin*	5.99	28.8092° N 80.7964° W	Green	Rare	2	5, 11	5	5
12	South Twin*	6.28	28.8071° N 80.7948° W	Green	Absent	0	5, 11	11, 16	5
13	Channel*	8.18	28.7922° N 80.7854° W	Brown	Abundant	20	5, 11	5, 16	12
14[B]	[B6]	8.65	28.7884° N 80.7832° W	Brown	Abundant	12	5, 11	11	–
15[B]	[B7]	8.87	28.7865° N 80.7825° W	Brown	Abundant	8	5, 11	5	12
16[C]	[B8]	9.31	28.7828° N 80.7806° W	Brown	Abundant	16	5, 11	4	10
17[C]	[C1]	9.48	28.7816° N 80.7793° W	Brown	Abundant	22	9, 10	5	11
18[C]	[C2]	9.58	28.7810° N 80.7785° W	Brown	Abundant	25	9, 10	7	–

Table 4.1 (continued)

Island[1]	Name[2]	ICW position (km)	Latitude Longitude	Dominant anole	Invasion status	Total brown anole count[3]	Census dates (January) 2007	2008	2009
19^{D}	[C3]	10.08	28.7769° N 80.7765° W	Green	Absent	0	9, 10	4	10
20^{D}	[C4]	10.30	28.7752° N 80.7753° W	Green	Absent	0	9, 10	7	–
21^{D}	[C5]	10.45	28.7738° N 80.7749° W	Green	Absent	0	9, 10	4	–
22^{D}	[C6]	10.66	28.7724° N 80.7736° W	Green	Absent	0	9, 10	7	11
23^{E}	[C7]	11.01	28.7696° N 80.7719° W	Green	Absent	0	9, 10	4	–
24^{E}	[C8]	11.19	28.7681° N 80.7712° W	Green	Absent	0	9, 10	7	9
25^{E}	[C9]	11.53	28.7655° N 80.7693° W	Green	Absent	0	9, 10	13	10[5]
26^{E}	[D1]	11.88	28.7626° N 80.7674° W	Green	Absent	0	7, 12	8	11
27^{E}	[D2]	12.14	28.7607° N 80.7662° W	Green	Absent	0	7, 12	13	–
28	Cedar Ring*	12.38	28.7589° N 80.7647° W	Brown	Abundant	11	7, 12	8	9
29	Dud*	12.70	28.7563° N 80.7631° W	Brown	Abundant	37	7[5], 12	13	7
30^{F}	[D5]	13.11	28.7535° N 80.7603° W	Green	Rare	1	7, 12	9, 15	–
31^{F}	[D6]	13.30	28.7523° N 80.7592° W	Green	Absent	0	7, 12	8	9
32	Osprey	13.60	28.7501° N 80.7573° W	Green	Absent	0	7, 12	9, 15	7
33^{G}	[D8]	13.97	28.7477° N 80.7543° W	Green	Rare[6]	0	7, 12	8	–
34^{G}	[D9]	14.18	28.7465° N 80.7526° W	Green	Rare	1	7, 12	9, 15	7

[1] Islands denoted by the same letter belong to the same block of marsh-connected islands

[2] Names with asterisks are from Stuart et al. (2014) and associated research. Brackets signify sample codes for unnamed islands. Remaining names assigned by N.W. Turnbough

[3] Brown anole counts are adjusted for observer bias (see Chapter 2)

[4] Island 9 (Raw Bar) lacked both green and brown anoles and was excluded from all analyses

[5] Census excluded from analyses due to the presence of a hawk

[6] Status based on brown anoles observed after the anole counts

Table 4.2 Time and weather conditions for bird censuses.

Variable[1]		Year 2006	 2007	 2008
Time (h)	Mean	0935	0846	0904
	SD	1.08	0.75	0.77
	Range	0730–1120	0733–1009	0749–1017
Temperature (°C)	Mean	16.0	21.1	19.3
	SD	4.9	3.2	4.2
	Range	4.2–24.4	11.0–25.0	6.6–24.8
Sky[2]	Mean	1.5	2.6	1.8
	SD	1.0	1.4	1.1
	Range	1.0–4.0	1.0–5.0	0.5–4.5
Wind[3]	Mean	0.5	1.0	0.6
	SD	0.9	1.0	0.9
	Range	0.0–2.5	0.0–3.0	0.0–3.0

[1] Time and weather data represent census starting conditions in 2006 and the average of starting and ending conditions in 2007 and 2008

[2] Classed 1 = clear, 2 = mostly clear or hazy, 3 = partly cloudy, 4 = mostly cloudy, or 5 = cloudy or foggy

[3] Classed 0 = still, 1 = mild, 2 = moderate, or 3 = strong; half-steps (e.g., 1.5) were allowed

Table 4.3 Environmental covariables used in xeric habitat and forest habitat bird analyses.

Habitat	Covariable	Description
Xeric	Xhab_1	First habitat structure PC, describing 41.6% of the total variation in (1) square-root-transformed xeric habitat area, (2) proportion of xeric habitat covered by vegetation, (3) xeric vegetation height class, (4) mean point count visibility, (5) proportion of xeric habitat perimeter open to island shorelines, and (6) mean forest depth. Indicator of general island scrubbiness: positively correlated with variable (5) and negatively correlated with variables (2), (3), and (6).
	Xhab_2	Second habitat structure PC, describing 30.4% of the total variation in variables (1)–(6) listed above. Measure of habitat visibility: positively correlated with variable (4) and negatively associated with variable (2).
	Xveg_1	First vegetation composition PC, describing 54.4% of the total variance in xeric-weighted (2*xeric:1*forest) plant cover estimates. Corresponded to a dominance tradeoff among the two most abundant plant species: positively correlated with cabbage palm cover and negatively correlated with red cedar cover.
	Xveg_2	Second vegetation composition PC, describing 18.6% of the total variance in xeric-weighted (2*xeric:1*forest) plant cover estimates. Corresponded to a tradeoff among subdominant plant species, possibly related to sand/shell substrate grain size: positively correlated with saw palmetto cover, negatively correlated with wax myrtle and Brazilian pepper cover.
	Xveg_Div	Simpson's diversity index of xeric-weighted (2*xeric:1*forest) plant species cover.
Forest	Fhab_1	First habitat structure PC, describing 63.9% of the total variation in (1) proportion of xeric habitat perimeter open to island shorelines, (2) mean forest depth, (3) square-root-transformed forest habitat area, (4) forest vegetation height class, and (5) mean forest understory density. Identical to Fhab_1 in Chapter 2. Indicator of island "forestedness": positively associated with variables (2), (3), and (4), and negatively correlated with variable (1).
	Fhab_2	Second habitat structure PC, describing 20.8% of the total variation in variables (1)–(5) listed above. Identical to Fhab_2 in Chapter 2. Measure of forest understory density: positively correlated with variable (5).
	Fveg_1	First vegetation composition PC, describing 53.3% of the total variance in forest-weighted (2*forest:1*xeric) plant cover estimates. Corresponded to a tradeoff between red cedar dominance and both cabbage palm and Brazilian pepper cover: positively correlated with cabbage palm and Brazilian pepper cover, and negatively correlated with red cedar cover.
	Fveg_2	Second vegetation composition PC, describing 20.3% of the total variance in forest-weighted (2*forest:1*xeric) plant cover estimates. Corresponded to a tradeoff between wax myrtle cover and palm and palmetto cover, possibly related to sand/shell substrate grain size: positively correlated with wax myrtle cover and negatively correlated with both cabbage palm and saw palmetto cover.
	Fveg_Div	Simpson's diversity index of forest-weighted (2*forest:1*xeric) plant species cover.

Table 4.4 Mean avian activity densities, by species and year. Values represent across-island averages of observed (unadjusted) activity densities.

		Mean activity density (individuals / ha)			
Habitat	Species	2006	2007	2008	All years[1]
Xeric					
	Arthropod-consuming birds:				
	Yellow-rumped Warbler (*Setophaga coronata*)	9.17	31.34	24.49	21.71
	Northern Cardinal (*Cardinalis cardinalis*)	0.18	2.44	1.93	1.41
	Gray Catbird (*Dumetella carolinensis*)	0.15	0.27	0.83	0.36
	Carolina Wren (*Thryothorus ludovicianus*)	0.11	0.12	0.41	0.18
	Palm Warbler (*Setophaga palmarum*)	0.07	0.06	0.36	0.15
	Common Yellowthroat (*Geothlypis trichas*)	0.15	0.21	0.08	0.15
	Other species[2]	0.07	0.12	0.50	0.20
	Doves:				
	Common Ground-Dove (*Columbina passerina*)	0.29	0.57	0.70	0.46
	Mourning Dove (*Zenaida macroura*)	0.15	0.12	0.54	0.23
Forest					
	Arthropod-consuming birds:				
	Yellow-rumped Warbler (*Setophaga coronata*)	–	30.95	25.75	30.28
	Common Yellowthroat (*Geothlypis trichas*)	–	1.80	3.19	2.21
	Northern Cardinal (*Cardinalis cardinalis*)	–	2.46	1.51	2.19
	Gray Catbird (*Dumetella carolinensis*)	–	0.75	1.66	1.18
	Palm Warbler (*Setophaga palmarum*)	–	0.25	0.25	0.24
	House Wren (*Troglodytes aedon*)	–	0.12	0.08	0.15
	Carolina Wren (*Thryothorus ludovicianus*)	–	0.16	0.00	0.11
	Other species[3]	–	0.12	0.91	0.47
	Doves:				
	Common Ground-Dove (*Columbina passerina*)		0.21	0.21	0.18
	Mourning Dove (*Zenaida macroura*)		0.06	0.08	0.06

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[1] Calculated as the average of across-year island means; because some islands were not censused in 2008, reported all-year averages are not equivalent to the simple average of reported yearly means

[2] Species [all-year mean activity density]: Blue-gray Gnatcatcher [0.08], House Wren [0.05], Orange-crowned Warbler [0.03], Prairie Warbler [0.02], and White-eyed Vireo [0.01]

[3] Species [all-year mean activity density]: Blue-gray Gnatcatcher [0.09], Orange-crowned Warbler [0.09], Pine Warbler [0.06], Prairie Warbler [0.06], Red-winged Blackbird [0.09], White-eyed Vireo [0.02], and Yellow Warbler [0.06]

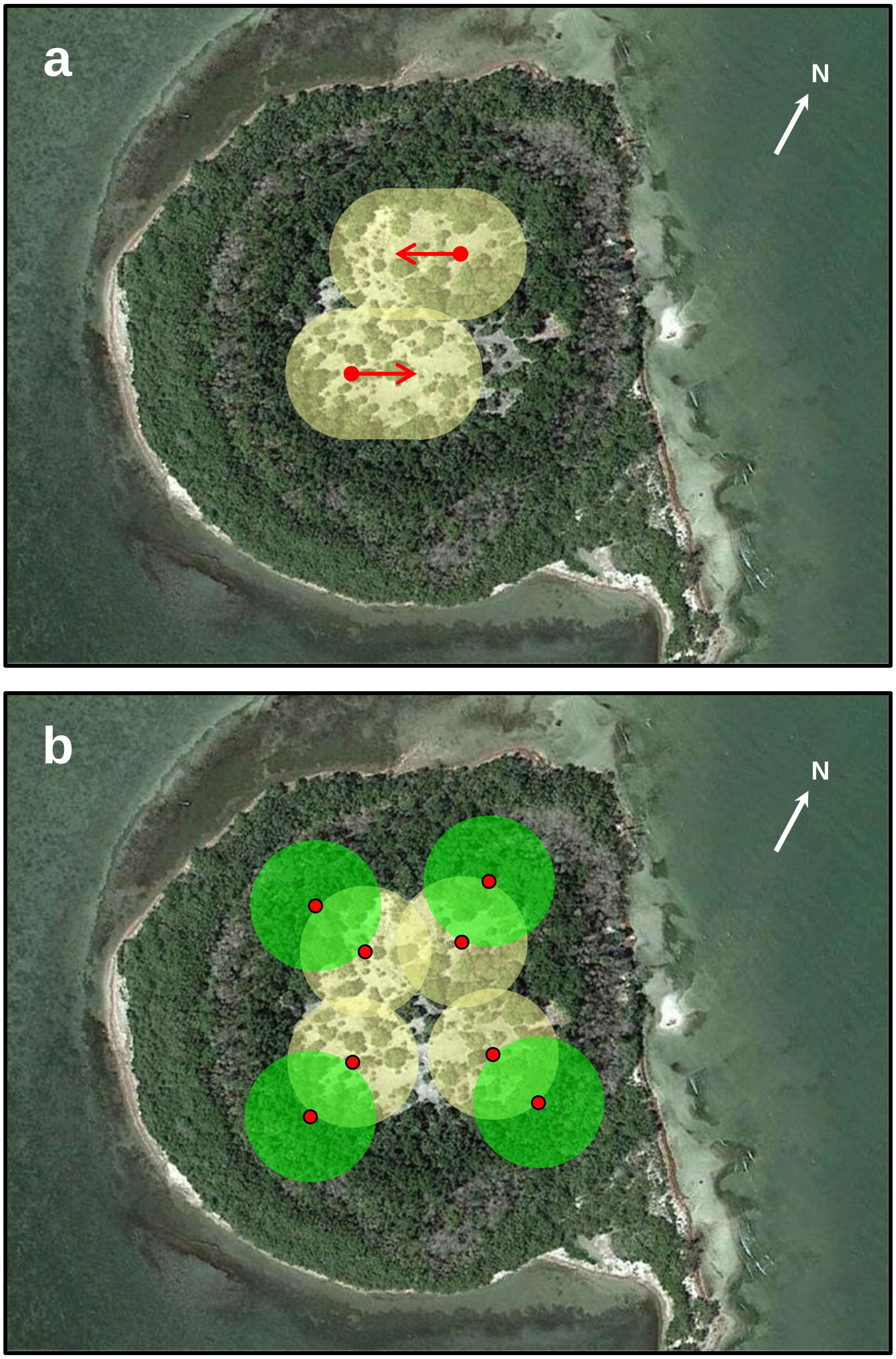

Figure 4.1 Configuration of (a) 2006 transect counts and (b) 2007–2008 point counts in bird censuses. Imaged island is “North Twin”, oriented such that the right margin of the image runs parallel to the Intracoastal Waterway. Censuses in all years began in the northeastern (upper-right) quadrant and proceeded counterclockwise to the southeastern (lower-right) quadrant. Arrows pointing true north are scaled to a length of 20 m. Island image captured in March 2013 and provided courtesy of Google Earth.

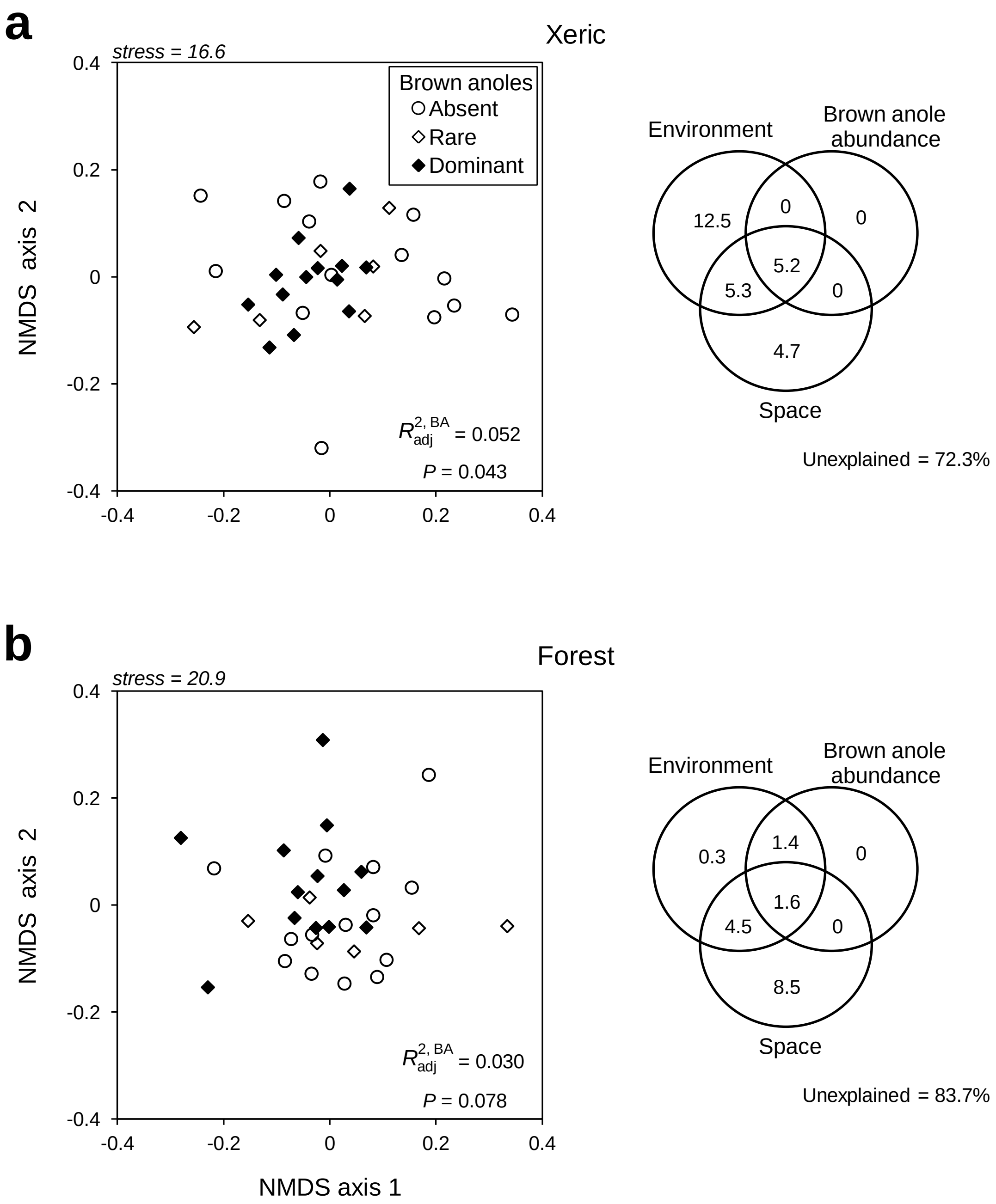

Figure 4.2 Dissimilarity NMDS plots and partitioned variation fractions (% explained) for arthropod-consuming bird communities in (a) xeric and (b) forest habitats.

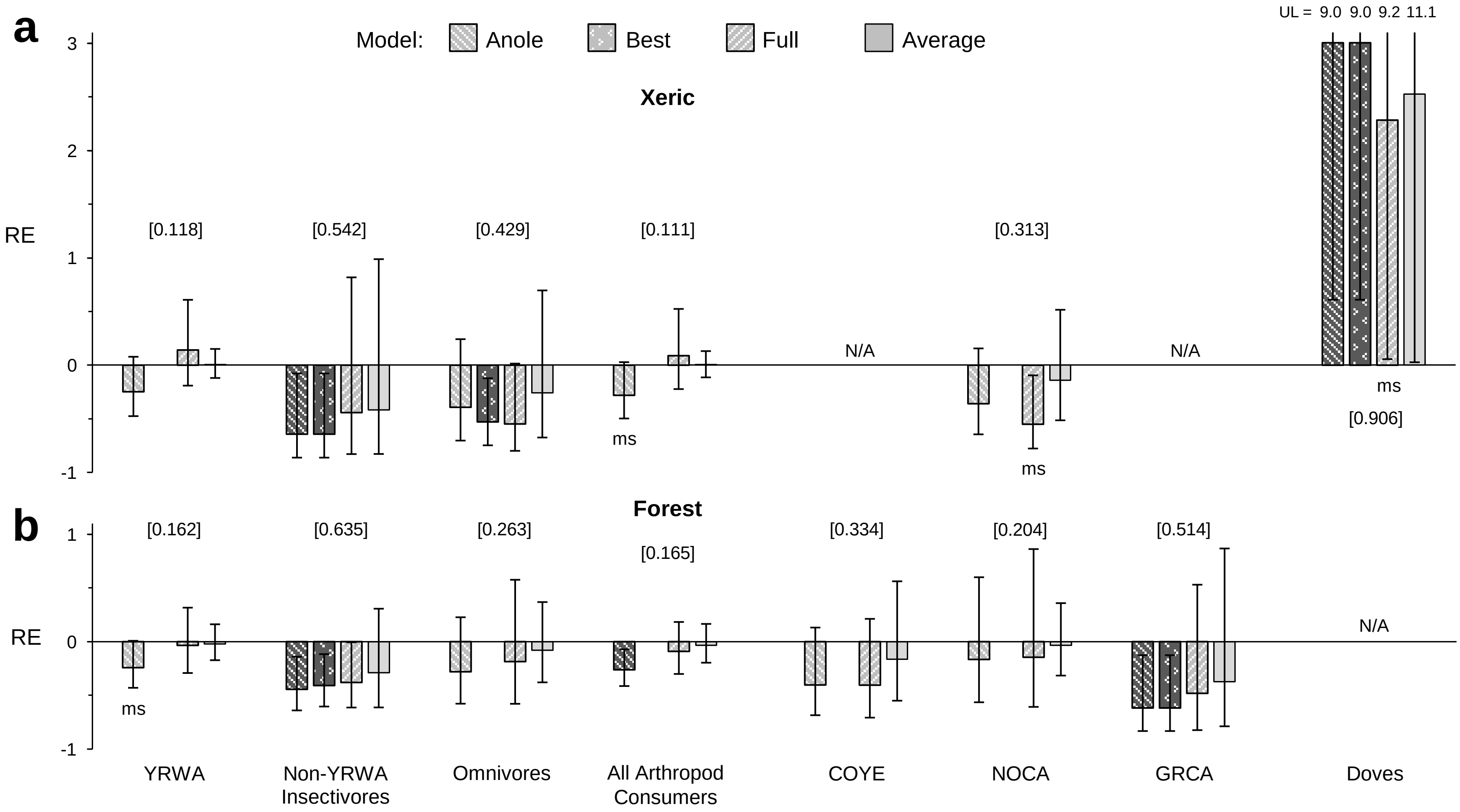

Figure 4.3 Anole, best, full, and averaged model replacement effect (RE) estimates for avian activity densities in (a) xeric and (b) forest habitats. Error bars denote 95% confidence intervals; upper limit (UL) values exceeding the figure scale are shown. Significance ($P < 0.05$) in the parametric bootstrap test is indicated by darker shading; "ms" denotes marginal significance ($P < 0.10$). Bracketed numbers are BA_{Abund} AICc weights. COYE = Common Yellowthroat, GRCA = Gray Catbird, NOCA = Northern Cardinal, YRWA = Yellow-rumped Warbler, All Arthropod Consumers = Insectivores + Omnivores, N/A = not analyzed.

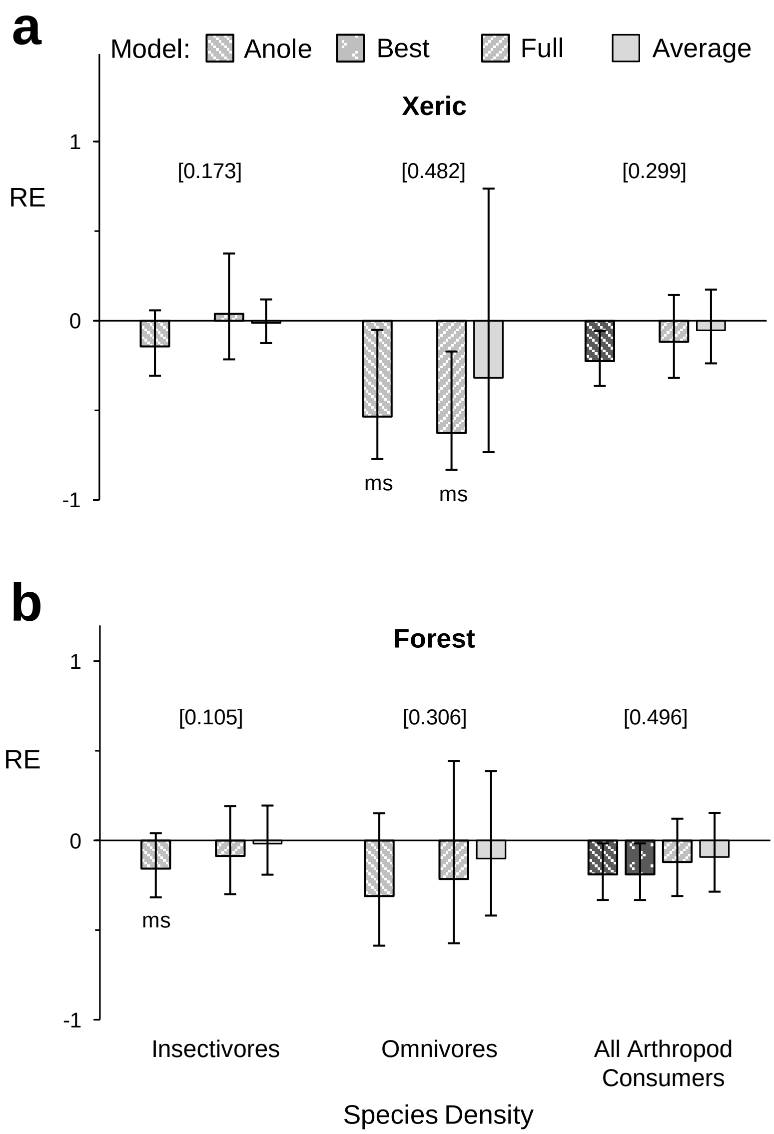

Figure 4.4 Anole, best, full, and averaged model replacement effect (RE) estimates for avian species density estimates in (a) xeric and (b) forest habitats. Other figure details as in Figure 4.3.

CHAPTER 5:

SUMMARY AND CONCLUSIONS

The community-wide impacts of brown anole invasions in Florida depend upon the degree to which brown anoles are functionally equivalent to the green anoles they displace. In open and structurally-simple habitats, the sheer increase in lizard density and biomass that accompanies brown anole invasion and green anole displacement suggests that populations of these two species must have differing food web-mediated effects, but what those differential effects might be and whether differences in per-capita effects contributed to them were, prior to this dissertation, unstudied. The research presented in the previous three chapters addressed these uncertainties and yielded findings that were, in several instances, quite unexpected and surprising.

In Chapters 2 and 4, I took advantage of a "natural" experiment—a mosaic of invasions within a system of small spoils islands—to assess whether arthropod communities, and the winter avifaunal assemblages that feed on them, varied in accordance with the dominant anole species operating in island food webs. One of the advantages offered by this system was that islands were large enough to capture the population dynamics of resident arthropod species as well as factors that affected these dynamics, such as within-island spatial heterogeneity in habitat structure and vegetational composition. Thus, the system likely afforded a more accurate picture of actual invasion impacts than could be obtained in small-scale manipulative experiments, for example a field enclosure study. However, an unfortunate drawback of this natural experiment approach was the substantial correlation, and thus statistical confounding, that occurred between brown anole abundance (a proxy for green anole displacement status) and certain attributes of island habitats and spatial positioning. To improve inferences in this system, I used analysis techniques that characterized the extent of explanatory overlap between brown anole abundance and both environmental and spatial covariable sets.

Island arthropod communities did indeed covary with brown anole abundance (and thus the identity of the dominant anole species), indicating, as expected, that green anole and brown anole populations are not functionally equivalent in island food webs. In general, the observed arthropod response patterns were well explained as direct and indirect food web effects of increased anole predation pressure following brown anole invasion. In both ground-active and foliage-dwelling arthropod communities, larger-bodied species of arthropod orders known to be frequently consumed by brown anoles tended to be negatively associated with brown anole abundance, and this trend resulted in negative associations between brown anole abundance and both the total abundance and biomass of foliage-dwelling arthropods. By contrast, smaller-bodied arthropods, which are less likely to serve as anole prey, tended to be positively associated with brown anole abundance; in most instances, these positive associations probably represented indirect food web effects mediated by brown anole predation on larger predatory arthropods. Interestingly, brown anole abundance was strongly associated with the composition of ground-nesting ant assemblages, and the available evidence suggests that brown anole ant consumption was at least partially responsible for the pattern. Until recently, the possibility that anoles might alter ant communities was completely unexplored; given the important role ants play in a wide variety of ecological processes, any such alterations may have far-reaching consequences. Another interesting and unexpected finding was the absence of the most consistently documented food web effect of increased anole abundance—a negative effect on web spider abundance—, which suggests that green anoles have stronger per-capita effects on web spiders than do brown anoles. Although the degree to which brown anole abundance uniquely explained arthropod response variation (i.e., independently of environmental or spatial covariables) differed among the significantly associated responses, in most cases brown anole abundance was incorporated into the parsimony-maximizing best model, and in several cases it significantly explained unique variation in the full model that incorporated all explanatory covariables.

Winter avifaunal assemblages also covaried with brown anole abundance in ways that were generally well explained as food web-mediated effects of post-invasion increases in anole predation pressure on arthropods. As might be expected from the negative associations between brown anole abundance and foliage-dwelling arthropod abundance and biomass, insectivorous (predominantly foliage-gleaning) bird abundances were negatively associated with brown anole abundance, and these associations tended to be stronger for avian insectivores of larger body size and more insectivorous diet. The data were noisy, however, and evidence that the observed patterns reflected exploitative competition for prey was relatively weak. Brown anole abundance did not significantly explain unique response variation independently of environmental covariables for any analyzed response, and best model support for the competition mechanism was called into question by the occurrence of a relatively strong and seemingly spurious association between the abundances of brown anoles and granivorous birds (i.e., doves). Competition between dense anole populations and insectivorous birds may have been responsible for the depauperate insectivore avifauna of the West Indies, and the seemingly strong potential for brown anole invasions to negatively impact avian insectivores may carry conservation implications. Additional study of avifaunal responses to brown anole invasion in the spoils islands system is therefore warranted. Further invasion of this system should degrade the collinearity that existed at the time of this dissertation research between brown anole abundance and island habitat characteristics; if negative associations between the abundances of brown anoles and avian insectivores persist at such a later point in time, the baseline associations documented in Chapter 4 will help to strengthen the inference of exploitation competition for prey.

The palm enclosure experiments of Chapter 3 were designed to assess the degree to which the perching and foraging behavioral differences of green and brown anoles affected their relative per-capita effects on arthropod prey that differed in microhabitat use and other autecological characteristics. Because both green and brown anoles are (like most anole species) opportunistic and visually-oriented generalist predators, their perching and foraging behaviors are probably the most important factors affecting their individual-level functional similarity in downstream food web processes. Although similarly-sized males of both species differed significantly in every measured aspect of their behavioral use of small cabbage palms (i.e., perch height, perch type usage, movement frequency, movement distance, and travel rate), they had, quite surprisingly, statistically indistinguishable effects on all but one of seven arthropod response taxa. Moreover, neither the significantly greater effect of green anoles on *Nephila* orb web spiders nor the probable (but nonsignificant) greater effect of brown anoles on *Phidippus* jumping spiders appeared to have been driven by differences in the way green and brown anoles perched and foraged on the palms, but rather by differences in their use of the enclosure net (*Nephila*) or boldness to attack dangerous prey (*Phidippus*). At first glance, these findings seem to suggest that green anole and brown anole individuals are functionally very similar in their effects on arthropod prey assemblages, and such a prospect may be true for scrubby habitats that lack tall vegetation. However, many anole-occupied habitats in the southeastern U.S. possess trees reaching at least 4 m in height, and in such habitats, the greater use of higher perches (e.g., above 2 m) by green anoles is likely to spread both their individual and average foraging efforts across a broader range of vegetational strata, thus diluting (relative to brown anoles) their per-capita effects on arthropods occurring on the ground or in the lower vegetation. Such a possibility remains to be tested.

This dissertation adds to the meager list of studies in which functional similarity has been assessed for closely-related terrestrial predators. One of the insights it reveals is that differences in abundance alone may be an insufficient basis for predicting the major impacts of predator displacements, even when the species involved are ecologically-similar congeners. This is perhaps most clearly illustrated by the apparent absence of an invasion impact on the total abundance of foliage-dwelling web spiders on spoils islands (though there may have been species-level abundance impacts). Because brown anoles have been repeatedly shown to have strong negative impacts on web spiders (particularly orb-web weavers; see references in Chapter 2), and similar effects have been found for other species of *Anolis*, one might expect (as did I) that negative effects on web spider abundances would be a relatively failsafe prediction for the large increases in total *Anolis* density that accompany brown anole invasion of island habitats. The failure of this prediction highlights the potential for differential per-capita interaction rates to influence population-level functional similarity; the palm enclosure experiments of Chapter 3 highlight the difficulty ecologists may encounter in predicting per-capita effect differentials from differences in trait values. The functional similarity of individual green and brown anoles in the enclosure experiments suggests that their differential microhabitat use and foraging behavior yield similar prey resource returns for habitat volumes at least the size of the enclosures, though the mechanism that permits this similarity is still a matter of conjecture. The extent to which this finding and others obtained in this dissertation reflect or depart from generalities that may occur among ecologically-similar species of *Anolis* or other groups of interest (e.g., arboreal lizards, terrestrial vertebrates, congeneric predators) is a subject that will require additional case studies and meta-analyses. The potential for such studies to advance our understanding of ecological systems along several fronts makes them a promising avenue for further research.

VITA

Nathan W. Turnbough was born on February 9, 1977, in Anaheim, California. A few years later, he moved with his family to the town of Oroville, California, where he grew up and gained mild notoriety as the local lizard-catcher. After graduating Oroville High School in 1995, Nathan attended Point Loma Nazarene University in San Diego, from which he earned a Bachelor of Arts degree in Biology in 1999. While at Point Loma, he conducted undergraduate research on breeding colonies of the endangered California Least Tern and differential gene expression in mouse germ cell lines. After Point Loma, Nathan delayed and eventually declined his acceptance into the Molecular and Cellular Biology doctoral program at the University of Arizona in order to remain near his soon-to-be fiancée, Jessica Lynne Brewton, whom he married in 2000. While his wife finished her undergraduate degree, Nathan worked as a research assistant in an immunology lab at The Scripps Research Institute in La Jolla, California. In 2002, Nathan returned to his first love in biology and entered the doctoral program in Ecology and Evolutionary Biology at the University of Tennessee, Knoxville, for which he conducted the research described in this dissertation. Several years and two beautiful daughters later, he finished this endeavor and was awarded the Doctor of Philosophy degree in Ecology and Evolutionary Biology in December 2016.