Population Regulation of Frogs and Lizards in a Lowland Wet Neotropical Forest: Integrating Alternative Hypotheses

by

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Abstract

Populations can be regulated in space and time from the “bottom-up” by resources (e.g., food), from the “top-down” by predation, or from parallel factors, such as interactions with conspecifics or heterospecifics. Amphibians and reptiles are species rich and abundant in lowland wet forests of Central America, and are important components of trophic communities as low or mid-level consumers of arthropods, and as prey to a diverse assemblage of vertebrate and invertebrate species. Theory describing population and community structure of Neotropical amphibians and reptiles has been generated largely from studies of a species-rich assemblage of frogs (Craugastoridae, Dendrobatidae) and anole lizards (Dactyloidae) that occur terrestrially on the forest floor and have generally supported hypotheses of bottom-up regulation mediated by resources, such as leaf-litter and prey abundance. Because trees regulate the input of leaf litter into terrestrial systems, a conceptual model has been suggested where leaf-abscission phenology of trees regulates patch dynamics of terrestrial frogs and lizards through forests in ways consistent with bottom-up regulation (the litter-mosaic hypothesis). However, a comparative review of anole life history in mainland Central American and Caribbean island habitats has described an alternative, top-down hypothesis of population regulation, where anoles in Central America are more greatly influenced by predation than anoles in Caribbean islands (the mainland-island model). Additionally, studies of the island anole *Dactyloa aenea* have demonstrated that juveniles are attracted to conspecifics when settling habitat, and conspecific attraction may be an additional parallel factor influencing forest dynamics of anoles and frogs in Central America.

In an effort to generate a more integrative conceptual model describing population regulation and forest dynamics of frogs and lizards assemblage in Central America, I tested three hypotheses describing bottom-up, top-down, and parallel population regulation of a model assemblage at La Selva Biological Station, Costa Rica. First, I tested the litter-mosaic hypothesis that leaf-drop phenology of trees regulates population cycles and patch dynamics of terrestrial arthropods, frogs (*Craugastor bransfordii*, *Oophaga pumilio*), and lizards (*Norops humilis*). I used a comparative experimental approach, where I (1) compared seasonal abundance cycles of terrestrial litter and fauna beneath two tree species differing in phenology of leaf abscission (*Castilla elastica*, *Dipteryx panamensis*), and (2) experimentally manipulated leaf abscission beneath *C. elastica* with litter supplementation. I observed seasonal patterns of leaf litter, arthropods, and vertebrate abundance, but these patterns did not vary between tree species. Experimental supplementation caused elevated abundance of *N. humilis* in manipulated *C. elastica* plots relative to controls, as a result of demographic shifts in either apparent survival, immigration, or recruitment. My results suggest the litter-mosaic hypothesis can be refined and restricted to describing spatiotemporal variance of terrestrial anoles, while excluding frogs. Second, to better understand how predators influence prey frog and lizard ecology, I tested the mainland-island model prediction that predation exerts stronger effects than food resources for anoles and, by extension, frogs in Central America. I modeled the relative contribution of food, microhabitat, and predatory spiders (Ctenidae) to frog and anole occupancy. Frog occupancy was most strongly influenced by predators, an effect which increased at reduced biomass of leaf litter. Anoles occupied sites independent of predators, an observation inconsistent with the mainland-island model. All species were positively associated with leaf-litter depth and had elevated detection when predators were present. Third and last, I used eighteen months of mark-recapture

observations of *O. pumilio* in a homogenous, fallow cacao plantation to test predictions of the conspecific attraction hypothesis. I found that juveniles settled habitat and used space in significant association with adults with previous history in plots, in ways consistent with conspecific attraction of juveniles and strong male territoriality.

Together, my results contribute to our understanding of patch dynamics for terrestrial frogs and lizards in Neotropical wet forests. My experimental results suggest that *Norops humilis* populations respond to pulses of terrestrial litter in ways consistent with the litter-mosaic hypothesis, but the *O. pumilio* and *C. bransfordii* do not. Dispersal of *O. pumilio* and other frogs through the landscape may be driven in part by conspecific attraction. Because predatory spiders exert stronger effects on the occupancy of terrestrial frogs at lower abundance of terrestrial litter, seasonal declines in frog abundance during the wet season may be driven in part by elevated predation pressure when leaf litter is scarce. Predator-prey models reject a large literature invoking predation as the dominant force shaping ecology of diverse mainland anoles, and suggest similar mechanisms may regulate the ecology and evolution of mainland and island anoles.

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Chapter 1

General Introduction

Abstract. In this dissertation, I describe a diverse assemblage of frogs and lizards that occurs in terrestrial leaf-litter environments in wet tropical forests of Central and South America, which has been the focus of a large literature examining vertebrate population and community regulation. The focal assemblage includes terrestrial frogs of the families Craugastoridae and Dendrobatidae, and terrestrial anole lizards in the family Dactyloidae, and I review literature describing factors influencing population and community ecology of the assemblage. In particular, I describe the litter-mosaic hypothesis, a conceptual model in which frog and lizard abundance is bottom-up regulated by leaf abscission of deciduous trees, mediated by tree-driven seasonal variation in microhabitat and food resources. The litter-mosaic hypothesis suggests that leaf-drop phenology drives patchiness of habitat quality for frogs and lizards in both space and time, and is similar to patch-mosaic models. I then introduce the mainland-island model of anole population regulation, an alternative hypothesis of top-down regulation, which suggests that predation is the dominant regulatory mechanism of anoles and, by extension, frogs in Central American forests. Last, I describe conspecific attraction, a parallel mechanism that may contribute to patterns of frog and lizard dispersal and space use in a patch-mosaic model.

Key words: frogs, anoles, food resources, predation, conspecific attraction.

POPULATION REGULATION

Ecology is the study of the distribution and abundance of organisms, and a fundamental goal of ecology is to understand processes that influence population size of species in space and time (e.g., Pulliam 1988). A helpful conceptual framework for classifying mechanisms of population regulation has described three fundamentally different categories of population regulation: bottom-up, top-down, and parallel regulation (*sensu* Hunter and Price 1992, Laundré et al. 2014). Bottom-up regulation occurs when populations are regulated by resources that are consumed, such as food or water, or used in important ways, such as for reproduction (e.g., Guyer 1988). Top-down regulation occurs when populations are regulated by higher-level consumers (i.e., predators consuming prey (e.g., Brown and Heske 1990). Last, parallel interactions occur when populations are regulated by interactions among individuals, that may have negative or positive effects on the population (e.g., negative – competition; e.g., positive – Allee effects; Laundré et al. 2014). Description of the relative importance and interactive effects between bottom-up, top-down, and parallel regulatory mechanisms is critical to understanding the distribution and abundance of organisms. It is within this conceptual framework that I view processes influencing the abundance of organisms in my dissertation.

THE FOCAL ASSEMBLAGE

In diverse rain forest communities of the New World tropics, amphibians and reptiles are a conspicuous component of vertebrate biodiversity, and two radiations in particular contribute greatly to species richness of Neotropical vertebrate diversity – brachycephaloid frogs (Padial et al. 2014) and dactyloid lizards (anoles; Nicholson et al. 2012). Together, these frogs and anoles have provided a valuable model system for developing and testing ecological theory relating to population, community, and evolutionary ecology. Species have adaptively radiated to occupy diverse habitats throughout the Neotropics, across terrestrial and arboreal axes, and between lotic (flowing water) and lentic (standing water) aquatic environments. Species have evolved convergent morphologies repeatedly to exploit novel habitats, so patterns of anole and brachycephaloid frogs are consistent with definitions of adaptive radiation (Hedges 1989, Losos et al. 1998, Losos 2009, Glor 2010). However, despite being on two divergent branches on the Tree of Life, ecological features of brachycephaloid frogs and anoles occurring in terrestrial, forest-floor environments can be highly similar, and members of these lineages frequently have been considered as a cohesive assemblage of ecologically similar species. In general, many species within this terrestrial frog and lizard assemblage occur in leaf litter on the forest floor, where they consume similar arthropod food resources (Toft 1980, Lieberman 1986, Whitfield and Donnelly 2006), select similar microhabitats and oviposition sites to limit desiccation (Toft 1985, Seebacher and Alford 2002, Schlaepfer 2003, Socci et al. 2005), and are eaten by similar predators (Greene 1988). Given the species richness of this assemblage and its conserved ecology, the diverse terrestrial frog and lizard assemblage allows for an opportunity to understand the degree to which similar mechanisms regulate the assemblage's ecology as a whole.

A common thread among studies examining ecology of the terrestrial frog and lizard assemblage has identified leaf litter as an important resource regulating abundance. Numerous studies have documented a positive relationship between leaf-litter abundance and frog and lizard density (Scott 1976, Lieberman 1986, Guyer 1988, Fauth et al. 1989, Whitfield et al. 2007), and Whitfield et al. (2014) provided the first experimental demonstration of standing leaf litter as a density-limiting factor, although this effect varied among the frog and lizard species examined. Thus, literature supports the idea that leaf litter regulates the frog and lizard assemblage in ways consistent with bottom-up regulation of populations (*sensu* Hunter and Price 1992).

Many of the above-cited studies have been conducted at one long-term research site, La Selva Biological Station, in Costa Rica (hereafter, La Selva; McDade et al. 1994). La Selva is a private reserve owned by the Organization for Tropical Studies (OTS) in the Caribbean lowlands of northeastern Costa Rica, ~3 km south of Puerto Viejo de Sarapaquí, Heredia Province (10.42˚N, 84.02˚W). Elevation at La Selva ranges from 30–130 m asl. The site is characterized by an average temperature of 25.8˚C, receives ~4 m of precipitation per y (Sanford et al. 1994), and is classified within Holdridge's Tropical Wet Forest life zone (McDade and Hartshorn 1994). Rainfall is seasonal with most rain occurring during the wet season (May–December) relative to the 'dry season' (January–April). La Selva is ~1600 ha in area, of which 1100 ha is primary old-growth forest. Tree species richness is high at La Selva: single hectare plots can support 79–107 species. The understory is dominated by palms (Sanford et al. 1994), and is classified within Holdridge's Tropical Wet Forest life zone (Hartshorn 1972, 1983, Lieberman and Lieberman 2007).

La Selva is home to a diverse community of amphibians and reptiles that has been relatively well-studied, and comprehensive reviews have been provided elsewhere (Donnelly 1994, Guyer 1994, Guyer and Donnelly 2005). Amphibian diversity at La Selva has been described by a partition into three distinct ecological assemblages: a swamp assemblage, a riparian assemblage, and the terrestrial leaf-litter assemblage (Donnelly 1994); reptiles at La Selva also mirror this trichotomy with species showing habitat associations in swamp, riparian, and forest habitats (B.F., pers. obs.).

In this dissertation, I focus on understanding patterns and processes influencing the population and community ecology of the terrestrial leaf-litter assemblage by integrating studies of three species – *Craugastor bransfordii* (Brown Robber Frog; Craugastoridae), *Oophaga pumilio* (Strawberry Poison Frog; Dendrobatidae), and *Norops humilis* (Ground Anole; Dactyloidae). I selected these study species for two reasons. First, basic natural history is relatively well-described for all three species, and they are relatively similar ecologically: they consume arthropods, live and lay eggs in leaf litter on the forest floor, and are consumed by similar predators. Second, I selected these species because successful experimental studies have been done on each populations, indicating that experimental approaches can be useful for testing hypotheses about population regulation.

THE LITTER-MOSAIC HYPOTHESIS

Leaf production in tropical forests is generally highest during the dry season when herbivorous arthropod abundance is lowest and new leaves are flushed synchronously to saturate herbivores (Coley and Barone 1996). As a result, many tree species rapidly senesce moribund leaves and undergo significant leaf-drop events, with leaf litter accumulating to the greatest depths in the late dry or early wet season (Frankie et al. 1974, Levings and Windsor 1984). As the wet season advances, decreased leaf-drop and increased decomposition causes litter standing crops to decrease. As a result, litter depth varies in a predictable fashion across seasons. Litter provides the trophic base for the brown food web and its arthropod consumers (Kaspari and Yanoviak 2008), dry season litter-drop events cause arthropod abundance to increase also until both peak in the early wet season (Toft 1980, Lieberman and Dock 1982, Levings and Windsor

1984). Further, seasonal abundance of arthropods, in turn, is associated with increased arthropod predation (Janzen and Schoener 1968, Lieberman 1986, Toft 1980, Lieberman and Dock 1982, Guyer 1988). Given that litter regulates the abundance of arthropods, it is logical to assume that it also can indirectly moderate density of forest-floor herpetofauna through arthropod prey resources (e.g., the anole *Norops humilis*; Guyer 1988).

While the seasonal trend in decreasing litter depth occurs generally, some tree species vary their leaf-drop phenology, with some defoliating during the wet season (Frankie *et al.* 1974). As Neotropical tree species differ in the phenology of leaf-drop events and individuals of different tree species can be dispersed widely throughout forests (Clark and Clark 1987), patches of thick litter containing high arthropod abundance may be widespread through primary forest. Guyer (1988) hypothesized that litter-drop events at the spatial scale of single canopy trees may regulate abundances of arthropod predators, such as leaf-litter amphibians and reptiles. Increased population size could result from demographic responses to litter fall events beneath single forest trees, and tree species differing in leaf-drop phenology should support different cycles of herpetofaunal abundance throughout the year. In this conceptual model, herpetofaunal abundance through primary forest is a mosaic of sites at different stages depending on the leaf-drop phenology of the most proximate tree, and the asynchrony of leaf-drop phenology facilitates population and community dynamics throughout forest (hereafter, the litter-mosaic hypothesis; Guyer 1988).

THE MAINLAND-ISLAND MODEL

A large literature supports the idea that the focal assemblage is influenced by resources in ways consistent with bottom-up regulation, although little empirical work has considered the potential effects of predators as mechanisms of top-down regulation (*sensu* Hunter and Price 1992). This pattern is surprising because (1) an extremely diverse assemblage of organisms consumes small vertebrates in Neotropical ecosystems (Greene 1988), and (2) a long-standing hypothesis suggests that anole species occurring on mainland Central America are generally limited by predation when compared to species on Caribbean islands, which are generally limited by competition for food resources (Andrews 1979). This hypothesis was inferred from the observations that, relative to anole populations on Caribbean islands, mainland anoles are characterized by decreased abundance, lower survival, increased prey size and growth rates, and decreased foraging time for abundant food resources (Andrews 1979). The observed life-history differences are assumed to reflect differing ways that mainland and island populations are regulated, with mainland populations being dominated by predation while island populations are dominated by competition for limited food resources (hereafter, the mainland-island model, Andrews 1979, Losos 2009).

Detailed studies of the anole *Norops apletophallus* (formerly *N. limifrons*) in Panama are generally consistent with roles of predation in regulating abundance of anoles. Studies have reported that ants (*Solenopsis*) are the most common predator of anole eggs (Andrews 1982), ant predation of eggs likely influences variation in anole population size (more-so than adult survival or fecundity; Andrews 1988, Andrews and Wright 1994), and that rainfall influences intensity of ant depredation on eggs (Chalcraft and Andrews 1999). Juvenile *N. apletophallus* and craugastorid frogs also are preyed upon opportunistically by insectivorous birds in this ecosystem, frequently in association with swarms of army ants (Poulin et al. 2001).

Alternatively, one study suggested importance of bottom-up food limitation for *N. apletophallus* (Wright 1979).

At La Selva, an diverse assemblage of vertebrate predators consumes small terrestrial frogs and lizards (Greene 1988, Guyer and Donnelly 1990, Donnelly and Guyer 1994), but observations to date suggest that invertebrates are the most abundant predator of leaf-litter amphibians and reptiles. In particular, large spiders of the family Ctenidae – commonly referred to as ‘wandering’ spiders, because of low site fidelity and a lack of webs for prey capture – are common generalist predators occupying terrestrial environments in lowland Neotropical wet forests. Ctenids attack and consume terrestrial and arboreal frogs in the families Centrolenidae, Craugastoridae and Hylidae, but reject the poisonous frog *Oophaga pumilio* (Hayes 1983, Szelistowki 1985, Lapinski and Tschapka 2013, Murray et al. 2016). Ctenids also can consume small reptiles, being the most frequently observed predators during a detailed study of the anole *Norops humilis* (Guyer 1988), and ctenids were dominant predators of metamorphic hylid frogs emerging from an ephemeral swamp system (Donnelly and Guyer 1994). The latter study reported a strong pulse in metamorphosis of frogs, and the authors hypothesized that synchronous metamorphosis and emergence may have evolved as a mechanism to satiate terrestrial predators (e.g., spiders; Donnelly and Guyer 1994). Thus, accumulating literature suggests that spiders play an important role as vertebrate predators across Neotropical wet forests (Hayes 1983, Guyer 1988), but no study to date has examined how abundant ctenid spiders or other diverse predators influence terrestrial frog and lizard populations in a predator-prey context.

A controversial factor influencing local-scale ecology and habitat selection of individuals is the role that individuals play in shaping the distribution of conspecifics. A large literature suggests that conspecifics are competitors and individual fitness declines with increasing conspecific density (Brown 1969; Rosenzweig 1985, 1991; Muller et al. 1997). This hypothesis predicts that, to minimize intraspecific competition, individuals seeking habitat should avoid occurring in space near conspecifics. However, contrary evidence suggests that individuals can be attracted to conspecifics (conspecific attraction; Stamps 1988), because (1) conspecifics serve as cues of habitat quality (conspecific cueing; Stamps 1987), (2) colonists may benefit from living in aggregations after territories are established because aggregated individuals may better protect territories, reduce predation, or attract mates (Stamps 1988, 1994; Muller et al. 1997, Boulinier and Danchin 1997), and/or (3) individuals may reduce costs associated with searching for habitat (prospection; Reed et al. 1999). Conspecific attraction is particularly applicable to territorial species because presence of territorial residents may indicate high-quality habitat that is for occupancy and/or defense (Stamps 1987). In the conspecific attraction model, probability of settlement is increased in the presence of conspecifics (Donahue 2006). For conspecific attraction to be adaptive, fitness increases accrued from settlement with conspecifics must outweigh the energetic costs associated with higher densities and increased intraspecific competition (citation). Conspecific attraction predicts that individuals with little or no experience should be more attracted to habitat with higher density of conspecifics than experienced individuals already within the habitat (Stamps 1988; Donahue 2006).

Using an array of field experiments, Stamps (1987, 1988) demonstrated that juvenile anoles (*Dactyloa aenea*) were attracted to cues from conspecifics when settling habitat. Since those pioneering studies, additional support for the conspecific attraction model has been shown for other taxa, including invertebrates (Meadows and Campbell 1972, Crisp 1976, Muller 1998, Donahue 2006), fish (Sweatman 1985, 1988), amphibians (Gautier et al. 2006, Pizzatto et al. 2015), and birds (Muller et al. 1997, Danchin et al. 1998, Etterson 2003, Ward and Schlossberg 2004). However, a recent review of vertebrate social behavior emphasized the need for more studies of conspecific attraction (Doody et al. 2013).

Conspecific attraction may be an important and underappreciated factor influencing local-scale abundance patterns of terrestrial frogs and lizards in lowland Neotropical wet forests. Conspecific attraction has been demonstrated for *D. aenea* in a Caribbean island ecosystem (Stamps 1987, 1988), hence this factor may also apply to mainland anoles at La Selva. Conversely, the importance of conspecific cueing is less understood with respect to frogs, particularly in the tropics. Conspecific attraction may facilitate dispersal dynamics where individuals may be incentivized to occupy space in ways not predicted by conventional models of bottom-up (resource) or top-down (predation) regulation (citation).

OVERVIEW

My dissertation explores three competing hypotheses describing population regulation of frogs and lizards in wet Neotropical forests outlined above. I studied three focal species within the terrestrial frog and lizard assemblage (*Craugastor bransfordii*, *Oophaga pumilio*, *Norops humilis*) because they are relatively abundant, easy to capture, and information describing their natural history and population ecology is available. In Chapter 2, I tested the litter-mosaic hypothesis (Guyer 1988) that leaf-drop phenology of trees regulates population cycles of terrestrial frogs and lizards using a field experimental approach. In Chapter 3, I evaluated the role of predators in shaping local-scale abundance of frogs and lizards by modeling the relative contribution of food, microhabitat, and predatory spiders (Ctenidae) toward frog and anole occupancy; this study was an empirical test of the mainland-island model of anole population regulation (Andrews 1979). In Chapter 4, I used a large mark-recapture study of *O. pumilio* in a homogenous cacao plantation to test predictions of the conspecific attraction hypothesis. Last, in Chapter 5, I integrated the results of my studies to describe a revised conceptual model for population regulation of terrestrial frogs and lizards in lowland Neotropical wet forests; I outlined future research topics, given my results and within this conceptual framework.

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Chapter 2

Leaf-drop phenology as a template for terrestrial arthropods and their vertebrate predators in lowland Neotropical forests: a test of the litter-mosaic hypothesis

Abstract. Energy input into terrestrial ecosystems varies in space and time, in large part because of spatial and phenological differences of tree species and patterns of leaf abscission. In lowland wet Neotropical forests, deciduous canopy tree species differ in patterns of leaf drop: most species abscise leaves during the dry season, whereas other species drop leaves in the wet season. Because litter-fall events provide the trophic base for decomposing microorganisms and their arthropod consumers, and abundance of a model vertebrate organism was reported to be limited by food resources, the litter-mosaic hypothesis predicts that abundance of terrestrial frogs and lizards is caused by seasonal variation of leaf abscission of canopy trees. The hypothesis also predicts that tree species differing in leaf-drop phenology should support different abundance cycles of species annually. Here, I tested the litter-mosaic hypothesis at La Selva Biological Station, Costa Rica by: (1) quantifying the abundance of leaf litter, terrestrial arthropods, and herpetofauna beneath replicate plots of two tree species (*Dipteryx panamensis*, *Castilla elastica*) with contrasting patterns of leaf drop, and (2) manipulating leaf abscission phenology beneath *C. elastica* with a leaf-litter supplementation experiment. I observed strong seasonal variation in standing leaf-litter depth, with more abundant litter during the dry season relative to the wet season, although patterns of terrestrial litter did not vary between tree species. Abundance of four dominant arthropod taxa followed a similar seasonal pattern, but did not vary by tree species. I estimated the abundance of three vertebrates – the frogs *Craugastor bransfordii* and *Oophaga pumilio*, and the lizard *Norops humilis* – using hierarchical *N*-mixture models for open populations. Variation of frog and lizard abundance was best characterized by season and did not vary predictably by tree species. Experimental manipulation of litter caused elevated *N. humilis* abundance in manipulated plots relative to controls, apparently the result of increased immigration, apparent survival, and/or recruitment. Model selection suggested that both frog species were unaffected by litter supplementation. Comparative analysis between *C. elastica* and *D. panamensis* suggested that seasonal rhythms and litter admixture among neighboring trees overrides individual effects of tree species during the study. However, experimental manipulation of *C. elastica* supported the hypothesis that tree leaf-drop phenology affected *N. humilis* abundance. My data suggest that the litter-mosaic hypothesis should be refined and restricted to describe spatiotemporal variance of terrestrial anoles, and the model organism from which it was inferred.

Key words: *arthropods,* Craugastor bransfordii*, leaf litter,* Norops humilis*, Neotropics,* Oophaga pumilio*, population ecology, food resources.*

INTRODUCTION

Leaf production by trees in seasonal tropical forests is generally highest during the dry season when herbivorous arthropod abundance is lowest, and new leaves are flushed synchronously to saturate herbivores and decrease potential leaf damage (Coley and Barone 1996). Many tree species rapidly abscise old, senesced leaves and undergo significant leaf-drop in the dry season; as a result, terrestrial litter accumulates to its greatest depths toward the end of that season (Frankie et al. 1974, Levings and Windsor 1984, Spain 1984). As the wet season begins, decreased leaf drop, increased decomposition, and the mechanical action of rainfall all contribute to decreases in standing leaf-litter crops, and these features cause terrestrial leaf litter to vary predictably across seasons. Leaf-abscission events cause significant pulses of nutrients into the terrestrial community and provide the trophic base for the brown food web (citation) and its arthropod constituents (McGlynn et al. 2007, Kaspari and Yanoviak 2009). Abundant dry-season litter causes arthropod abundance to increase until both peak in the early wet season (Toft 1980, Lieberman and Dock 1982, Levings and Windsor 1984). Seasonal arthropod increases also correlate with increases in small vertebrates who consume arthropods, such as lizards and frogs, whose numbers respond to elevated prey (Janzen and Schoener 1968, Wright 1979, Toft 1980, Lieberman and Dock 1982, Lieberman 1986, Guyer 1988). Thus, it appears that leaf-drop phenology of trees can moderate density of forest-floor vertebrates, as mediated by arthropod prey resources, in ways consistent with bottom-up control (Hunter and Price 1992).

In wet Neotropical forests, numerous studies have identified a relationship between standing leaf litter and abundance of a diverse assemblage of terrestrial frogs and lizards (Scott 1976, Lieberman 1986, Guyer 1988, Fauth et al. 1989, Heinen 1992, Whitfield et al. 2007). Distribution of leaf litter is a vital aspect to the life history of this vertebrate assemblage, which relies on microhabitat selection in leaf litter to access arthropod food resources (Toft 1980, Lieberman 1986, Whitfield and Donnelly 2006), avoid desiccation (Seebacher and Alford 2002, Schlaepfer 2003, Socci et al. 2005), minimize predation (Greene 1988, Cooper et al. 2008a, b), and reproduce. Indeed, an experimental manipulation at La Selva Biological Station, Costa Rica, provided the first experimental evidence demonstrating standing leaf-litter depth to be a density-limiting factor for terrestrial frogs and lizards, although the effect varied among species (Whitfield et al. 2014).

Given the strong seasonally dynamic pattern of standing leaf litter (Lieberman and Dock 1982) and the connection between litter and life history of terrestrial frogs and lizards in the Neotropics, abundance of frogs and lizards is predicted to vary seasonally relative to leaf litter in lowland wet forests, such as La Selva Biological Station (hereafter, La Selva). The prediction was supported by a survey of primary forest habitats at La Selva, which showed a weak but significant seasonal effect of elevated frog and lizard abundance in the dry season relative to the wet season (Lieberman 1986). A similar seasonal pattern was observed in a mark-recapture study of the anole *Norops humilis* inhabiting a cacao (*Theobroma cacao*) plantation system at La Selva, which is characterized by a strongly seasonal leaf-drop phenology in the dry season (Guyer 1988). This study used repeated surveys in plots and observed a stronger seasonal effect with less variance among months for anole abundance, a pattern that was linked with the dry-season leaf abscission of *T. cacao* (Guyer 1988). Leaf abscission of most Neotropical tree species occurs in the dry season, although some species defoliate during the wet season (Frankie et al. 1974). Since tree species vary in leaf-drop phenology and individuals of different species can be dispersed widely throughout forests (Clark and Clark 1987), areas of thick litter with increased arthropod abundance may be distributed in patches throughout forests, with patches varying over time. Therefore, vertical studies with random sampling of sites in forests sampled at many time points may not account for important spatial and temporal heterogeneity in litter observed in horizontal studies of permanent plots sampled across time (Guyer 1988, 1990).

Guyer (1988, 1994) argued that the appropriate scale to study population and community dynamics of arthropod and arthropod predators is at the scale of single forest trees in lowland Neotropical wet forests. In this conceptual model, litter-drop events at the spatial scale of single forest trees drive elevated abundance of terrestrial arthropods, and increased arthropod availability beneath trees, in turn, drives increased abundance of frogs and lizards by increasing (1) immigration of individuals from a floating population, and (2) reproductive output of females in plots. Alternatively, seasonal reductions in litter and associated food should lower survival and increase emigration, and thus decrease abundance at sites. This assertion could apply to tree species with varying leaf-drop phenology, such that seasonal abundance cycles should differ drastically beneath tree species that abscise leaves at different times in the year. Together, the Guyer (1988) model suggests that abundance of leaf-litter organisms throughout primary forests is a patchy mosaic of sites at differing stages, depending on the time of the year and the leaf-drop phenology of the proximate tree (hereafter, the litter-mosaic hypothesis, Guyer 1988).

In this study, I sought to understand how tree leaf-drop phenology influences seasonal variation of arthropods, frogs, and lizards at La Selva, Costa Rica, by testing three predictions of the litter-mosaic hypothesis (Guyer 1988, 1994). First, if litter fall events at the scale of single trees regulates population cycles of arthropods and their predators, then abundance of standing leaf litter should correlate with increased abundance of arthropods and their predators, caused by demographic shifts in recruitment, survival, immigration, and/or emigration associated with litter abundance variation. Second, tree species differ in leaf-drop phenology, so seasonal variation of litter abundance should differ below different tree species, and tree species-specific patterns of litter abundance should drive different abundance cycles of arthropods and their predators. Third, altered phenology of leaf abscission should also result in altered abundance cycles of arthropods and arthropod predators.

To test the first two predictions of the litter-mosaic hypothesis, I quantified the abundance of terrestrial leaf litter, arthropods, and vertebrate arthropod predators (frogs and lizards) in replicate plots for two tree species with contrasting patterns of leaf abscission

(*Castilla elastica*, *Dipteryx panamensis*) over a seasonal period. Because *C. elastica* and *D. panamensis* differ in seasonality of leaf fall, the hypothesis predicts that trees are characterized by different abundance cycles of leaf litter, arthropods, and arthropod predators (predictions 1 and 2; Figure 1). To test the third prediction, I experimentally manipulated leaf fall by supplementing leaf litter beneath *C. elastica* trees during the late wet season when litter abundance is low. If leaf-drop phenology limits cycles of associated animal abundance, then simulation of leaf-abscission via litter supplementation should increase the abundance of leaf-litter organisms as a result of altered demographic processes, compared to control plots.

METHODS

Study area

La Selva Biological Station is a private reserve owned by the Organization for Tropical Studies (OTS) in the Caribbean lowlands of northeastern Costa Rica, ~3 km south of Puerto Viejo de Sarapaquí, Heredia Province (10.42˚N, 84.02˚W). Elevation at La Selva ranges from 30–130 m asl. The site is characterized by an average temperature of 25.8˚C, receives ~4 m of precipitation annually (Sanford et al. 1994), and is classified within Holdridge's Tropical Wet Forest life zone (McDade and Hartshorn 1994). Rainfall is seasonal with most rain occurring during the wet season (May–December) relative to the dry season (January–April). La Selva is ~1600 ha in area, of which 1100 ha is primary, old-growth forest. Tree species richness is high at La Selva: single hectare plots can have 79–107 species, and the understory is dominated by palms (Hartshorn 1972, 1983, Lieberman and Lieberman 2007).

Canopy tree species in the lowland tropical wet forest of Costa Rica are characterized by diverse phenological patterns of leaf abscission and flushing (Frankie et al. 1974). My experimental study examined two tree species with contrasting patterns of abscission. *Dipteryx panamensis* (Fabaceae) is a canopy or emergent canopy species occurring on well-drained upland ridge tops that drops its leaves during the dry season (February–March). *Castilla elastica* (Moraceae) is a canopy species occurring in alluvial, riparian, and plateau habitats and drops leaves at the start of the wet season (May–June). Both *D. panamensis* and *C. elastica* are relatively abundant at La Selva, occurring in densities of 1–10 individuals per ha (Hartshorn and Poveda 1983). Leaf morphology also differs between the species: *C. elastica* leaves are relatively large and simple, while *D. panamensis* is a legume with alternate leaflets which cumulatively are of comparable size as *C. elastica*.

Study taxa

The leaf-litter arthropod community at La Selva is a diverse assemblage, although the dominant groups are mites (Acari), spiders (Araneae), beetles (Coleoptera), springtails (Collembola), millipedes (Diplopoda), ants (Formicidae), and crickets (Orthoptera; Lieberman and Dock 1982, McGlynn et al. 2007). Arthropods are seasonally abundant in the dry season at La Selva (Lieberman and Dock 1982), although there is high spatial variation in abundance, which has been tied to nutrient availability (McGlynn et al. 2007).

Three species of terrestrial frogs and lizards are abundant at La Selva and were the focal vertebrate taxa in my study: the frogs *Craugastor bransfordii* (Bransford's Litterfrog) and *Oophaga pumilio* (Strawberry Poison Frog) and the anole *Norops humilis* (Ground Anole).

Craugastor bransfordii utilizes a diverse prey base that includes beetles, spiders, mites, and isopods. *Oophaga pumilio* is a specialist that feeds almost exclusively on ants and mites, groups that comprise 50 and 40 percent of its diet, respectively (Lieberman 1986, Donnelly 1991). *Norops humilis* is a generalist predator of arthropods in primary forest (Lieberman 1986, C. Guyer pers. comm.).

Study design

I selected replicate individuals of *Dipteryx panamensis* (N = 8) and *Castilla elastica* (N = 6) that were tall (i.e., canopy or emergent-canopy height), occurred in primary forest, occurred in plots without significant intrusion by understory trees or lianas (allowing for adequate searching), were independent of each other (minimum distance between individual = 60 m), and were spatially interspersed across the alluvial landscape at La Selva. I selected individuals with broad diameters at breast height in an attempt to study trees with maximal effect size on the terrestrial animal community. I established gridded plots around each tree consisting of 21 cells per plot; each cell was 3 m x 3 m in area, which together generated plot areas of 189 m^2 per plot). Cells were marked using PVC tubing; the central-most grid cell contained the base and buttresses of the tree (Figure 2). I selected plots of this area because it is of similar size to plots used successfully in other experimental manipulations of amphibian and reptile populations at La Selva (Guyer 1988, Donnelly 1989, Reider et al. 2013, Whitfield et al. 2014).

I assessed the abundance of standing leaf litter and arthropods in each plot monthly during February–November, 2014. To do so, I randomly selected four tubes within the PVC grid and used a 0.30 m x 0.30 m (area = 0.09 m^2) quadrat to collect leaf litter and arthropod samples immediately adjacent to each tube. I laid the quadrat adjacent to each tube at a randomly selected anti-cardinal directions (NE, SE, SW, NW), such that a corner of the quadrat touched the base of the tube. Leaves were cut quickly along the perimeter of the quadrat using a large knife, and all litter and invertebrates were removed and placed into a large Ziploc® bag. Any woody material >0.5 cm in diameter was excluded. I brought the samples into the laboratory, placed them into Berlese funnels (Tullgren modification; Edwards 1991), and used a 75W light bulb to dry the litter over 48 h (or longer, as necessary to completely dry the litter) to induce arthropods to migrate from the drying litter into a vial containing 95% ethanol. I assumed that all arthropods contained in the litter were extracted and abundance of arthropods were therefore detected perfectly. I used a dissecting microscope to sort arthropods into groups and identified them to the lowest practical taxonomic group (Appendix A), following the methods of prior diet studies of the focal vertebrate taxa (Lieberman 1986, Donnelly 1991, Whitfield and Donnelly 2006). I then counted the number of individuals in each lot to quantify abundance of each group in each sample. Taxonomic lots were deposited into the Auburn University Museum of Natural History (Appendix A). I attempted to collect litter and arthropod samples monthly for both trees in the study, but was unable to collect samples in March and April, 2014, for both tree species and in November, 2014, for *D. panamensis*.

After leaf litter was dried and arthropods were removed, I measured leaf-litter mass (g) from Berlese samples with an electronic balance. I also quantified litter abundance by (1) measuring the distance from the top of the soil to the top layer of litter (mm; Vernier calipers), and (2) counting the number of individual leaves in the litter column that were pierced by the metal shaft of the Vernier calipers (Reider et al. 2013, Whitfield et al. 2014). I collected these measures within the center of grid cells in each plot bimonthly during the study.

I surveyed amphibians and reptiles using diurnal visual-encounter searches of the forest floor and other substrates up to 2 m above ground. I attempted to capture all individuals detected, identified them to species and sex, measured snout-vent length (SVL, nearest mm), determined mass (nearest 0.05 g), and recorded the grid cell location where each animal was first sighted (see Guyer and Donnelly 2012). I also recorded female reproductive status of *C. bransfordii* from August–November. Care was taken to have minimal disturbance on litter microhabitats during sampling. Plots were sampled monthly from February–November 2014, except for April. Repeated surveys (N = 3) were performed within each month, except for March (N = 2). The first survey was conducted on a randomly selected day, and repeated surveys were performed on the two following days.

Supplementation experiment with C. elastica

From 28–30 May 2014, I collected *Castilla elastica* leaves from beneath trees located outside of the study area. Leaves were collected if they were freshly abscised, lacked mechanical damage, and had experienced no decomposition. Leaves were picked individually, manually shaken to remove macroinvertebrates, placed in large plastic bags, and then transported to an air-conditioned laboratory where leaves were spread across the floor and allowed to dry over a 3-d period (Cardelús 2010). After drying, leaves (191 kg total) were stored in plastic bags in an air-conditioned laboratory for three mo.

Three of the six *C. elastica* study trees were assigned randomly to an experimental supplementation treatment. During 5–8 September 2014, ~3 mo after natural leaf abscission for *C. elastica*, I supplemented 62–64 kg of dried *C. elastica* leaves to each plot in the experimental supplementation treatment group. Leaves were spread homogeneously throughout plots in an effort to mimic natural leaf-drop (Figure 3). I also performed a sham manipulation in control plots by walking through plots with large plastic bags and mimicking the action of spreading leaves on the ground. While experimental treatments were randomly selected, the assignment of experimental treatment and control plots were relatively interspersed in the forest. In months prior to the experimental treatment (February–August), all *C. elastica* plots were pooled for analyses; however, after the experimental manipulation, experimental plots were analyzed separate from control plots.

Statistical approach

I considered observed measures of leaf litter abundance (dried mass, g; depth, mm) and arthropod abundance (individuals per litter sample) to indicate true abundance of these variables in plots by assuming no measurement bias (litter, arthropods) or false detection rate (arthropods). However, observed measures of amphibians and reptiles, such as counts, often are inappropriate estimates of abundance because of imperfect detection (Heyer et al. 1994, Mazerolle et al. 2007, McDiarmid et al. 2012). To account for low detection probability of terrestrial frogs and lizards, I used hierarchical *N*-mixture models that estimate detection probability from count data to estimate abundance of species within local populations. Classic *N*-mixture models (Royle 2004) use a repeated sampling scheme within a time period where local populations are assumed closed to demographic changes (births/deaths, immigration/emigration); detection probability is estimated from counts and used to infer abundance (Royle 2004). Recent extension of the *N*-mixture model has allowed for hierarchical modeling of populations that are open to demographic processes, where variance in abundance through time is modeled because of demographic processes, such as apparent survival (mortality/emigration), recruitment term (birth), and immigration (Dail and Madsen 2011, Hostetler and Chandler 2015). These hierarchical *N*-mixture models for open populations require two hierarchal sampling levels, primary and secondary sampling periods. Among primary periods, populations are open to demographic changes, and models estimate two demographic processes that cause changes in abundance between primary periods: a survival process (mortality/emigration) and recruitment processes (birth, immigration). Primary sampling periods typically encompass multiple secondary sampling periods, and models assume that populations are closed to demographic changes within primary periods. Iterative sampling within primary periods is then used to estimate detection probability. Thus, *N*-mixture models for open populations estimate abundance through estimates of demographic rates and detection probabilities. In the present study, the primary sampling period was month, and the second sampling units were individual surveys within months. Plots were the unit of replication within tree species and experimental treatment groups, and abundance of species was estimated among all grid cells within plots.

To understand whether population dynamics varied between *C. elastica* and *D. panamensis* plots in ways predicted by the litter-mosaic hypothesis, I used *N*-mixture abundance models to estimate how abundance and population structure varied seasonally in each plot. For each of the focal vertebrate species, I tallied the number of juveniles, males, and females encountered during each survey, and built *N*-mixture abundance models for open populations (Hostetler and Chandler 2015), which estimated detection probability and abundance of age classes across entire tree plots throughout the study. I generated a set of candidate models that described hypotheses about how initial abundance (N_1), population growth (λ) or apparent survival (ω), and detection probability (p) could vary by tree species or month (N = 9 models;

Table 1). Initial exploratory analyses strongly supported monthly variation in detection; thus, I built all models to include that parameter. For each species-age class, I built the nine candidate models during five different iterations in which I specified five different hypothetical population dynamics: (1) a 'trend' model for exponential growth, in which abundance (N_t) was estimated as a function of N_{t-1} and the finite rate of population growth (λ), (2) an 'autoregressive' model in which population growth (λ) was modeled as a function of abundance during the previous time step (N_{t-1}), (3,4) two models for density-dependent population growth, the Ricker-logistic (Ricker) model and the Gompertz-logistic (Gompertz) model, in which λ was the maximum instantaneous population growth rate around an equilibrium abundance (i.e., carrying capacity, K), and (5) a null model lacking any temporal trend (Dail and Madsen 2011, Fiske and Chandler 2011, Hostetler and Chandler 2015). This procedure resulted in 45 candidate models of hypothetical population dynamics and detection for each age-sex group of the focal vertebrate species. All models were specified with a zero-inflated Poisson distribution. I explored different values of the tuning parameter K until abundance estimates did not increase, and ultimately built models at $K = 100$. All models were ranked with Akaike's Information Criterion corrected for small sample size (AIC_c; Hurvich and Tsai 1989); the model with the lowest AIC_c was identified as the top model and selected for inference (Burnham and Anderson 2010). I applied empirical Bayes methods to the top model to estimate $N_{j,i}$ – the abundance at each site (j) during each month (i). I calculated log-transformed population growth (λ) vertebrate age-sex classes in plots by dividing model-estimated abundance for each age-sex class in a given month t (N_t) by abundance from the previous month (N_{t-1}).

To understand how variance in abundance of dried leaf litter, arthropods, and vertebrates varied seasonally and among study treatments, I built linear mixed-effect (LME) regression models with covariate structure describing how response variables (dried litter mass, arthropod abundance, vertebrate abundance) varied by month, tree species treatment (*C. elastica*, *D. panamensis*; *C. elastica* [control], *C. elastica* [supplemented]), and a tree species treatment*month interaction. I built a saturated model with all hypothesized effects (tree species + month + tree species*month interaction), and then built four additional models comprising each possible combination of candidate model terms, and including a null model (i.e., an all-subsets analysis). I specified random effects for models in two ways. First, to understand if animal communities exhibited general responses to litter fall, I built models for all arthropods and vertebrates, which included random effects of taxonomic group (arthropods) or species identity (vertebrates) nested within plot. For analyses of leaf-litter mass, individual arthropod taxa, or individual frog and lizard species, plot was specified as the only random effect. Models were ranked using AIC_c, and model parameter coefficients were averaged using model weights. Second, I evaluated whether model-averaged coefficients exerted significant effects on response variables if (1) the predictor variable was included in a top-model set ($\Delta AIC_c < 2.00$), and (2) if full model-averaged 95% CI did not overlap zero (Burnham and Anderson 2010); if effects met both of these two criteria, I considered effects as significant and described effect size of parameters with 95% CI.

All analyses were performed in the statistical program R (R Core Team 2016). I used the package ‘unmarked’ (Fiske and Chandler 2011) to build *N*-mixture abundance models and estimate posterior abundance with the function *pcountOpen* and *ranef*. The LME models were performed using the functions *lme* in the package ‘nlme’ (Pinheiro et al. 2016), and all-subsets and model-averaging analyses were performed using the functions *dredge* and *model.avg* from the package ‘MuMIn’ (Barton 2016).

Seasonal comparison between C. elastica *and* D. panamensis

To test the prediction that abundance of leaf litter corresponds with increased abundance of arthropod assemblages, I built linear mixed-effect regression models (LMEs) with covariate structure describing arthropod abundance as a result of dry litter mass, tree species identity, and litter mass*tree species interaction terms. The hypothesis predicts that litter mass correlates positively with arthropod abundance. However, because litter arthropods are limited by litter nutrients (McGlynn et al. 2007) and leaves from the two focal tree species differed in nutrient concentration (e.g., Cardelús et al. 2009), I included a tree species identity term in models to test if tree species have different relationships of litter mass and arthropod abundance (i.e., Analysis of Covariance). I included tree plot as a random effect. When fixed-effect model parameters were non-significant, I removed parameters in favor of simple models, and only reported parameters from reduced models.

In addition, I analyzed whether abundance patterns of litter, arthropods, and vertebrates differed in ways consistent with the hypothesis that timing of leaf abscission differentially regulates these systems. Specifically, because litter fall of *D. panamensis* occurs earlier in the year than *C. elastica*, I predicted that abundance of litter, arthropods, and vertebrates beneath *D. panamensis* should increase earlier in the year than litter and associated fauna beneath *C. elastica*. If tree species with distinctive patterns of leaf-drop phenology generated distinct seasonal abundance cycles of leaf litter and terrestrial fauna, I expected that (1) LME models for leaf litter and arthropods would describe significant variation explained by tree species*month interaction terms in the data from February–August, and (2) model selection analysis for *N*-

mixture models should identify models with seasonal dynamics of frogs and lizards that differ between *C. elastica* and *D. panamensis* plots.

To better understand factors influencing vertebrate population variation, I used abundance estimates derived from *N*-mixture models to calculate population growth (λ; above) and then used a LME all-subsets analysis to test predictions of the litter-mosaic hypothesis. I developed a global candidate model that described hypotheses (below) for factors influencing population growth of frogs and lizards, assuming seasonal population regulation by tree species, as mediated through leaf litter and food resources. The candidate model described vertebrate λ as a function of a tree species*month interaction term and additive effects of leaf litter and food resources. I defined food resources as the sum of Acari, Araneae, Coleoptera, Isopoda, and Formicidae, the primary food sources for the focal vertebrates (Lieberman 1986, Donnelly 1991). Leaf-litter mass and food abundance were log+1 transformed to increase normality and decrease heterogeneity of variance. I modeled the candidate global model using an LME modeling framework, with a random effect of tree plot nested within age-sex class within species. I then used an all-subsets analysis and model-averaging to test 19 alternative models, including a null model, to rank competing models with AIC_c and averaged parameter effects across all models using model weight. I reported parameter effects for which 85% confidence intervals did not overlap zero. To understand species-specific variation in population growth, I built the same 20 models for each vertebrate species separately, but modeled food resources as specific to each species' diet, following the literature (Lieberman 1986, Donnelly 1991): *C. bransfordii* and *N. humilis* food resources were modeled as the sum of Acari, Araneae, Coleoptera, and Isopoda, and *O. pumilio* food was modeled as the sum of Acari and Formicidae.

Supplementation experiment with C. elastica

The third prediction of the litter-mosaic hypothesis suggests that experimental alteration of leaf drop phenology should cause elevated abundance in treatment plots relative to unmanipulated control plots; specifically, elevated habitat quality from litter supplementation should increase reproduction and/or decreases in mortality and emigration, thereby increasing the abundance of individuals in supplemented relative to control plots. I tested this prediction in four ways. First, I tested for predictable increases in habitat quality by measuring how litter and arthropod food resources varied between supplemented compared to unmanipulated control *C. elastica* plots during August (pre-treatment) and September–November (treatment) using the LME model approach, as outlined above.

Second, I built a candidate set of eleven *N*-mixture models for open populations with autoregressive population dynamics, where model parameters (recruitment [λ], apparent survival [ω], immigration [ι], and detection probability [*p*]) varied as a result of litter supplementation; Appendix C). I specified autoregressive population dynamics here because (1) the model structure estimated recruitment, apparent survival, and immigration, three demographic parameters predicted by the Litter-mosaic hypothesis to increase as a result of elevated leaf litter, and (2) the model was linear in nature, and I did not expect exponential or non-linear dynamics during the three-months post-supplementation. I used counts of juveniles, females, and males summed together, because these data more closely approximated a Poisson distribution and goodness-of-fit analyses and thus indicated that the more-parameterized models would converged better with the data. Therefore, I specified a Poisson distribution for models; however, count data for *N. humilis* were still characterized by a considerable proportion of zeroes, so I modeled that species with a zero-inflated Poisson distribution. I used model selection to identify which models received the strongest support (ΔAIC < 2.00), and considered leaf-drop phenology to influence vertebrate demography when experimental treatment parameter(s) were included in the top model or models with equivocal support (model weight).

Third, I used abundance estimates from *N*-mixture models to calculate population growth (λ) for vertebrates and used a LME all-subsets analysis to test if litter and/or food resources (arthropod abundance) correlated with changes in vertebrate population size in supplemented plots. Last, I used LME models to test for treatment-based increases in reproduction. Specifically I measured the proportion of observed gravid female *C. bransfordii* in all plots and tested whether supplemented plots were responsible for differences in egg input among litter supplemented *C. elastica* plots, control *C. elastica* plots, and *D. panamensis* plots.

RESULTS

Seasonal comparison between C. elastica *and* D. panamensis

Abundance of leaf litter in *C. elastica* and *D. panamensis* plots varied strongly among months during the study, but effects of tree species identity and tree species*month interactions were not significant (Figure 4). Relative to leaf litter abundance in February, litter abundance was higher in May ($\beta = 23.7$; 15.0–32.5, 95% CI), June ($\beta = 23.8$; 15.0–33.0), and August ($\beta = 26.4$; 17.0–35.8); in addition, litter abundance in May was higher than in August ($\beta = 20.4$; 7.4–33.4), but was not higher than June.

Linear mixed-effects models described significant relationships between variation in litter abundance and arthropods. For each 10-g increase in litter abundance, I observed a 70.7

individual (69.1–72.3; 95% CI) increase in abundance of arthropods ($P < 0.0001$). Specifically, for each 10 g increase in dried leaf litter, I observed a 23.0 individual (14.6–31.4) increase in acarine abundance ($P < 0.0001$), a 10.6 individual (8.1–13.1) increase in collembolan abundance ($P < 0.0001$), a 1.0 individual (0.6–1.3) increase in spider abundance ($P < 0.0001$), a 4.9 individual (3.0–6.9) increase in ant abundance ($P < 0.0001$), a 1.3 individual (0.9–1.7) increase in coleopteran abundance ($P < 0.0001$), and a 0.2 individual (0.1–0.3) increase in orthopteran abundance ($P < 0.0001$). Models including factors of tree species identity and litter mass*tree species interaction terms did not support significant effects of tree species identity or tree species*litter mass interactions, so these parameters were removed in favor of simple model structure.

In general, arthropod abundance varied seasonally, but not by tree species identity or month*tree species interaction terms. An overall analysis of the six numerically dominant arthropod groups revealed that, relative to February, abundance was higher in May ($\beta = 37$; 25–49), June ($\beta = 26$; 14–39), and August ($\beta = 17$; 4–30); abundance in May was higher than that observed in August ($\beta = 20$; 7–33). Effect of tree species identity or month*tree species interactions were not supported because 95% confidence intervals overlapped zero. Specific arthropod groups showed similar seasonal patterns, which also did not vary by tree species or month*tree species interactions (Figure 5; Appendix B). Relative to February, mite abundance in plots was higher in May ($\beta = 152$; 88–215), June ($\beta = 114$; 48–180), and August ($\beta = 112$; 43–181; Figure 5A). Collembolan abundance also was elevated in May ($\beta = 60$; 41–79) and June ($\beta = 25$; 6–45) relative to February, but there was an interaction in which *D. panamensis* trees had decreased collembolan abundance in May relative to that observed in *C. elastica* plots ($\beta = -27$; 2–52; Figure 5B). Similarly, other less-dominant arthropod groups exhibited seasonal patterns similar to mites and collembolans: spiders were more abundant in May (β = 5; 2–9) and June (β = 4; 1–8) than in August, coleopterans were more abundant in May (β = 6; 2–9) and June (β = 9; 5–12) than in February, and orthopterans were more abundant in May than in August (β = 0.3; 0.1–0.8).

Among the 45 candidate *N*-mixture abundance models built to evaluate population dynamics of *C. bransfordii*, *O. pumilio*, and *N. humilis*, ten models did not converge or could not be fitted given the varying population dynamics (Appendix B). The model selection procedure identified support for population dynamics that varied by species and age-sex groups, including trend, Ricker exponential, autoregressive, and no trend dynamics (Table 2). Model weights indicated that top-models used for inference were generally ~1.5 times more-strongly supported than other models in the top-model set for each species age-sex class (Table 2).

Abundance estimates derived from top models described species-specific patterns of population structure and seasonally variable abundance for *C. bransfordii*, *O. pumilio,* and *N. humilis*. Models estimated populations of *C. bransfordii* to be dominated by juveniles over adults, whereas populations of *O. pumilio* and *N. humilis* were generally characterized by higher abundance of adults than juveniles (Figure 6). Model estimates suggested that *C. bransfordii* juveniles become more abundant in the wet season, female abundance varied slightly but did not show a strong seasonal signal, and male abundance was higher under *D. panamensis* relative to in *C. elastica* plots, but seasonally variable in both. Relative to *C. bransfordii,* abundance of *O. pumilio* and *N. humilis* exhibited higher seasonal variation. Juvenile *O. pumilio* were more abundant during the dry season, whereas female and male abundances increased in the wet season. Further, patterns of male abundance suggested an interaction between season and tree species, in which male *O. pumilio* abundance was higher in *D. panamensis* than *C. elastica* plots during the late wet season. Juveniles of *N. humilis* were more abundant in *D. panamensis* plots during the dry season, but exhibited decreased population growth in those plots and declined in the wet season until abundance in litter beneath both trees was equivalent. Female *N. humilis* showed a strong pattern of seasonally higher abundance in the dry than wet seasons, although it did not vary by tree species, and males showed no seasonal trend in abundance and no difference in abundance between tree species (Figure 6).

An all-subsets analysis of vertebrate λ in *C. elastica* and *D. panamensis* plots from February to August identified seasonality as the greatest source of variation in plots. Considering all three species as a random effect, λ was higher during the dry season (i.e., from March–May) than during the wet season (i.e., from May–June or from July–August). Separate analysis of each species identified three species-specific patterns: (1) relative to during the dry season in March–May, λ of *O. pumilio* decreased during the ring the wet season (June: β = -0.47,-0.28–0.67; August: β = -0.64, -0.43–0.85), (2) λ of *O. pumilio* was positively correlated with arthropod abundance in plots (β = 0.010; 0.009–0.143), and (3) λ of *N. humilis* increased in August relative to May (β = 0.004, 0.009–0.133) and, relative to *C. elastica* populations, *N. humilis* showed decreased λ in *D. panamensis* plots.

Supplementation experiment with C. elastica

Experimental supplementation of *C. elastica* litter produced a significant increase of 21.3 g (1.3–41.0, 95% CI) of dried leaf litter in treatment plots relative to controls (Figure 4); strong variation was not observed across months or by treatment*month interaction terms. A linear mixed-effects model for total arthropod abundance described a supplementation*month interaction, with arthropod abundance increasing with each successive month post supplementation ($\beta = 7$; -6–21, 95% CI); however, the confidence intervals around the effect overlapped zero. Analyses of most individual arthropod groups also found no effects of experimental supplementation or month*treatment interactions on abundance (Figure 5), except for a coleopteran abundance increased in supplemented plots over time ($\beta = 4.5$; 0.1–10.5), and a weak month*treatment interaction for mites ($\beta = 31$; -43–107).

Model selection of candidate *N*-mixture models for the three vertebrate species supported effects of litter supplementation on *N. humilis*, but not for *C. bransfordii* or *O. pumilio* (Table 3). The top-model set for *N. humilis* identified three top models with equivocal support (model weight = 0.15–0.16); these models included supplementation effects on apparent survival, recruitment, and immigration. Abundance estimates for *N. humilis* derived from the three top models were comparable to each other and described an increase of 13.5 individuals (11.8–15.2, 95% CI) in supplemented plots relative to controls ($P < 0.0001$). Top models for *C. bransfordii* and *O. pumilio* did not describe differences in population demography or abundance between supplemented and control plots; rather, the top two models for both species either were the null model or included a single parameter of differing detection between supplemented and control plots (Table 3).

An all-subsets model-averaging analysis of vertebrate λ in experimental *C. elastica* plots did not support an effect of litter supplementation on λ. Model selection identified a null model as the most strongly supported (model weight = 0.83), with no effects of litter, food, month, experimental treatment, or month*treatment interactions; model averaging similarly identified no parameter effects on λ. However, there were species-specific responses to supplementation (Figure 8). The average model for *N. humilis* described an effect in which λ of *N. humilis* was elevated in supplemented plots relative to controls during September (β = 0.08, 0.02–0.67). Model selection analysis for frogs suggested that litter supplementation did not influence variation in λ: *C. bransfordii* was best described by a null model of no effects on λ (model weight = 0.72), whereas λ for *O. pumilio* was best described by monthly decreases irrespective of supplementation (β = -0.20; -0.14–0.33; model weight = 0.72).

Proportions of gravid female *C. bransfordii* in plots were best explained by monthly variation (Table 4). Specifically, there was an increase in the proportion of gravid females with each successive month from August–November, (β = 0.05; 0.02–0.16); in contrast, tree treatment groups and interactions between month and treatment groups did not explain significant variation in egg production of *C. bransfordii*.

DISCUSSION

In this study, I conducted an experimental test of whether tree species and single-canopy trees provide a template for understanding the local-scale population dynamics of terrestrial arthropods and their vertebrate predators in a complex wet tropical forest. Given the observation that seasonal abundance of one vertebrate species, the ground anole *Norops humilis*, cycled seasonally in concert with patterns of leaf abscission and food availability in an abandoned cacao plantation system at La Selva, Guyer (1988) hypothesized that leaf-drop phenology of canopy trees regulates abundance of terrestrial vertebrates mediated through the arthropod food web. Because leaf input into the terrestrial system from deciduous trees largely causes changes in population density of members of the terrestrial arthropod community, the litter-mosaic hypothesis suggests that patches of food resources for frogs and lizards vary in space and time because of differing phenology of leaf abscission among tree species. The hypothesis was exciting because it potentially explained high spatial and temporal variation in population and community structure of frogs and lizards in primary forest at La Selva (Lieberman 1986) and other lowland wet Neotropical forests. The idea that individual trees influence population and community structure of arthropods and their vertebrate predators is supported by studies of amphibians and reptiles in plantation monoculture systems, which reported that plantation tree species differ in population structure and community assembly of their associated litter herpetofauna (e.g., Heinen 1992, Gardner et al. 2007, Folt and Reider 2013, Mendenhall et al. 2014), and studies describing insular effects of canopy trees and their buttresses on arthropods and herpetofauna (Whitfield and Pearce 2004, Adams et al. 2016).

My comparative study of *C. elastica* and *D. panamensis* was consistent with the first key prediction of the litter-mosaic hypothesis. I found a positive correlation between litter abundance and arthropod abundance for the six numerically dominant arthropod taxa, consistent with the well-supported model of leaf litter nutrients providing the trophic base for arthropod consumers in the brown food web (McGlynn et al. 2007, Kaspari and Yanoviak 2009). However, when comparing seasonal patterns of leaf litter, arthropods, and vertebrates beneath *C. elastica* and *D. panamensis* trees, results of my observational study revealed that litter abundance did not vary by tree species in ways consistent with the second prediction of this hypothesis. While *C. elastica* generally had higher standing litter throughout the year than *D. panamensis*, results did not identify a significant tree species*month interaction term; this is inconsistent with the prediction of contrasting seasonal patterns of litter beneath tree species with dissimilar phenology. Further, patterns of arthropod abundance also did not vary beneath the study tree species in ways predicted by the litter-mosaic hypothesis, and instead followed patterns comparable to the observed pattern of leaf litter that varied between the dry and wet seasons.

Last, vertebrate abundance in *C. elastica* and *D. panamensis* plots did not vary in ways predicted by the litter-mosaic hypothesis.

The positive relationship between seasonal litter and seasonal arthropod abundance was consistent with bottom-up regulation of arthropod abundance in the litter-mosaic hypothesis. However, I was unable to test the second prediction because patterns of standing litter beneath trees did not differ seasonally in the way I anticipated from my review of the literature. Thus, my comparative study of abundance cycles could not discern patterns of leaf litter, arthropod, and vertebrate abundance beneath the two tree species, and whether tree species with contrasting leaf abscission patterns regulate population cycles differently remains to be tested in a natural forest system.

When I first established the study plots in January 2014, leaf litter was already abundant in many plots prior to leaf abscission of the dominant tree. The high litter load indicates that significant leaf-drop events had happened recently before the start of the study and the abscission events of (1) *D. panamensis* during February-March and (2) *C. elastica* during May-June. This observation also suggests that any patchy effects of leaf abscission from different tree species were not stronger than the overall effect of leaf fall from other neighboring trees close to plots. If true, then litter admixture from neighborhood trees likely would mask effects of tree species identity on the litter footprint beneath single canopy trees. Further, while results of my experiment suggested an effect of leaf-drop phenology on population demography of *N. humilis* (below), two observations suggest that seasonal rhythms of the forest swamped effects of individual tree species on the terrestrial animal assemblage: (1) I observed significant litter present in plots prior to leaf abscission for both tree species (i.e., in February 2014), and (2) I observed low variance in standing litter between the two focal tree species, despite differing timing of leaf fall for those species.

The litter-mosaic hypothesis predicts that leaf fall increases arthropod abundance, and , in turn, elevated food resources for arthropod predators causes increased predator abundance by (1) increasing immigration to areas from a floating population, and/or (2) increasing apparent survival in areas of abundant litter, through decreased mortality and decreased emigration. As an explicit test of the third prediction, I supplemented litter in *C. elastica* plots to test for predictable increases in arthropod and vertebrate abundance. Experimental supplementation of leaf litter in *C. elastica* plots appeared to cause a strong and significant effect on the abundance of litter in supplemented trees relative to controls, although this increase did not ramify strongly through the food web as predicted by the litter-mosaic hypothesis. Litter supplementation caused apparent increases in abundance of arthropod taxa relative to controls (Figure 5), but these changes were not supported strongly by statistical analysis. It is possible that the marginal increase in arthropods is a true and strong effect affected by low sample size and statistical power (N = 3 plots/experimental treatment); however, because I observed such a strong effect of litter on arthropod abundance among all pooled samples, I interpret the supplementation to have driven an increase in arthropod abundance. Model estimates of vertebrate abundance suggested that *C. bransfordii* and *O. pumilio* abundance did not increase in supplemented plots, although *N. humilis* did increase. Three demographic models for *N. humilis* received equal support as top models, each describing a different demographic parameter that was elevated in litter supplemented plots (recruitment, apparent survival, immigration). These models suggested that elevated *N. humilis* abundance was driven by a demographic shift in supplemented plots. If increased arthropod abundance in supplemented plots was, in fact, biologically significant, then increases in leaf litter and/or arthropod food resources could have caused *N. humilis* to respond by increasing reproduction on litter-supplemented plots (i.e., recruitment model), immigrating to such plots (i.e., immigration model), and/or remaining on such plots or experiencing decreased mortality on such plots (i.e., apparent survival model). Because I did not observe an increase in the number of egg production or hatchlings in experimental plots (B.F., pers. obs.), I suspect this effect was driving by either higher adult immigration or apparent survival.

The litter-mosaic hypothesis was largely derived from an experimental study in which Guyer (1988) used meat bait stations in cacao plantation plots to experimentally increase food resources for *N. humilis* populations. Increased food availability for lizards caused populations to double in size; given that cycles of terrestrial leaf litter also relate to arthropod food resources for lizards, Guyer (1988) hypothesized that patterns of tree species leaf-drop phenology may provide the ideal template for understanding local-scale abundance of *N. humilis* and other terrestrial arthropod predators in this system. In my study, *N. humilis* populations responded to experimental supplementation of litter in ways consistent with the litter-mosaic hypothesis, by increasing abundance and altering population dynamics. However, because *C. bransfordii* and *O. pumilio* did not, my results do not support the generality included in the litter-mosaic hypothesis.

Whitfield et al. (2014) performed a 16-mo experimental removal and supplementation study of leaf litter at La Selva in random forest plots, and my experimental results are similar in several ways. Whitfield et al. (2014) found that *O. pumilio* abundance increased in supplemented plots, while *C. bransfordii* and *N. humilis* abundance declined in removal plots. In my study, there was a marginal increase in *O. pumilio* abundance in supplemented plots relative to controls, but the observed effect was weak and not strongly supported by statistical inference. Unfortunately, my experiment only manipulated litter in a single direction (supplementation), and natural decomposition processes likely did not diminish litter to the levels observed in the litter removal experiment of Whitfield et al. (2014); thus, I was not able to address how experimental removal of leaf fall may have influenced populations of *C. bransfordii* and *N. humilis* similar to those effects observed by Whitfield et al. (2014). My results may have differed from those of Whitfield et al. (2014) given the differing magnitude of experimental effects. Specifically, my supplementation elevated litter in a single pulse, similar to the temporal scale of elevated litter driven by leaf abscission of deciduous trees; this temporal scale is much shorter than the prolonged, 16-mo supplementation by Whitfield et al. (2014).

My results supported an important role of leaf-drop phenology in regulating abundance of *N. humilis*, but not necessarily because of increased arthropod prey for *N. humilis*. Analyses of vertebrate λ were best explained by seasonal variation; λ was only predicted by increases in food resources for *O. pumilio*, and λ was not correlated to litter abundance. This result was consistent with other studies suggesting that food resources are not limiting for terrestrial frogs and lizards in Central American rain forests (Andrews 1979, Whitfield and Donnelly 2006), and that factors other than food may influence variation in frogs and lizard abundance.

Vertebrate abundance estimates were largely characterized by seasonally varying abundance and population structure. Relative to the dry season, juveniles and females of *N. humilis* became less abundant during the wet season, and *O. pumilio* populations become adult dominated. The seasonal pattern of declining wet season abundance of *N. humilis* is consistent with Guyer (1988), who measured increases in population size during the dry season, and other researchers have observed strong seasonal patterns in which *N. humilis* is most abundant during the dry season at La Selva (S. Whitfield, pers. comm.). In both *C. elastica* and *D. panamensis* plots, counts and model-estimated abundance of *N. humilis* was highest at the start of the study in

February, prior to the leaf abscission of either tree species. This result suggests that an uncharacterized event happens late in the wet season or early in the dry season to increase abundance of *N. humilis*, prior to leaf abscission by *D. panamensis* and possibly other deciduous species with a similar early dry-season abscission phenology.

My seasonal estimates of abundance and λ for *N. humilis* were generally consistent with established patterns in the literature where this species is more abundant in the dry season than the wet (Guyer 1988, S. M. Whitfield pers. comm.). Analyses of λ here described *N. humilis* populations as declining during the dry season (May-June), until the middle of the wet season when λ increases again. This result suggests that λ begins at the end of the wet season, a feature which is not predicted by seasonal abundance of food resources in sites that is elevated at the end of the dry season. Thus, population growth of *N. humilis* did not appear to be driven by food resources. The wet season at La Selva extends from May to December, but is frequently punctuated by a short period of diminished rainfall during September or October, known locally as the '*veranillo*' (little-summer; Sanford et al. 1994). Guyer (1988) observed increased abundance of *N. humilis* during the *veranillo*, but my models were unable to resolve population differences over this period. Future studies should provide explicit tests of alternative demographic mechanisms potentially influencing seasonal λ and abundance of *N. humilis*, such as variance in recruitment, survival, or reproductive effort (i.e., quiescence, Braker and Greene 1994).

My analytical approach estimates abundances of terrestrial frogs and lizards using models that accounted for imperfect detection. A large literature from La Selva has used count data to make inferences about population and community structure of frogs and lizards (Fauth et al. 1989, Heinen 1992, Whitfield and Pearce 2004, Watling 2005, Whitfield et al. 2007, Folt and

Reider 2013, Reider et al. 2013); results of these studies may have been hindered by issues associated with imperfect detection of study organisms (Mazerolle et al. 2007). My study represents an attempt to remedy this shortcoming. Future studies attempting to measure abundance of terrestrial frogs and lizards at La Selva and other Neotropical forests should seek to account for imperfect detection when estimating the abundance (MacKenzie et al. 2006), potentially by using flexible approaches which can estimate complex population demographics (e.g., Hostetler and Chandler 2015).

The scope of my study largely was designed to view population dynamics through the lens of bottom-up regulation by resources. However, frog and lizard populations may be limited by factors other than food, such as interactions with predators (i.e., top-down factors) or with conspecifics (i.e., parallel factors, Laundré et al. 2014; e.g., conspecific attraction, Stamps 1988). For example, Whitfield and Donnelly (2006) found evidence suggesting that there is no seasonal change in availability of arthropod prey for amphibians and reptiles at La Selva, Costa Rica. Frog and lizard abundance may be strongly influenced by other deterministic factors that have received little attention to date in mainland Neotropical forests, including predators. Predation may be a potent force driving abundance, demography, and life history of species such as *C. bransfordii* and *N. humilis*, which exhibit cryptic coloration presumably in response to significant levels of historical or current predation. Alternatively, parallel factors such as competition or conspecific attraction may influence the local-scale abundance in ways not anticipated by hypotheses of resource limitation (Stamps 1988, Doody et al. 2013). These respective hypotheses would predict either abundance which, independent of resources, is distributed uniformly distributed or aggregated in space. Future studies should examine how local-scale ecology of frogs and lizards are influenced by purely social interactions among individuals, which might explain seemingly non-deterministic spatial and temporal patterns in this diverse ecosytem.

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Table 1. Candidate model set of *N*-mixture abundance models for open populations (Dail and Madsen 2011, Hostetler and Chandler 2015) built to examine how population dynamics of juvenile, female, and male *Craugastor bransfordii*, *Oophaga pumilio*, and *Norops humilis* varied in plots around single trees (*Castilla elastica*, *Dipteryx panamensis*) at La Selva, Costa Rica. Each model was built five times with different specifications for population dynamics: no trend, trend, autoregressive, Ricker, and Gompertz (see Methods). Models represent different hypotheses where initial abundance (N_1) and/or population growth rate (λ; trend, Ricker, Gompertz models) or apparent survival of individuals (ω; no trend, autoregressive models) could vary by tree species (Tree), and detection probability varied by Month and/or Tree. Model structures which did not converge or could not be built given model specifications were removed from the analysis. See Appendix B for the full model set and list of omitted models.

Model number	Model structure
1	N~1, λ~1, p~Month
2	N~Tree, λ~1, p~Month
3	N~1, λ~Tree, p~Month
4	N~1, λ~1, p~Month+Tree
5	N~Tree, λ~1, p~Month+Tree
6	N~1, λ~Tree, p~Month+Tree
7	N~Tree, λ~Tree, p~Month
8	N~Tree, λ~Tree, p~Tree
9	N~Tree, λ~Tree, p~Month+Tree

Table 2. Number of parameters (K), Akaike's Information Criterion (AIC), ΔAIC, and model weight (wm) for the top-model set (ΔAIC < 2.00) of 45 N-mixture abundance models (Appendix D) built to estimate abundance of terrestrial frogs and lizards at La Selva, Costa Rica.

Species	Sex	Population dynamic	Model structure	K	AIC	ΔAIC	w_m
C. bransfordii	J	Trend	N~1, λ~1, p~Tree+Month	14	1584.20	0.00	0.16
		Trend	N~Tree, λ~1, p~Month	14	1584.96	0.77	0.11
		Trend	N~1, λ~Tree, p~Tree+Month	15	1585.92	1.72	0.07
		Trend	N~Tree, λ~1, p~Tree+Month	15	1585.92	1.73	0.07
	F	Ricker	N~1, λ~1, p~Month	14	1134.80	0.00	0.16
		Gompertz	N~1, λ~1, p~Month	14	1136.04	1.24	0.09
		Ricker	N~Tree, λ~1, p~Month	15	1136.27	1.47	0.08
		Ricker	N~1, λ~Tree, p~Month	15	1136.37	1.57	0.07
	M	No Trend	N~Tree, ω~1, p~Month	13	1028.92	0.00	0.34
		No Trend	N~1, ω~1, p~Month	12	1029.88	0.96	0.21
O. pumilio	J	Autoregressive	N~1, ω~1, p~Month	14	573.85	0.00	0.11
		Trend	N~1, λ~Tree, p~Month	14	574.08	0.23	0.10
		No Trend	N~1, ω~1, p~Month	12	574.21	0.36	0.09
		Trend	N~1, λ~Tree, p~Tree+Month	15	574.64	0.79	0.08
		Trend	N~Tree, λ~Tree, p~Month	15	574.65	0.80	0.08
		No Trend	N~Tree, ω~1, p~Month	13	575.53	1.68	0.05
		Autoregressive	N~Tree, ω~1, p~Month	15	575.62	1.77	0.05
		Autoregressive	N~1, ω~1, p~Tree+Month	15	575.78	1.93	0.04
	F	Trend	N~Tree, λ~Tree, p~Tree	8	1025.64	0.00	0.47

	M	Ricker	N~Tree, λ~Tree, p~Tree	9	712.24	0.00	0.26
		Gompertz	N~Tree, λ~Tree, p~Tree	9	713.15	0.91	0.17
		No trend	N~1, ω~1, p~Tree+Month	13	713.71	1.47	0.13
N. humilis	J	Trend	N~Tree, λ~Tree, p~Tree	8	501.57	0.00	0.23
	F	Trend	N~Tree, λ~Tree, p~Tree	8	481.01	0.00	0.17
		No trend	N~1, ω~1, p~Tree+Month	13	481.67	0.66	0.12
		Gompertz	N~Tree, λ~Tree, p~Month	16	482.38	1.37	0.09
		No trend	N~Tree, ω~1, p~Month	13	482.84	1.84	0.07
	M	No trend	N~1, λ~1, p~Month	12	585.27	0.00	0.11
		Ricker	N~1, ω~1, p~Month	14	585.42	0.15	0.10
		No trend	N~Tree, ω~1, p~Month	13	586.13	0.87	0.07
		No trend	N~1, ω~1, p~Tree+Month	13	586.20	0.93	0.07
		Ricker	N~1, λ~1, p~Tree+Month	15	586.30	1.03	0.07
		Ricker	N~Tree, λ~1, p~Month	15	586.68	1.41	0.06

Table 3. Number of parameters (K), Akaike's Information Criterion (AIC), ΔAIC, and model weight (w_m) for the top-model set (ΔAIC < 2.00) of 11 autoregressive *N*-mixture abundance models built to evaluate if experimental manipulation of leaf-drop phenology influenced population demography of terrestrial frogs and lizards at La Selva, Costa Rica. Demography for three vertebrate species (*Craugastor bransfordii*, *Oophaga pumilio*, *Norops humilis*) were modeled in plots around individual *Castilla elastica* trees that were either experimentally supplemented with leaf litter (Treatment group; N = 3) or not (control group; N = 3; see Methods). *N* = initial population size; λ = recruitment; ω = apparent survival; *p* = detection probability; ι = immigration.

Species	Model structure	K	AIC	ΔAIC	w_m
C. bransfordii	*N*~1, λ~1, ω~1, *p*~Treatment, ι~1	6	379.21	0.00	0.24
	N~1, λ~1, ω~1, *p*~1, ι~1	6	380.00	0.79	0.16
	N~1, λ~Treatment, ω~1, *p*~Treatment, ι~1	6	380.58	1.37	0.12
	N~1, λ~1, ω~Treatment, *p*~Treatment, ι~1	6	380.61	1.39	0.12
O. pumilio	*N*~1, λ~1, ω~1, *p*~Treatment, ι~1	6	265.91	0.00	0.21
	N~1, λ~1, ω~1, *p*~1, ι~1	6	266.40	0.49	0.16
	N~1, λ~1, ω~Treatment, *p*~Treatment, ι~1	6	267.06	1.15	0.12
	N~1, λ~1, ω~Treatment, *p*~1, ι~1	6	267.62	1.71	0.09
	N~1, λ~1, ω~1, *p*~Treatment, ι~Treatment	6	267.63	1.72	0.09
	N~1, λ~1, ω~1, *p*~1, ι~Treatment	6	267.89	1.98	0.08
N. humilis	*N*~1, λ~1, ω~Treatment, *p*~1, ι~1	6	216.41	0.00	0.16
	N~1, λ~1, ω~1, *p*~1, ι~Treatment	6	216.42	0.01	0.16
	N~1, λ~Treatment, ω~1, *p*~1, ι~1	6	216.52	0.11	0.15
	N~1, λ~1, ω~1, *p*~1, ι~1	6	217.75	1.34	0.08
	N~1, λ~1, ω~Treatment, *p*~Treatment, ι~1	6	218.06	1.65	0.07
	N~1, λ~1, ω~1, *p*~Treatment, ι~1	6	218.24	1.83	0.06
	N~1, λ~1, ω~1, *p*~Treatment, ι~Treatment	6	218.24	1.83	0.06
	N~1, λ~Treatment, ω~1, *p*~Treatment, ι~1	6	218.28	1.87	0.06

Table 4. Candidate set of models describing variation in relative egg production by *Craugastor bransfordii* in plots around individual *Castilla elastica* (*Castilla*; N = 6) and *Dipteryx panamensis* (*Dipteryx*; N = 8) trees at La Selva Biological Station, Costa Rica, during August–November 2014. Three randomly selected *Castilla elastica* plots were supplemented with 63–65 kg of dried *C. elastica* litter between August and September; three were unmanipulated controls. See Methods for details.

Model	df	*ll*	AIC_c	ΔAIC_c	w_m
Month	4	-5.97	20.80	0.00	0.56
Null	3	-7.48	21.47	0.67	0.40
Month+Tree	6	-6.96	27.83	7.02	0.02
Tree treatment	5	-8.48	28.29	7.49	0.01
Month*Tree treatment	8	-5.79	31.01	10.21	0.00

Figure legends

Figure 1. A conceptual model describing seasonal patterns of terrestrial leaf litter (A), arthropods (B), and arthropod predators (vertebrates; C) beneath two trees differing in leaf-drop phenology in lowland tropical wet forests, *Dipteryx panamensis* and *Castilla elastica*, and for an experimental manipulation of leaf litter beneath *C. elastica* trees (*C. elastica* [+]). A null model describing the total, overall seasonal rhythm of the forest also is included (black line; Lieberman 1986). Vertical lines indicate leaf abscission events for *D. panamensis* in February-March (black dash), *C. elastica* during May-June (grey dash), and litter supplementation beneath *C. elastica* (grey dots).

Figure 2. Graphical representation of gridded plots used to georeference areas around study trees. Trees were located in the center of plots (grey star), and PVC tubes (black dots) were placed at regular intervals (3 m; grey line) to generate 21 distinct cells. The black square indicates a hypothetical randomly selected quadrat position to sample leaf-litter and arthropod abundance (not to scale); the black arrow indicates northing.

Figure 3. Before (A) and after (B) experimental supplementation of dried leaf litter to a plot around a *Castilla elastica* tree. Leaves were spread homogeneously and provided a biologically relevant manipulation of natural leaf-drop events by that tree species.

Figure 4. Temporal variation of leaf litter abundance (dry mass; g) in plots around individual *Castilla elastica* (*Castilla*; N = 6) and *Dipteryx panamensis* (*Dipteryx*; N = 8) trees at La Selva Biological Station, Costa Rica, during February–August 2014. *Castilla elastica* plots were randomly assigned into experimental [*Castilla* (+); N = 3] or control plots [*Castilla* (c); N = 3]

on 1 September 2014, and experimental plots were supplemented with 63–65 kg of dried *C. elastica* litter. *Castilla elastica* plots were monitored from September–November, while monitoring of *D. panamensis* plots was discontinued during that time. See Methods for details.

Figure 5. Abundance of terrestrial arthropods (Acari – mites, top left; Araneae – spiders, top right; Coleoptera – beetles, bottom left; Collembola – springtails, bottom right) in leaf-litter samples from plots around individual *Castilla elastica* (N = 6) and *Dipteryx panamensis* (N = 8) trees at La Selva Biological Station, Costa Rica. Samples were collected from leaf litter processed in Berlese funnels and counted using a dissecting microscope. *Castilla elastica* (*Castilla*) and *D. panamensis* (*Dipteryx*) were sampled from February–August 2014; in September 2014, *C. elastica* plots were assigned randomly into supplemented [*Castilla* (+)] or control plots [*Castilla* (c)], and supplemented receiving 63–65 kg of additional dried *C. elastica* litter. After supplementation, *C. elastica* plots were monitored from September–November, while sampling in *D. panamensis* was discontinued. See Methods for details.

Figure 6. Monthly structure of age-sex classes (juveniles, females, and males) of three terrestrial vertebrates (*Craugastor bransfordii, Oophaga pumilio, Norops humilis*) in replicate plots around individual *Castilla elastica* and *Dipteryx panamensis* trees at La Selva Biological Station, Costa Rica. Three *C. elastica* plots were supplemented with 63–65 kg of dried *C. elastica* dried leaf litter at the start of September [*Castilla* (+)]; the other three plots remained as unmanipulated controls [*Castilla* (c)]. Population structure was inferred using *N*-mixture abundance models for open populations (Hostetler and Chandler 2015).

Figure 7. Monthly population growth rate (λ) for age-sex classes of *Craugastor bransfordii*, *Oophaga pumilio*, and *Norops humilis* replicate plots around individual *Castilla elastica* and

Dipteryx panamensis trees at La Selva Biological Station, Costa Rica. Three *C. elastica* plots were supplemented with 63–65 kg of dried *C. elastica* dried leaf litter during 1–3 September 2014 [*Castilla* (+)]; the other three plots were used as unmanipulated controls [*Castilla* (c)].

Figure 8. Model-estimated population size and population growth rate (λ) for whole-species populations of *C. bransfordii*, *O. pumilio*, and *N. humilis* in plots around *C. elastica* trees that were supplemented with leaf litter at the start of September [*Castilla* (s+)] or not [*Castilla* (c)].

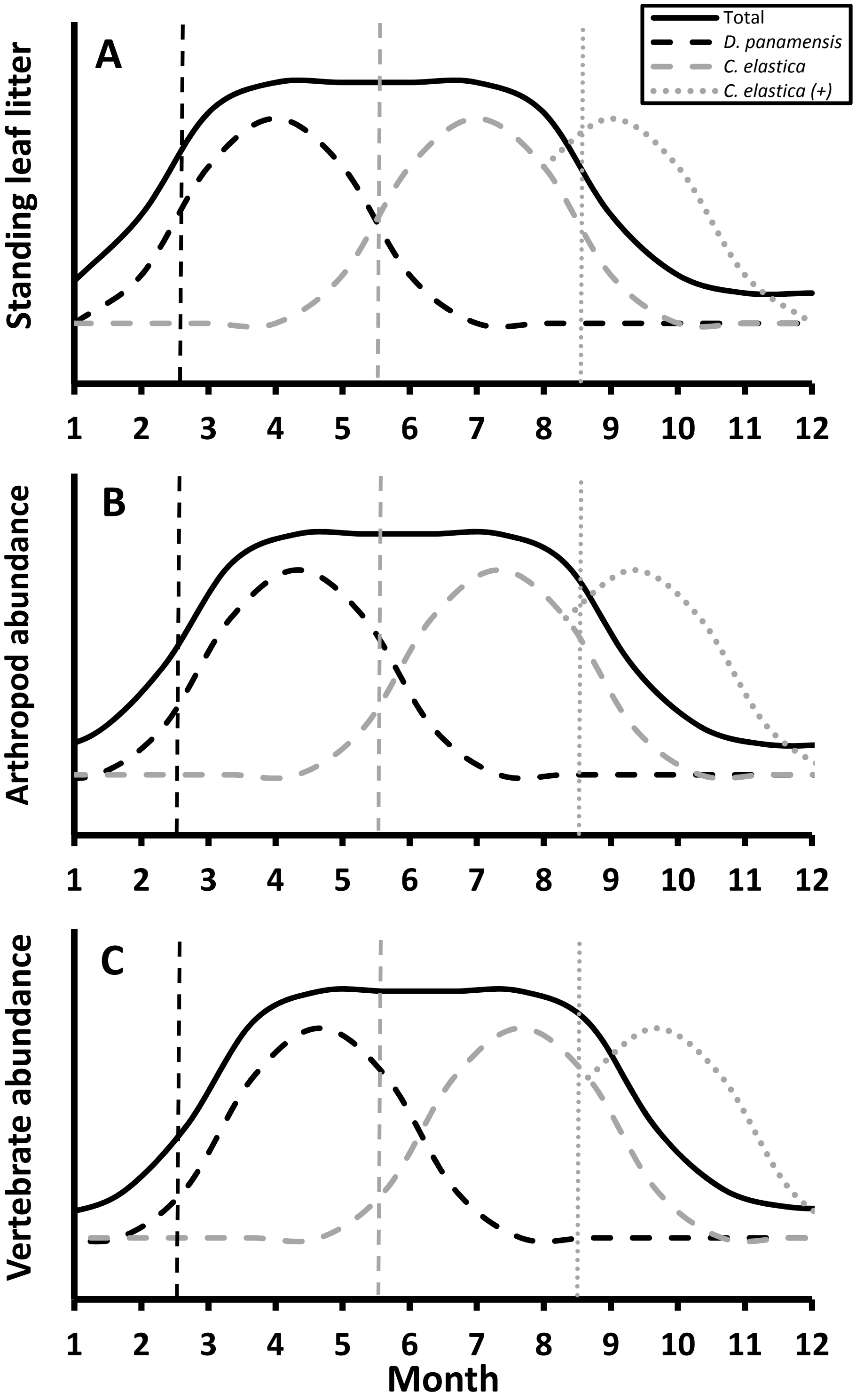

Total
D. panamensis
C. elastica
C. elastica (+)
A
Standing leaf litter
B
Arthropod abundance
C
Vertebrate abundance
1 2 3 4 5 6 7 8 9 10 11 12
Month

Figure 1

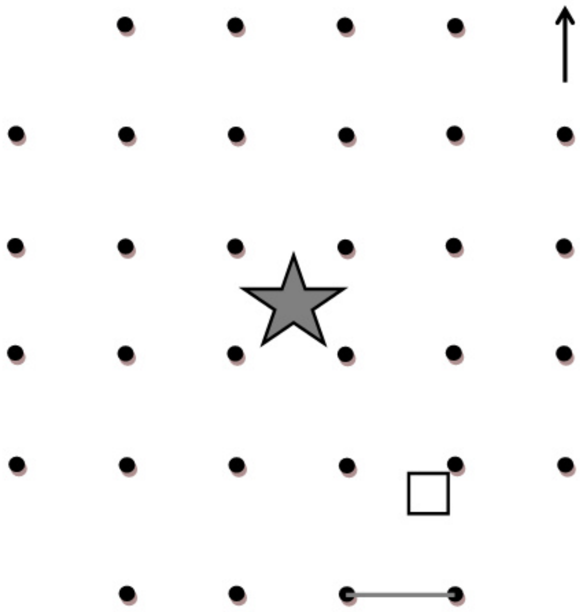


Figure 2

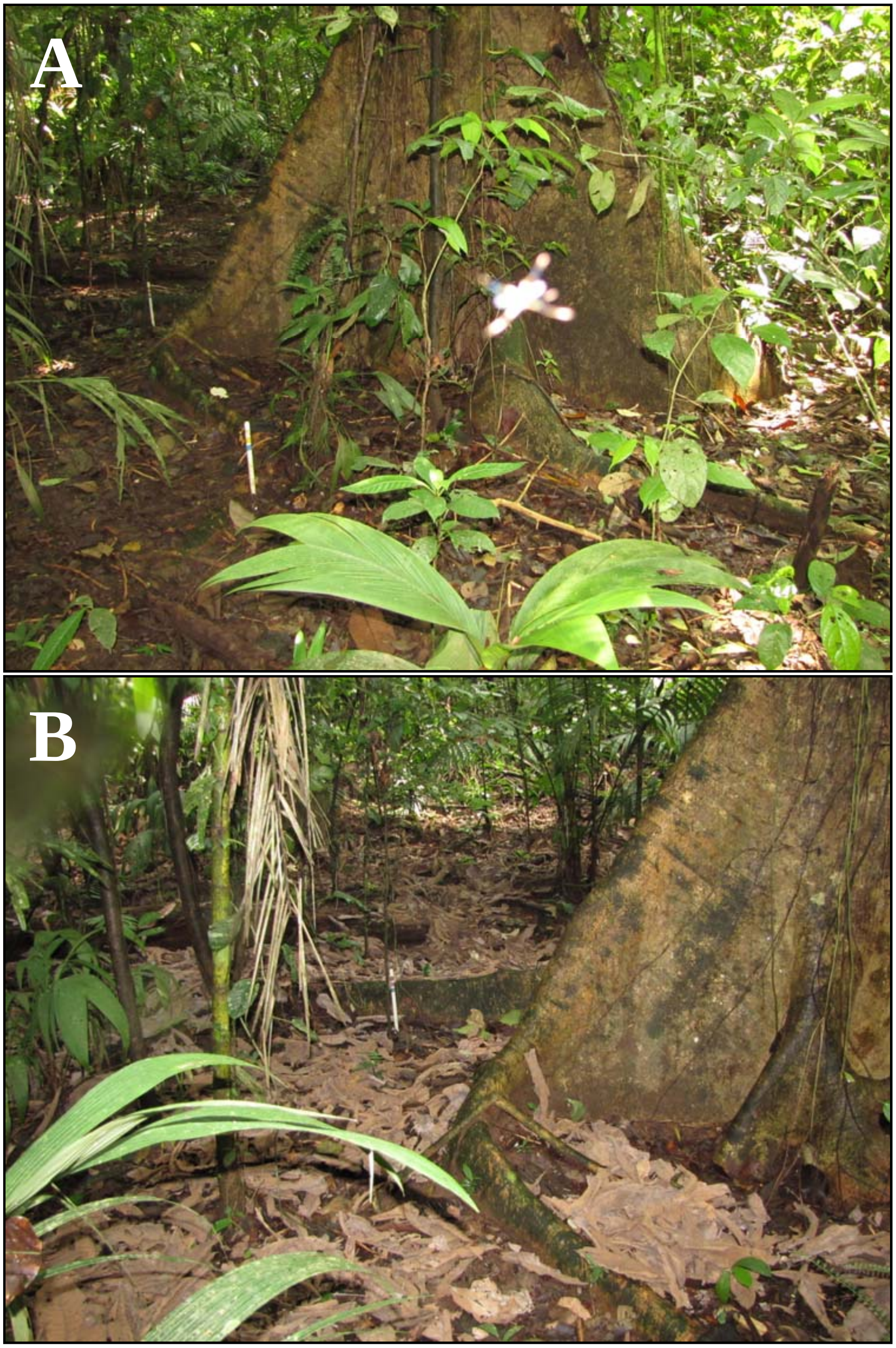
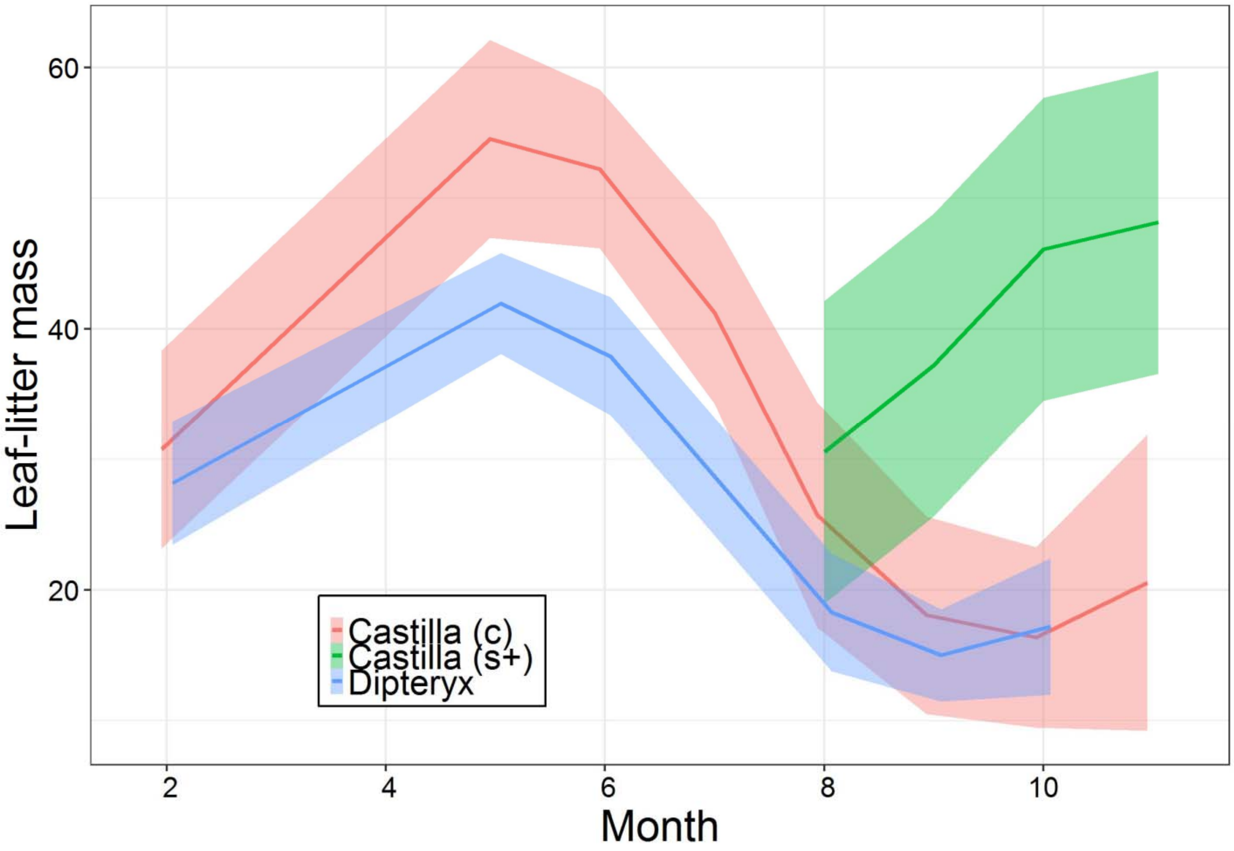


Figure 3



60
40
20
Leaf-litter mass
2
4
6
8
10
Month
Castilla (c)
Castilla (s+)
Dipteryx

Figure 4

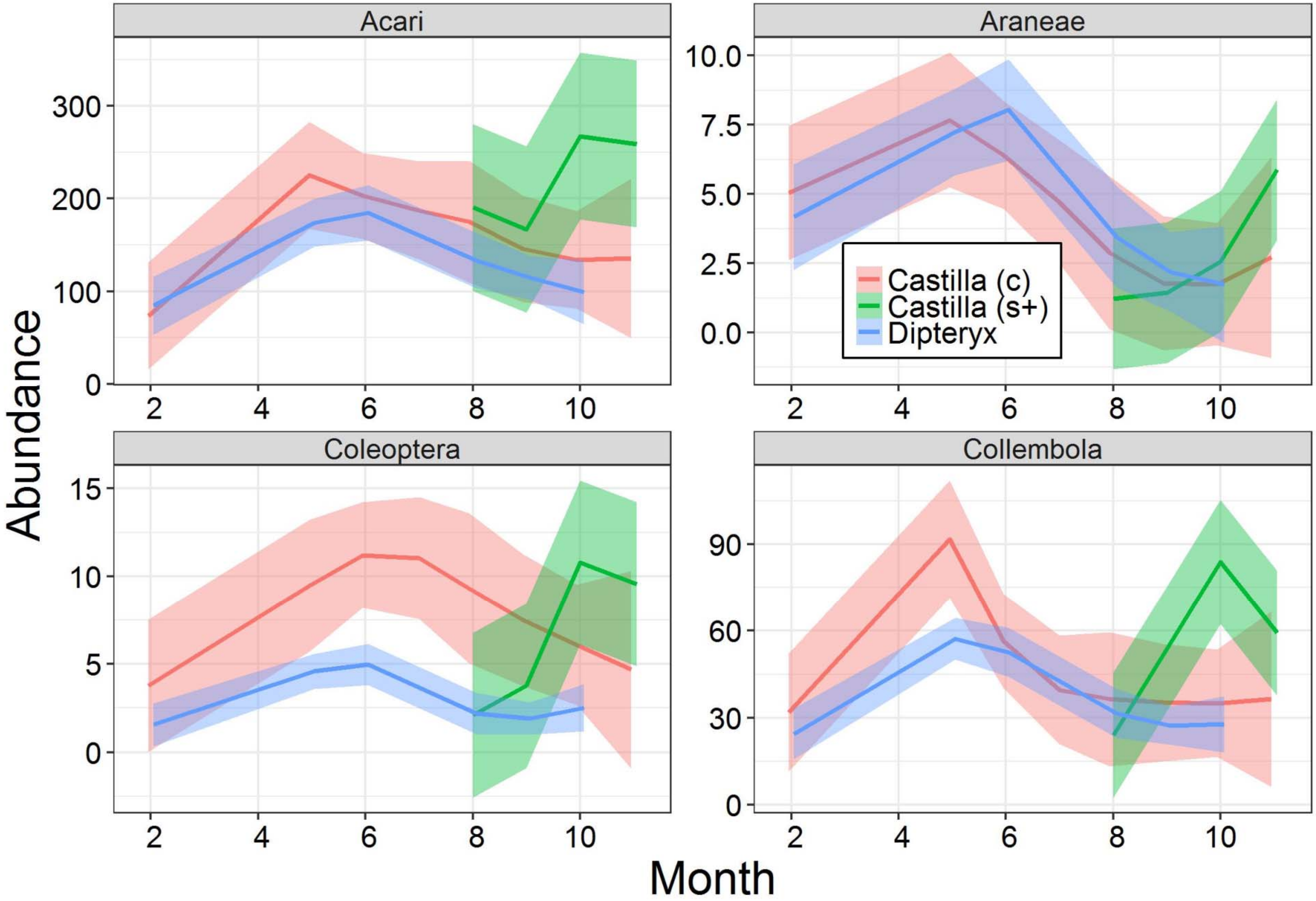
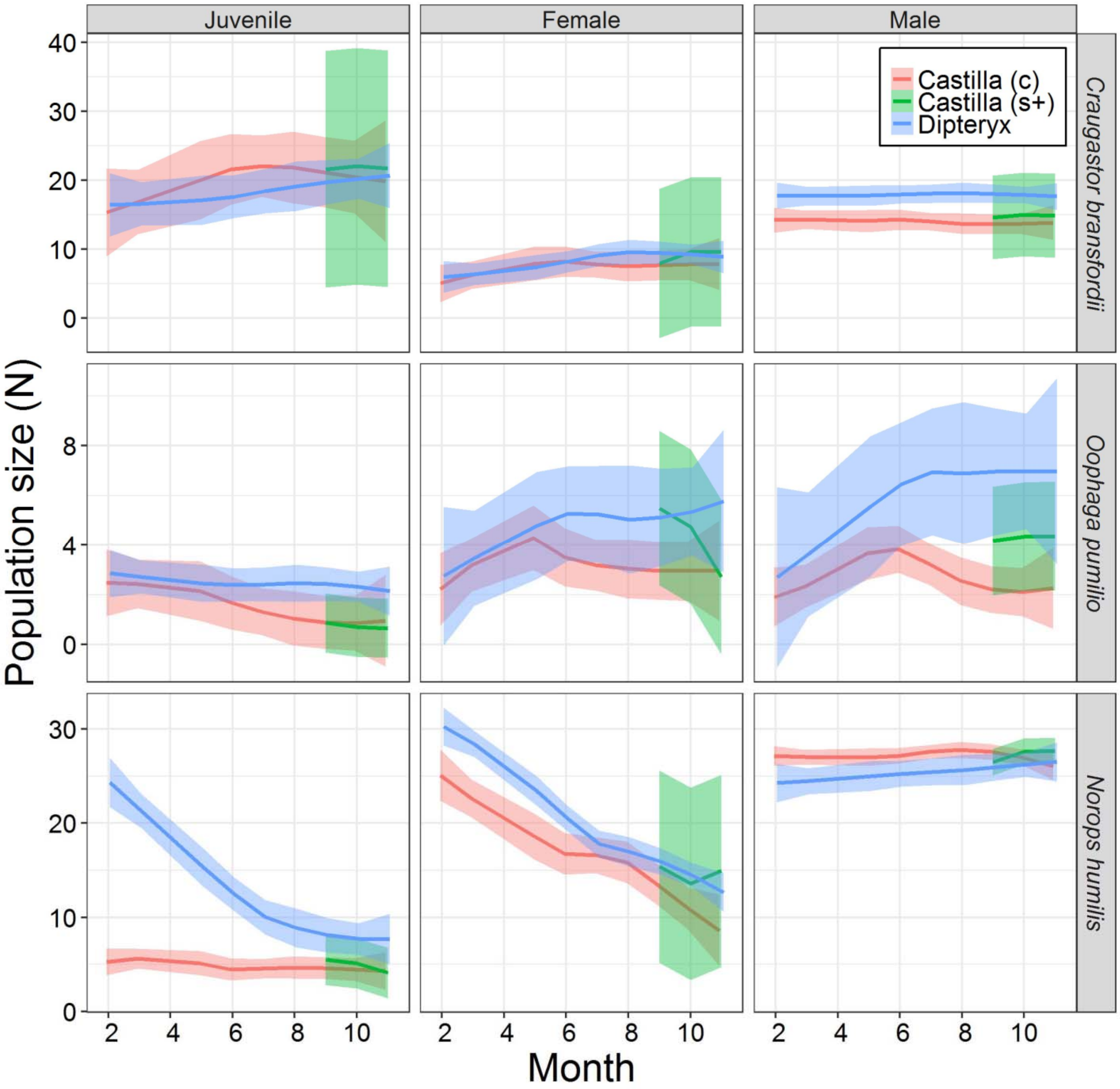

Acari
Araneae
Coleoptera
Collembola
Abundance
Month
300
200
100
0
10.0
7.5
5.0
2.5
0.0
15
10
5
0
90
60
30
0
2
4
6
8
10
Castilla (c)
Castilla (s+)
Dipteryx

Figure 5



Juvenile
Female
Male
Craugastor bransfordii
Oophaga pumilio
Norops humilis
Castilla (c)
Castilla (s+)
Dipteryx
Population size (N)
Month
40
30
20
10
0
8
4
0
30
20
10
0
2
4
6
8
10

Figure 6

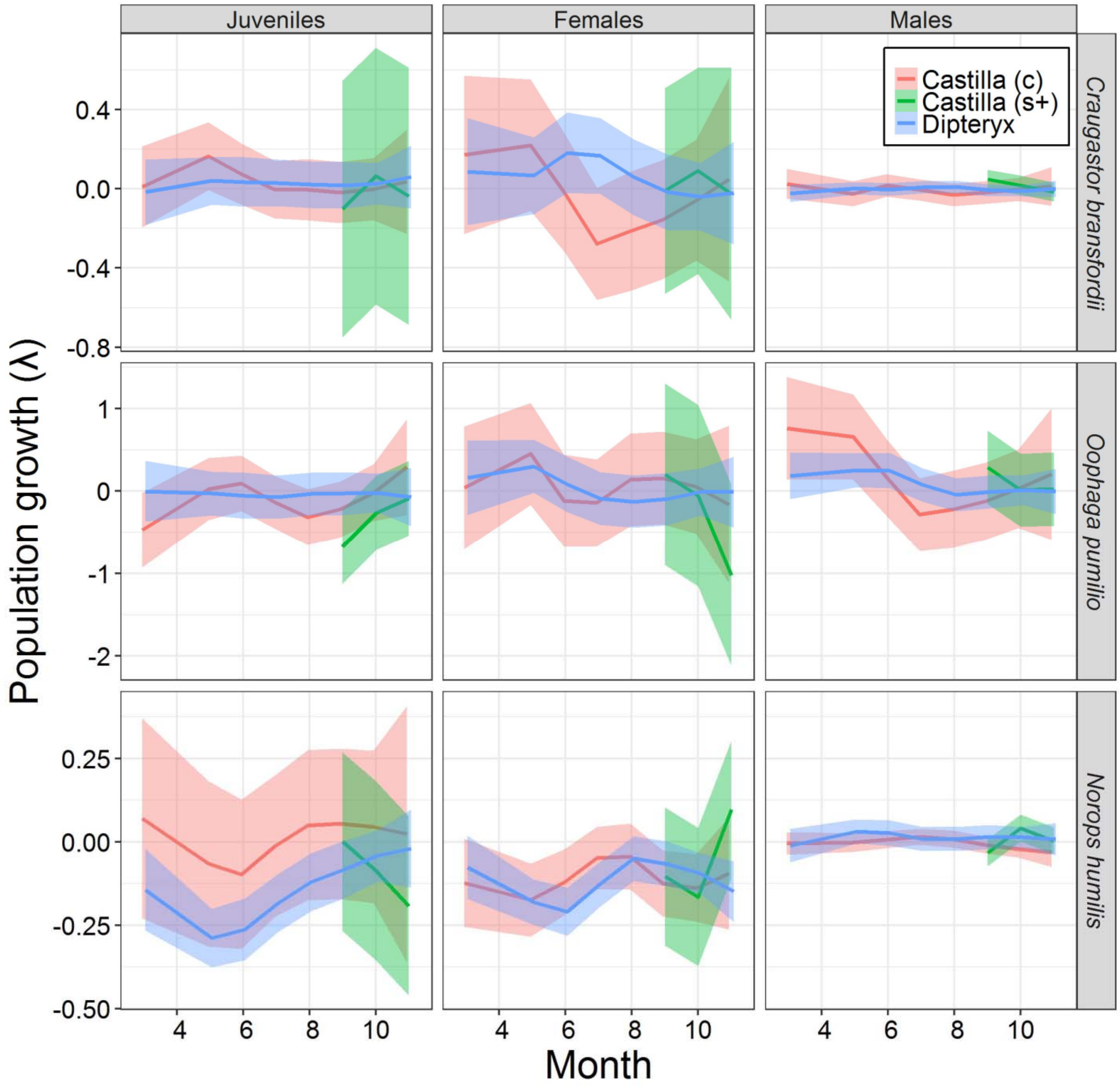

Juveniles
Females
Males
Craugastor bransfordii
Oophaga pumilio
Norops humilis
Castilla (c)
Castilla (s+)
Dipteryx
Population growth (λ)
Month
0.4
0.0
-0.4
-0.8
1
0
-1
-2
0.25
0.00
-0.25
-0.50
4
6
8
10

Figure 7

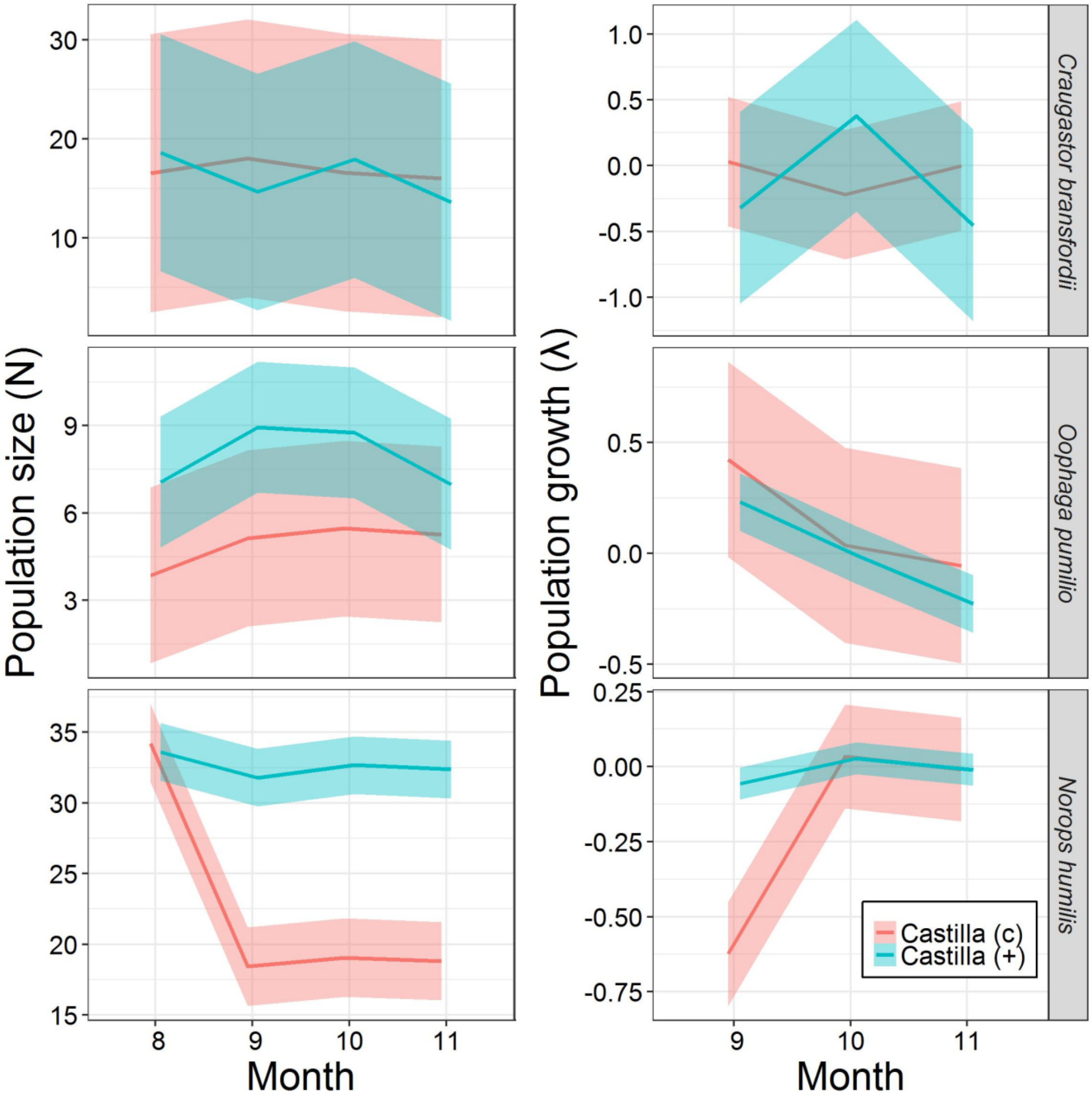

Population size (N)
Population growth (λ)
Craugastor bransfordii
Oophaga pumilio
Norops humilis
30
20
10
9
6
3
35
30
25
20
15
1.0
0.5
0.0
-0.5
-1.0
0.5
0.0
-0.5
0.25
0.00
-0.25
-0.50
-0.75
8
9
10
11
Month
9
10
11
Month
Castilla (c)
Castilla (+)

Figure 8

Appendix A. Museum accession numbers for arthropod specimens collected, examined, and deposited into the Auburn University Museum of Natural History after the study.

Phylum	Subphylum	Class	Order	Family	Museum numbers
Arthopoda	Chelicerata	Arachnida	Araneae		AUMS 17701–18730
Arthropoda	Chelicerata	Arachnida	Parasitiformes		AUMS 17948–17949
Arthopoda	Chelicerata	Arachnida	Opiliones		AUMS 17950–18075
Arthopoda	Chelicerata	Arachnida	Pseudoscorpiones		AUMS 18076–18215
Arthopoda	Chelicerata	Arachnida	Ricinulei		AUMS 18216–18221
Arthopoda	Chelicerata	Arachnida	Acariformes		AUMS 18222–18532
Arthopoda	Myriapoda	Chilopoda			AUMS 18533–18565
Arthopoda	Myriapoda	Diplopoda			AUMS 18566–18731
Arthopoda	Hexapoda	Entognatha	Collembola		AUMI 129401–129708
Arthopoda	Hexapoda	Insecta	Coleoptera		AUMI 129709–129945, 129965
Arthopoda	Hexapoda	Insecta	Dermaptera		AUMI 129946–129958
Arthopoda	Hexapoda	Insecta	Blattodea		AUMI 129967–130019
Arthopoda	Hexapoda	Insecta	Mantodea		AUMI 130020–130021
Arthopoda	Hexapoda	Insecta	Diptera		AUMI 130022–130264
Arthopoda	Hexapoda	Insecta	Hymenoptera	Formicidae	AUMI 130265–130550
Arthopoda	Hexapoda	Insecta	Lepidoptera		AUMI 130583, 130585, 130586
Arthopoda	Hexapoda	Insecta	Thysanoptera		AUMI 130587–130705
Arthopoda	Hexapoda	Insecta	Hemiptera		AUMI 130706–130799
Arthopoda	Hexapoda	Insecta	Orthoptera		AUMI 129964, 130800–130866
Arthropoda		Malacostraca	Isopoda		AUMI 41161–41362
Mollusca		Gastropoda			AUMI 41093–41155
Onycophora				Peripatidae	AUMI 41156–41160
Annelida		Clitellata	Hirudinea		AUMI 41373–41439

Appendix B. Complete candidate set of N-mixture abundance models for open populations built to examine how population structure and dynamics of *Craugastor bransfordii*, *Oophaga pumilio*, and *Norops humilis* varied in tree plots at La Selva, Costa Rica. Models which either did not converge or were not permitted by the specified population dynamic were omitted from the analysis, and are indicated in the Omitted column.

Model	Dynamics	Model structure	Omitted
1	Autoregressive	N~1, ω~1, p~Month	
2	Autoregressive	N~Tree, ω~1, p~Month	
3	Autoregressive	N~1, ω~Tree, p~Month	x
4	Autoregressive	N~1, ω~1, p~Month+Tree	
5	Autoregressive	N~Tree, ω~1, p~Month+Tree	
6	Autoregressive	N~1, ω~Tree, p~Month+Tree	x
7	Autoregressive	N~Tree, ω~Tree, p~Month	x
8	Autoregressive	N~Tree, ω~Tree, p~Tree	x
9	Autoregressive	N~Tree, ω~Tree, p~Month+Tree	x
10	Gompertz	N~1, λ~1, p~Month	
11	Gompertz	N~Tree, λ~1, p~Month	
12	Gompertz	N~1, λ~Tree, p~Month	
13	Gompertz	N~1, λ~1, p~Month+Tree	
14	Gompertz	N~Tree, λ~1, p~Month+Tree	
15	Gompertz	N~1, λ~Tree, p~Month+Tree	
16	Gompertz	N~Tree, λ~Tree, p~Month	
17	Gompertz	N~Tree, λ~Tree, p~Tree	
18	Gompertz	N~Tree, λ~Tree, p~Month+Tree	
19	No trend	N~1, ω~1, p~Month	
20	No trend	N~Tree, ω~1, p~Month	
21	No trend	N~1, ω~Tree, p~Month	x
22	No trend	N~1, ω~1, p~Month+Tree	
23	No trend	N~Tree, ω~1, p~Month+Tree	
24	No trend	N~1, ω~Tree, p~Month+Tree	x
25	No trend	N~Tree, ω~Tree, p~Month	x
26	No trend	N~Tree, ω~Tree, p~Tree	x
27	No trend	N~Tree, ω~Tree, p~Month+Tree	x
28	Ricker	N~1, λ~1, p~Month	
29	Ricker	N~Tree, λ~1, p~Month	
30	Ricker	N~1, λ~Tree, p~Month	
31	Ricker	N~1, λ~1, p~Month+Tree	

32	Ricker	N~Tree, λ~1, p~Month+Tree
33	Ricker	N~1, λ~Tree, p~Month+Tree
34	Ricker	N~Tree, λ~Tree, p~Month
35	Ricker	N~Tree, λ~Tree, p~Tree
36	Ricker	N~Tree, λ~Tree, p~Month+Tree
37	Trend	N~1, λ~1, p~Month
38	Trend	N~Tree, λ~1, p~Month
39	Trend	N~1, λ~Tree, p~Month
40	Trend	N~1, λ~1, p~Month+Tree
41	Trend	N~Tree, λ~1, p~Month+Tree
42	Trend	N~1, λ~Tree, p~Month+Tree
43	Trend	N~Tree, λ~Tree, p~Month
44	Trend	N~Tree, λ~Tree, p~Tree
45	Trend	N~Tree, λ~Tree, p~Month+Tree

Chapter 3

Effects of invertebrate predators on vertebrate prey are strong but reject the mainland-island model of anole population regulation

Abstract. A fundamental goal of ecology and evolution is to understand mechanisms which regulate life-history and population dynamics, and how such mechanisms generate evolutionary diversity. For the species-rich radiation of anole lizards, research has suggested a dichotomy between population regulation in Caribbean island and Central-South American ecosystems, where island populations are regulated by competition for resources and mainland populations are regulated by predation. A recent experimental manipulation of competition and predation for island populations supported the mainland-island model, but comparable tests are needed to reconcile the role of predation in regulating anoles and another diverse radiation, terrestrial frogs, in mainland ecosystems. Here, I used multi-species occupancy models to test the mainland-island model with a frog and anole assemblage in Costa Rica for which spiders (Ctenidae) are a major predator. I modeled the relative contribution of food, microhabitat, and predators toward frog (*Craugastor bransfordii*, *Oophaga pumilio*) and anole (*Norops humilis*) occupancy and detection to test the predictions that (1) occupancy is more strongly influenced by predators than resources (food, leaf-litter), and (2) detection decreases when predators are present. Frog occupancy was most strongly influenced by predators and secondarily by leaf litter; predator effects on frogs increased as litter decreased. Anole occupancy was influenced by leaf litter, but not by predators. Detection probability of each species was elevated when predators were present. Results described strong effects of predators on a prey vertebrate assemblage in a Central American forest, but patterns of anole occupancy and detection were inconsistent with predictions of the mainland-island model. My results are contrary to a large literature invoking predation as the dominant force shaping ecology and evolution of mainland anoles, and suggest that mainland and island systems might be regulated more similarly than previously acknowledged.

Key words: *co-occurrence patterns, Ctenidae,* Craugastor bransfordii*, La Selva,* Norops humilis*, occupancy analysis,* Oophaga pumilio*, population regulation, predator-prey dynamics, spiders, Neotropics.*

INTRODUCTION

A fundamental goal of ecology and evolution is to understand the mechanisms which regulate life history and population dynamics, and how such mechanisms contribute to the evolution of diversity. In the New World tropics, anoles (Dactyloidae) are a species-rich and ecologically diverse lineage of lizards that are widely distributed across Central America, South America, and the Caribbean. Because anole species have repeatedly evolved convergent morphologies that adaptively exploit novel environments, patterns of anole diversification are consistent with definitions of adaptive radiation (Losos et al. 1998, Losos 2009, Glor 2010), and anoles have, therefore, been a focus of many studies investigating patterns and processes of adaptive diversification (Losos 2009).

In his seminal review of anoles, Losos (2009) argued that interspecific interactions – chiefly, competition (Losos 1994) – have been a dominant force contributing to evolution of the ecologically diverse radiation of anoles. However, a limitation of the Losos (2009) thesis is that the literature focuses heavily on anoles from Caribbean island systems, despite the fact that greater anole species richness occurs in mainland habitats of Central and South America than in Caribbean island systems. The disparity between Caribbean and mainland anole research is problematic, because a large body of literature has suggested that different processes regulate population ecology of anoles in mainland and island ecosystems (Andrews 1979a, Irschick et al. 1997, Losos 2009), such that inferences drawn from island anoles may not apply to more species-rich mainland populations. Specifically, a long-standing hypothesis suggests that anole species occurring in island ecosystems are generally limited by competition for food resources, whereas species in mainland habitats are limited by predation (Andrews 1979a). The Andrews (1979a) hypothesis was derived from observations that, relative to anole populations on Caribbean islands, mainland anoles are characterized by lower abundance, survival, and foraging time for food resources that are more abundant, exhibit increased prey size, and have increased growth rates. These life-history differences were thought to reflect differing ways that mainland and island populations are regulated, with elevated adult predation pressure for mainland populations generating *r*-selected demographic patterns (Andrews 1979a). By implicating predation as the most significant mechanism driving population ecology of the more species-rich mainland anoles, the mainland-island model for anole population regulation (hereafter, the mainland-island model; Andrews 1979a) is at odds with the paradigm that anole evolution is primarily driven by interspecific competition (Losos 2009).

Despite being proposed over three decades ago, empirical tests of the mainland-island model are rare. The best support to date comes from an experimental manipulation of population and predator density in whole-island populations of the anole *Norops sagrei* in the Caribbean (Calsbeek and Cox 2010). That study found competition to be the greatest source of natural selection for anoles; predators did not drive selection, but rather induced behavioral shifts in habitat use. While these results were consistent with mainland-island model predictions for island anoles, a comparable evaluation for mainland anoles is needed to better reconcile the roles of predation and competition for mainland anoles (Losos 2009, Calsbeek and Cox 2010).

In many diverse mainland forest ecosystems, anoles are part of a larger assemblage of small terrestrial vertebrates, which also includes the ecologically similar radiation of terrestrial brachycephaloid frogs (Padial et al. 2014). This assemblage occurs terrestrially on the forest floor, where these species use abundant arthropods as food resources (Toft 1980, Lieberman 1986, Whitfield and Donnelly 2006), take refuge from predators (Talbot 1979, Cooper et al. 2008a,b), select habitat to limit desiccation across life stages (Seebacher and Alford 2002, Schlaepfer 2003, Socci et al. 2005), and are eaten by similar predators (Greene 1988). Several studies have documented a positive relationship between standing leaf litter and abundance of terrestrial frogs and anoles in mainland ecosystems (Scott 1976, Lieberman 1986, Guyer 1988, Fauth et al. 1989, Heinen 1992, Whitfield et al. 2007), and Whitfield et al. (2014) provided the first experimental demonstration of standing leaf litter as a density-limiting factor, although the effect of litter varied among vertebrate species examined. Thus, a common thread among studies has identified leaf litter as a fundamental resource regulating abundance of the vertebrate assemblage, and several studies support the idea that litter regulates the frog and lizard assemblage in ways consistent with bottom-up regulation of populations (*sensu* Hunter and Price 1992).

Because of ecological similarities between anoles and terrestrial frogs in mainland ecosystems and the mainland-island model was generated in part using observations of non-anole species (Andrews 1979b), the mainland-island model can reasonably be extended to include predation as an important mechanism regulating the entire assemblage of mainland frogs and anoles. However, relative to studies of resource limitation (e.g., Whitfield et al. 2014 and citations therein), much less consideration has been given to the role of predation on mainland frogs and lizard populations. The lack of information on top-down effects is surprising because (1) mainland anoles and frogs are consumed by a diverse assemblage of predators (Greene 1988) conservatively estimated to be twice as that of a comparable island system (Losos 2009), and (2) the mainland-island model has suggested an important role of predation in driving life-history evolution of mainland anoles for over 30 y (Andrews 1979a).

At La Selva Biological Station, Costa Rica, observations suggest that, despite the diverse suite of vertebrate predators (Greene 1988), the most abundant predator of leaf-litter frogs and anoles may be invertebrates. In particular, large spiders of the family Ctenidae – commonly referred to as 'wandering' spiders, because of low site fidelity and they do not use webs for prey capture – are particularly common generalist predators occupying terrestrial environments in lowland Neotropical wet forests of Costa Rica. Ctenids attack and consume terrestrial and arboreal frogs in the families Centrolenidae, Craugastoridae, and Hylidae, but frequently reject the poisonous frog *Oophaga pumilio* (Hayes 1983, Szelistowki 1985, Donnelly and Guyer 1994, Lapinski and Tschapka 2013, Murray et al. 2016). Ctenids also are capable of consuming small reptiles, being the most commonly observed source of predation during detailed studies of the anole *Norops humilis* (Guyer 1988) and metamorphic hylid frogs emerging from an ephemeral swamp system (Donnelly and Guyer 1994). The latter study observed a strong pulse in metamorphosis of frogs, and hypothesized that this synchronous emergence may have evolved as a mechanism to satiate terrestrial spider predators (Donnelly and Guyer 1994, Guyer and Donnelly 2005). Recent studies from South America have also found that ctenids are opportunistic predators of small vertebrates (e.g., Menin et al. 2005). While the accumulating literature suggests that spiders play a general but important role as vertebrate predators across Neotropical wet forests (Hayes 1983, Guyer 1988, Donnelly and Guyer 1994, Menin et al. 2005), no study has examined the extent to which ctenid spiders influence terrestrial lizards or frogs in a predator-prey context (e.g., anoles; Losos 2009).

Classic analyses of interactions between species have frequently estimated abundance of focal species at sites and analyzed co-occurrence patterns to infer interspecific interactions. However, when species are detected imperfectly (detection probability < 1.0), analyses of co-occurrence patterns can be misleading and result in erroneous inferences (MacKenzie et al. 2006). Issues of low detection are particularly problematic for studies of mainland anoles, where population densities are low and individuals may be secretive because of a wariness of predators (Andrews 1979a, Losos 2009). To this end, recent advances in quantitative ecology has developed sampling and statistical methods that account for imperfect detection of individuals while estimating species occupancy or abundance at sites (occupancy modeling, and derivations; MacKenzie et al. 2006). In particular, such occupancy models have been expanded to include parameterizations that investigate relationships among co-occurring and potentially interacting species (MacKenzie et al. 2004); these multi-species occupancy models are flexible and can include covariates, to evaluate support for competing hypotheses, such as resources, in addition to interspecific interactions (Richmond et al. 2010). Most applications of multi-species occupancy models have investigated co-occurrence patterns between competing species (e.g., MacKenzie et al. 2004, Richmond et al. 2010, Steen et al. 2012), but the models also can examine hypothesized interactions between predators and prey (MacKenzie et al. 2006, Lazenby and Dickman 2013).

In this study, I used multi-species occupancy models to test for predator and resource effects on terrestrial anoles and frogs in a mainland Neotropical forest. I quantified patterns of site occupancy and detection for three small terrestrial vertebrates (one anole, two frogs) at La Selva, Costa Rica, and evaluated the degree to which vertebrate occupancy and detection was conditionally influenced by predatory spiders in the genus *Ctenus* (hereafter, ctenid spiders). Because predation has been hypothesized to exert a stronger effect on mainland anoles than does food resources (Andrews 1979a), I modeled the relative contribution of predators, food, and microhabitat resources toward frog and anole occupancy to (1) provide an empirical test of the mainland-island model, and (2) evaluate relative support for top-down and bottom-up forces in regulating component species in this vertebrate assemblage.

METHODS

Study site and taxa

La Selva Biological Station (hereafter, La Selva) is a private reserve owned by the Organization for Tropical Studies (OTS) in the Caribbean lowlands of northeastern Costa Rica (10.42˚N, 84.02˚W). The site is characterized by an average temperature of 25.8˚C, receives ca. 4 m of precipitation/yr, and is classified as a Tropical Wet Forest in the Holdridge life zone system (McDade and Hartshorn 1994).

I studied three common terrestrial vertebrates and ctenid spiders from La Selva as the focal taxa (Figure 1). *Craugastor bransfordii* is an abundant frog (Craugastoridae) in Caribbean forests of Nicaragua, Costa Rica, and Panama. Coloration of *C. bransfordii* is highly variable;

variation has been categorized into four distinct morphs defined by color and dorsal ridging patterns, three of which occur at La Selva (Savage and Emerson 1970). Cryptic coloration and immobility are thought to decrease predation while in the terrestrial leaf-litter environment (Savage and Emerson 1970, e.g., Cooper et al. 2008a). *Oophaga pumilio* is a poison frog (Dendrobatidae) that also occupies terrestrial habitats in Caribbean forests from Nicaragua to Panama (Savage 2002). The species is a dietary specialist, consuming ants and mites (Donnelly 1991); this diet provides alkaloid compounds that are sequestered into poison glands in the frog's skin that confers an antipredatory defense (Saporito et al. 2004, 2007a, Stynoski et al. 2014b). Across its geographic distribution, *O. pumilio* is brightly colored, which serves as an aposematic signal to reduce predation (Saporito et al. 2007b). *Norops humilis* is a terrestrial anole (Dactyloidae) that occurs primarily in Caribbean lowland and premontane forests from Honduras to Panama (Phillips et al. 2015). The species is a generalist predator that forages for arthropods within the leaf litter.

Ctenid spiders are common generalist predators occupying terrestrial environments in lowland Caribbean forests of Costa Rica. Three species in the genus *Ctenus* are conspicuous residents at La Selva (*Ctenus curvipes, Ctenus sinuatipes*, and an undescribed species) which consume small vertebrates (Szelistowski 1985, Guyer 1988, Lapinski and Tschapka 2013). In primary forest habitats like La Selva, these ctenid species are visual ambush predators that emerge from hidden sites in soil and leaf litter (Lapinski and Tschapka 2013) to attack frogs and lizards (C. Guyer, pers. comm., Figure 1). Identification of *Ctenus* species is difficult in the field because the species are morphologically similar and also exhibit high intraspecific variation. Thus, I recorded ctenid presence non-invasively and considered all ctenids as a single group in my analyses.

Because the focal vertebrates is relatively mobile compared to ctenids (B.F., pers. obs.), prey species should respond to predation threat through shifts in space or habitat use (i.e., the prey response dominates; Sih 1984). Therefore, if spider predation exerts a selective pressure on frogs and lizards, I predicted that, relative to sites where spiders were absent, the presence of spiders would decrease patterns of occupancy and detection of prey (Andrews 1979a, Losos 2009). However, because *O. pumilio* is chemically defended and ctenids have rejected *O. pumilio* during feeding trials (Szelistowki 1985, Murray et al. 2016), I also predicted that *O. pumilio* would occupy sites independent of spiders as a result of a lack of perceived predation threat.

Data collection

I established replicate gridded plots around individual canopy trees (N = 14) in primary forest habitat; plot grids consisted of 21 cells that were each 3 m x 3 m in area (189 m^2 total) and were marked using PVC tubing. I used plots of this area because comparable-sized plots had been successfully implemented in other studies of amphibian and reptile population ecology at La Selva (Guyer 1988, Donnelly 1989a,b, Whitfield et al. 2014).

Plot cells were sampled for frogs, lizards, and spiders in February, May, June, August, September, October, and November of 2014. I surveyed animals in each cell using diurnal visual-encounter searches of the forest floor and other substrates up to 2 m above ground. I walked methodically through plots to search all cells, and carefully prodded through the litter and other structures with a 1.2-m pole. Leaf-litter microhabitats were disturbed minimally during sampling. Plots were surveyed repeatedly (N = 3) each month. I conducted the first survey on a randomly selected day, and repeated surveys on the two consecutive days.

I quantified abundance of leaf litter and terrestrial arthropods in four plot cells monthly. For litter and arthropod samples, I used a 0.30 m x 0.30 m PVC-frame to delimit samples of litter, cut the perimeter of the litter with a utility blade, and collected the sample into one or more large sealable plastic bag. I brought the samples into the laboratory and dried them in Berlese funnels beneath heated incandescent bulbs; during the drying process, arthropods were driven downward from within the drying litter and collected in vials containing 95% ethanol. I then measured dried leaf-litter mass (g), and used a microscope to sort arthropods into taxonomic groups that are important in the diets of the study species (Whitfield and Donnelly 2006; Appendix A). I then used the frog, lizard, and spider survey data from the four cells/plot with resources covariates to model predator-prey occupancy.

Statistical analysis

I modeled how the spatial and behavioral ecology of frogs and lizards is influenced by predatory spiders and resources (leaf litter, arthropod food resources) using the Ψ^{Ba} parameterization of the multi-species, single-season occupancy model (MacKenzie et al. 2004, Richmond et al. 2010). The Ψ^{Ba} parameterization estimates the probability of occupancy of a dominant species (A) and a subordinate species (B,), and I assumed that spiders were dominant and frogs and lizards were subordinate. Using these models, I estimated the probability of occupancy of the dominant predatory organisms (Ψ^{A}) and the occupancy of each subordinate taxon when dominant predators were present (Ψ^{BA}) and absent (Ψ^{Ba}).

I evaluated co-occurrence patterns between ctenids and each focal vertebrate species separately. Preliminary analyses indicated that spiders and vertebrates consistently differed in patterns of occupancy and detection for each of the three predator-prey pairs (ctenids + *C. bransfordii*, ctenids + *O. pumilio*, ctenids + *N. humilis*). Thus, I used a model-building process that began with creating an initial model describing variance in occupancy and detection differing between dominant and subordinate species, and then built six models that included all combinations of Ψ parameters (Table 1) describing hypotheses of how predatory spiders influence occupancy and/or detection of potential prey vertebrates (Table 2). Using this model-building process, I evaluated whether occupancy of the subordinate species was affected by presence of the dominant species ($\Psi^{BA} \neq \Psi^{Ba}$) and whether detection probability of the subordinate species was influenced by detection (r^{BA}) and/or occupancy (r^{Ba}) of the dominant species (Table 2). My model-building process generated a balanced set of six models with even representation of predator effects ($\Psi^{BA} \neq \Psi^{Ba}$, r^{BA}, r^{Ba}) either present or absent in models.

To test Andrews' (1979a) prediction that anoles and frogs are more strongly influenced by predators than food resources, I built 36 additional models to evaluate how vertebrate occupancy and detection are explained by predators and resources. I expanded the initial six models (Table 2) to include covariate effects (litter mass, arthropod abundance) on occupancy, detection, and both occupancy and detection, in the presence and absence of predator effects. The second model-building process generated 42 total models with different combinations of predator, food resources, and null models in a completely balanced design (Appendix B). I modeled the arthropod covariate differently for each species depending on its diet (Lieberman 1986, Whitfield and Donnelly 2006): the sum of Acari, Araneae, Coleoptera, and Isopoda abundance for *C. bransfordii*, Acari and Formicidae for *O. pumilio*, and Araneae and Isopoda abundance for *N. humilis*. I transformed all covariates by log(x+1) to improve model convergence.

I evaluated how well each model fit the data using Akaike's Information Criterion corrected for small sample size (AIC_c; Hurvich and Tsai 1989) and calculated the probability a given model within a set is the best approximating model (model weight; w_m). I then used model weights to calculate model-averaged coefficients (± unconditional SE) and model-averaged parameter weights (w_p) across all models with $w_m > 0.025$. I considered parameters as explaining significant variation when they occurred in a model in the top model set ($\Delta AIC_c < 2.00$), unconditional SE estimates did not overlap, and $w_p > 0.70$ (Burnham and Anderson 2010).

When the analyses indicated significant predator-prey interactions in the top-model set by supporting the Ψ^{Ba} parameter in the top model, I calculated a species interaction factor (SIF). The SIF describes if the predator-prey pairs co-occur more frequently (SIF > 1) or less frequently (SIF < 1) than expected if species did not interact and occupancy probabilities were independent of each other (SIF ~ 1). I calculated the SIF using model-averaged parameter estimates and by following the SIF equation described by Richmond et al. (2010):

$$\mathrm{SIF} = \frac{\Psi^{\mathrm{A}} * \Psi^{\mathrm{BA}}}{\Psi^{\mathrm{A}}\left(\Psi^{\mathrm{A}} * \Psi^{\mathrm{BA}} + \left(1 - \Psi^{\mathrm{A}}\right) * \Psi^{\mathrm{Ba}}\right)}$$

I performed all analyses in the statistical Program R (R; R Core Team 2016). I built co-occurrence models using the function *occmod()* in the package 'RPresence' (MacKenzie and Hines 2016).

RESULTS

During February–November 2014, I made 988 detections of *C. bransfordii*, 329 detections of *O. pumilio*, 115 detections of *N. humilis*, and 270 detections of ctenid spiders during 2616 repeated surveys of 872 sites. Top-model sets of co-occurrence models for each predator-prey pair contained parameters describing interactions between predators and prey (Ψ^{Ba}, r^{BA}, r^{Ba}) and effects of leaf litter on occupancy and detection (Ψ^{LL}, p^{LL}; Table 3).

The top model for both frog species included the terms Ψ^{Ba}, Ψ^{LL}, r^{BA}, and r^{Ba} (Table 3), a model which indicated effects of predators (Ψ^{Ba}) and leaf litter (Ψ^{LL}) on frog occupancy and a predator effect on frog detection (r^{BA}). For *C. bransfordii*, the top model ($w_m = 0.41$) was over one and a half times more likely than other models. For *O. pumilio*, the top model ($w_m = 0.35$) was rivaled by an equivocally supported model, which included r^{Ba} ($w_m = 0.33$). The top model for *N. humilis* included the terms Ψ^{LL}, r^{BA}, r^{Ba}, and r^{LL} ($w_m = 0.28$), although a similar model without r^{LL} was also strongly supported ($w_m = 0.23$). Both those models were ~2 times more strongly supported than two similar models in the top-model set that included an additional term Ψ^{Ba} (Table 3).

Model averaging of parameters strongly supported three parameters for both frogs: Ψ^{Ba} (*C. bransfordii*, $w_p = 0.99$; *O. pumilio*, $w_p = 0.99$), Ψ^{LL} (*C. bransfordii*, $w_p = 0.98$; *O. pumilio*, $w_p = 0.97$), and r^{BA} (*C. bransfordii*, $w_p = 0.99$; *O. pumilio*, $w_p = 0.99$; Table 4, 5). While the parameter r^{Ba} was included in top-model sets for both species, it received low support by model averaging ($w_p < 0.70$) for both frog species. Model averaging supported three parameters for *N. humilis*: Ψ^{LL} ($w_p = 0.89$), r^{BA} ($w_p = 0.87$), and r^{Ba} ($w_p = 0.79$; Tables 4, 5). The parameters Ψ^{Ba} and r^{LL} were included in the top-model set, but they were not supported by model averaging ($w_p = 0.31, 0.60$, respectively).

Model-averaged coefficients described frog occupancy as increasing with leaf-litter mass and, relative to when spiders were present, frog occupancy was elevated when spiders were absent (Figure 2). Occupancy was more strongly predicted by the absence of predators (Ψ^{Ba}) than the abundance of leaf litter (Ψ^{LL}) or arthropods ($\Psi^{Arthropods}$) for both *C. bransfordii* and *O. pumilio* (Table 4). These patterns generated SIFs for frogs that described predator avoidance at sites with low leaf litter; however, at sites with increased leaf litter, co-occurrence patterns were independent between frogs and spiders (Figure 3). For *N. humilis*¸ Ψ^{LL} was the strongest predictor of lizard occupancy among parameters supported by model averaging; Ψ^{LL} had a weaker effect size (1.23 ± 0.53 SE) than Ψ^{Ba} (–2.64 ± 1.51 SE), but the latter parameter was not supported by model averaging ($w_p = 0.31$). Model-averaged coefficients described lizard occupancy as increasing with leaf-litter mass and, relative to when spiders were absent, lizard occupancy was elevated when spiders were present (Figure 2). This pattern suggests aggregated co-occupancy between *N. humilis* and spiders, but I did not calculate a SIF for *N. humilis* because Ψ^{Ba} received little support by model averaging.

Detection probability of spiders (p^A = 0.10–0.12) was lower than detection of *C. bransfordii* ($p^B = 0.29$) and *O. pumilio* ($p^B = 0.25$), but detection probability of both species increased at sites where spiders were occupants and were detected (r^{BA} = 0.45, 0.40, respectively; Figure 4). Detection probability was higher for spiders ($p^A = 0.09$) than *N. humilis* ($p^B = 0.06$); when spiders were present in plots, lizard detection was elevated when spiders were detected ($r^{BA} = 0.08$) and decreased when spiders were present but not detected ($r^{Ba} = 0.04$; Figure 4). Arthropod abundance received zero support as an effect on frog and lizard occupancy and detection (Table 4, 5).

DISCUSSION

Andrews (1979a) synthesized literature on anole population biology from comparable habitats in Central America and Caribbean islands, and argued that mainland anoles are generally limited by predators, whereas Caribbean anoles are limited by food resources. In my study, site occupancy of the anole *N. humilis* was not influenced by predators, but occupancy of both *C. bransfordii* and *O. pumilio* was more strongly predicted by the presence of predators than other resources. Specifically, both frogs exhibited decreased occupancy when spiders were present, suggesting that frogs selected habitat to reduce co-occurrence with spider predators. Occupancy of all three focal vertebrates was also strongly influenced by leaf-litter abundance at sites, and I observed an effect in which predator avoidance by frogs decreased as litter abundance increased. Variance in frog and lizard detection probability was also consistent with predator avoidance. Relative to when spiders were absent, detection of *C. bransfordii*, *O. pumilio*, and *N. humilis* was elevated when spiders were present and detected within plots, suggesting that frogs and lizards exhibit more vigilant behavior when spider predators were present and conspicuous in plots. These results were consistent with the hypothesis that spider predators exert strong effects on prey vertebrate occupancy and detection in Central American forests, but not in ways predicted by the mainland-island model for anole population regulation (below).

Using *N. humilis* as a model anole and by extending the mainland-island model to include ecologically similar terrestrial frogs, I tested two predictions of the mainland-island model: (1) occupancy of mainland is more strongly influenced by predators than food resources, and (2) mainland species are less detectable in the presence of predators, because of wariness of predators (Andrews 1979a, Losos et al. 1991, Losos 2009). However, an experimental supplementation of food for *N. humilis* demonstrated food limitation of mainland anoles (Guyer 1988) and provided an alternative hypothesis predicting occupancy and detection of mainland species to be positively influenced by food resources. Interestingly, my results for *N. humilis* supported neither of these hypotheses. While occupancy of both frog species was consistent with the mainland-island model, anole occupancy was more strongly predicted by the leaf-litter resource itself than by predators or food resources within litter; the lack of predator and food effects on anole occupancy is inconsistent with predictions of both the mainland-island model (Andrews 1979a) and the food limitation hypothesis (Guyer 1988). Rather, an observed effect of leaf litter on anole occupancy was most consistent with a model of limitation by litter (Whitfield et al. 2014). Instead, my results suggested a pattern of detection probability where anoles and frogs were more detectable in the presence of spiders but were not influenced by food. While predator-induced shifts in anole habitat use are well for island anoles (e.g., Schoener et al. 2002, Losos et al. 2004, Calsbeek and Cox 2010), predator-driven increases in detection are inconsistent with the mainland-island model, which predicted anoles to be less detectable in the presence of predators. Models did not describe increases of detection associated with food resources in ways anticipated by food limitation (Guyer 1988). Thus, in my study, predators and food resources did not influence patterns of occupancy and detection of frogs and anoles in ways anticipated either by the mainland-island model (Andrews 1979a) or the food-limitation hypothesis (Guyer 1988).

Losos (2009) speculated that the mainland-island model has not been falsified because work on anole population biology has declined in recent decades. However, other experiments and studies during this time have, in fact, generated observations inconsistent with the Andrews (1979a) hypothesis. If mainland anoles are limited by predators and island anoles are limited by food, then the Andrews (1979a) hypothesis predicts that (1) mainland populations experiencing demographic increases from elevated food resources should be negated by losses from dominant predation, and (2) island anoles experiencing demographic decreases from elevated predation should be matched by density-dependent demographic gains from increased resource availability. However, experimental food supplementation of *N. humilis* populations resulted in doubled population size relative to controls (Guyer 1988), and populations of the island anole *N. sagrei* exposed to experimental introduction of predators resulted in a halving of population size relative to controls (Schoener et al. 2002). These results demonstrate food can limit mainland anoles and predators can limit island anoles, respectively – observations that are inconsistent with the mainland-island model. Andrews (1979a) interpreted decreased apparent survival of mainland anoles as a consequence of higher predation rates by more species-rich mainland predator assemblages, including sites such as La Selva (Greene 1988) where predator richness can be >2 times that of comparable islands (Losos 2009). However, a few lines of logic question that assumption: (1) predator richness did relate to survival or predation intensity of a mainland anole (Wright et al. 1984), (2) no studies have empirically compared predation rates between mainland and island anoles, and (3) the primary citation used support strong mainland predation pressure on anoles by Andrews (1979a) is a single focal observation of a non-anole lizard, *Corytophanes cristatus*, that was not depredated (Andrews 1979b). Last, studies of *Norops apletophallus* (formerly, *Norops limifrons*) in Costa Rica were foundational in generating the mainland-island model (Andrews 1979a), but pioneering studies of the species in Panama are inconsistent with predation of adult in shaping population ecology. Rather, this literature described variation in abundance through space and time that was best predicted by egg mortality driven by interactions between ants (*Solenopsis* sp.) and rainfall (Andrews 1982, 1988, Andrews and Wright 1994, Chalcraft and Andrews 1999). Thus, accumulating literature along with my results are inconsistent with a number of predictions from the mainland-island model (Andrews 1979a), and instead suggest a more simple explanation – that mainland and island populations may be regulated more similarly than previously acknowledged, similar to the formation of native and naturalized communities of anoles in mainland and island habitats (Poe 2014).

Rather, the predator-prey models presented here suggest a new emerging hypothesis, in which behavioral decisions by mainland anoles may be effective at reducing predation pressure until other resources become limiting. One observation that led to the mainland-island model was that, relative to Caribbean island species, comparable mainland anoles spends less time foraging for more abundant food resources (Andrews 1979a) because anoles are allegedly wary of strong predation pressure (Losos et al. 1991; i.e., the growth/predation risk tradeoff, McPeek 2004). While the most frequent predators of *N. humilis* and other terrestrial anoles at La Selva are probably ctenid spiders (Guyer 1988), my models suggest that predation risk from spiders was so low as to have exerted no effect on anole occupancy, and instead litter abundance was a better predictor of occupancy. The lack of predator effects on occupancy may have resulted from shifts in anole habitat use to avoid predators without altering occupancy, similar to how island populations alter habitat use in response to introduced predators (Schoener et al. 2002, Calsbeek and Cox 2010). Altered patterns of *N. humilis* detection, when co-occurring at sites with ctenids, suggests that mainland anoles also exhibit behavioral responses to local predators. Anoles possess excellent eyesight and color vision (Fleishman and Persons 2001), and apparently high vigilance and shifts in habitat use of mainland anoles, such as *N. humilis*, may reduce predation pressure as a density-regulating factor for populations, to the point where resources can become limiting, such as food (Wright 1979, Guyer 1988) or leaf litter (Whitfield et al. 2014). If predator-induced vigilance decreases predation risk to the point where resources are limiting, then resource availability may ultimately drive mainland anole populations more strongly than predation.

In addition to demonstrating food limitation of *N. humilis*, Guyer (1988) observed seasonal abundance cycles of *N. humilis* populations in cacao plantations that oscillated in tandem with tree leaf-drop. Because seasonality of leaf litter drives arthropod abundance (Lieberman and Dock 1982) and *N. humilis* was found to be food limited, Guyer (1988) hypothesized that leaf-fall events at the scale of single canopy trees regulate abundances of terrestrial anoles and similar vertebrates. The Guyer (1988) hypothesis assumes that populations are regulated bottom-up by leaf-litter and/or food resources, and predicts that (1) anole and frog abundance through primary forest is a mosaic of sites at different stages depending on the leaf-drop phenology of the most proximate tree, and (2) low-resource patches should be vacated seasonally by individuals in search for areas of greater resource quality (hereafter, the litter-mosaic model; Guyer 1988). My results have implications for reinterpreting and revising the litter-mosaic model in two ways. First, site occupancy of all three species was influenced by abundance of leaf litter, but not arthropod abundance used as food. This result suggests that leaf litter alone may drive variance in the litter-mosaic model (i.e., Whitfield et al. 2014). Second, because frog occupancy was more greatly influenced by predators than by litter abundance, predators appear to be an underemphasized control on anuran ecology in a patch-mosaic context. Specifically, my results suggested that frog demography is most sensitive to the presence of predators and only secondarily influenced by the availability of resources, such as leaf litter. In the context of the litter-mosaic model (Guyer 1988), frogs may still be incentivized to occupy sites of diminished leaf litter or vacate sites with abundant litter, depending on the presence of predators. Thus, my results revise the litter-mosaic model by placing greater emphasis on leaf litter and predators as mechanisms influencing site occupancy of small terrestrial vertebrates in a patch-mosaic model.

Because terrestrial leaf-litter abundance is strongly seasonal in lowland Caribbean wet forests, the relationship between leaf litter and predator-prey interactions also has implications for understanding seasonal abundance cycles and amphibian declines at La Selva and other comparable wet tropical forests. Leaf-drop phenology of most trees causes standing leaf litter to reach its greatest depth at the end of the dry season (Frankie et al. 1974, Levings and Windsor 1984); as the wet season begins and advances, decreased leaf drop, increased decomposition, and mechanical action of rainfall and shredding action of insects cause standing litter to decrease. Because models suggested that predator-prey interactions vary across a gradient of litter abundance, ctenid spiders might exert greater effects on terrestrial frogs during periods of low leaf litter in the wet season when frogs may have reduced refugia in litter. This effect can be extended with implications for models of amphibian population decline at La Selva, a site that experienced a 75% decline over a 35-y period that was hypothesized as a result of climate-driven reductions in the abundance of standing leaf litter (Whitfield et al. 2007). Given observed increase in predator-prey interactions at lower levels of litter abundance at La Selva, climate-driven declines in litter could have driven increased predator-prey interactions and a shift in community composition toward decreased abundance of frogs and increased abundance of spider predators. Thus, models of resource-driven amphibian declines (Whitfield et al. 2016) should consider how altered predator-prey relationships may influence community dynamics in these ecosystems.

Because ctenid spiders are thought to avoid depredating *O. pumilio*, I predicted that *O. pumilio* would exhibit patterns of occupancy and detection independent of spiders. Contrary to this prediction, occupancy and detection patterns were consistent with spider avoidance and similar to those observed for a species thought to be frequently consumed by ctenids, *C.*

bransfordii. The spider-avoidance effect may be driven by (1) predation attempts by ctenids on *O. pumilio* that occasionally result in frog consumption (e.g., Summers 1999), (2) ctenid predation of *O. pumilio* eggs or tadpoles that have reduced chemical protection than adults (Stynoski et al. 2014a), and/or (3) an innate, general avoidance of spiders by frogs, because frogs have shared a long evolutionary history with spider predators. Because *O. pumilio* responded to spiders in ways consistent with predictions of a predator-prey relationship, my modeling results are at odds with behavioral studies of spider–*O. pumilio* interactions describing spiders as unimportant predators (Szelistowksi 1985, Murray et al. 2016).

My study is a hypothesis-testing endeavor, because it provided an empirical test of a necessary prediction of the Andrews hypothesis. However, a general limitation of the study was that the methods did not include a robust experimental design to provide a sufficient test of the hypothesis. In this sense, the results are limited in inference because other factors, not measured nor controlled, could have exerted influences in unanticipated ways. Another limitation is that I interpreted increased detection of vertebrates in the presence of spiders as evidence inconsistent with predictions of predator-induced wariness, but model-estimated detection estimates may not be the most ideal way to evaluate that prediction. If vertebrate detection by spiders differs from that of researchers, then vertebrates may be less detectable to spiders in ways consistent with that prediction of the mainland-island model. Last, I analyzed how vertebrate prey ecology was shaped by a single predator group, ctenid spiders, which is more narrow in scope than the extremely diverse mainland predator assemblage (Greene 1988, Losos 2009) implicitly implicated in driving population ecology of mainland anoles by the Andrews (1979a) hypothesis. While ctenids are the most frequently observed predator of *N. humilis* (Guyer 1988), other predators may have contributed in ways not measured and more consistent with the more diverse predation pressure implicitly described by Andrews (1979a).

In conclusion, my results provide correlative evidence for strong effects of predatory spider on prey vertebrates, although they were inconsistent with the mainland-island model of anole population regulation (Andrews 1979a). My results supported leaf litter as bottom-up factor regulating the terrestrial vertebrate assemblage in lowland wet tropical forests, but described a stronger and novel top-down effect of predators on anurans that has significant implications for improving models of patch dynamics, seasonal population cycles, and amphibian declines (Guyer 1988, Whitfield et al. 2014). While a large literature has suggested or assumed dominant bottom-up regulation of the terrestrial frogs and lizards in this system (Scott 1976, Toft 1980, Lieberman 1986, Guyer 1988, Fauth et al. 1989, Heinen 1992, Guyer 1994, Whitfield et al. 2007, Folt and Reider 2013, Whitfield et al. 2014), I provided the first evidence supporting a dominant effect of predators regulating this important assemblage. However, my results oppose a large literature invoking predation as the dominant force shaping ecology and evolution of mainland anoles (Andrews 1979a, Irschick et al. 1997, Losos 2009), and suggest that mainland and island systems might be regulated more similarly than previously thought.

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Table 1. Description of model parameters used to evaluate hypotheses describing two-species co-occurrence patterns, following Richmond et al. (2010). Species A are predators and are assumed to be dominant over the prey species B.

Parameter	Description
Ψ^{A}	Occupancy of the dominant species A
Ψ^{BA}	Occupancy of species B, given species A is present
Ψ^{Ba}	Occupancy of species B, given species A is absent
p^{A}	Detection probability of species A, given species B is absent
p^{B}	Detection probability of species B, given species A is absent
r^{BA}	Detection probability of species B, given both species are present and species A is detected
r^{Ba}	Detection probability of species B, given both species are present and species A is not detected
Ψ^{LL} p^{LL}	Effect of leaf litter (LL) on occupancy (Ψ)or detection (p) of both species
$\Psi^{Arthropods}$ $p^{Arthropods}$	Effect of arthropod food resources on occupancy or detection of both species

Table 2. Six models describing hypotheses for co-occurrence patterns between predator and prey species in forest plots at La Selva, Costa Rica. Species A is assumed to be dominant over species B. All models include terms describing species A and B differing in probability of occupancy and detection.

Model	Hypotheses
Ψ^{BA}, Ψ^{Ba}	Occupancy of species A affects the occupancy of species B
Ψ^{BA}, Ψ^{Ba}, r^{BA}	Occupancy and detection of species A affects the occupancy and detection of species B
Ψ^{BA}, Ψ^{Ba}, r^{BA}, r^{Ba}	Occupancy of species A affects the occupancy and detection of species B, whether or not species A is detected
Ψ^{BA}	No interactions between species affecting occupancy or detection; null model
Ψ^{BA}, r^{BA}	No interactions between species affecting occupancy; occupancy and detection of species A influences the detection of species B
Ψ^{BA}, r^{BA}, r^{Ba}	No interactions between species affecting occupancy; occupancy of species A affects the detection of species B, whether or not species A is detected

Table 3. Number of parameters (*k*), AIC$_c$, ΔAIC$_c$, and model weight (w_m) for 42 models built to describe how occupancy and detection patterns of *Craugastor bransfordii*, *Oophaga pumilio*, and *Norops humilis* are influenced by predatory ctenid spiders and resources (leaf-litter, arthropods) at La Selva, Costa Rica. See Table 1 for explanations of model parameters.

Species	Model	k	ΔAICc	w_m
C. bransfordii	$\Psi^{A}\ \Psi^{BA}\ \Psi^{Ba}\ \Psi^{LL}\ p^{A}\ p^{B}\ r^{BA}$	7	0.00	0.41
	$\Psi^{A}\ \Psi^{BA}\ \Psi^{Ba}\ \Psi^{LL}\ p^{A}\ p^{B}\ r^{BA}\ r^{Ba}$	8	0.81	0.27
	$\Psi^{A}\ \Psi^{BA}\ \Psi^{Ba}\ \Psi^{LL}\ p^{A}\ p^{B}\ r^{BA}\ p^{LL}$	8	1.70	0.18
	$\Psi^{A}\ \Psi^{BA}\ \Psi^{Ba}\ \Psi^{LL}\ p^{A}\ p^{B}\ r^{BA}\ r^{Ba}\ p^{LL}$	9	2.28	0.13
O. pumilio	$\Psi^{A}\ \Psi^{BA}\ \Psi^{Ba}\ \Psi^{LL}\ p^{A}\ p^{B}\ r^{BA}$	7	0.00	0.35
	$\Psi^{A}\ \Psi^{BA}\ \Psi^{Ba}\ \Psi^{LL}\ p^{A}\ p^{B}\ r^{BA}\ r^{Ba}$	8	0.13	0.33
	$\Psi^{A}\ \Psi^{BA}\ \Psi^{Ba}\ \Psi^{LL}\ p^{A}\ p^{B}\ r^{BA}\ p^{LL}$	8	1.73	0.15
	$\Psi^{A}\ \Psi^{BA}\ \Psi^{Ba}\ \Psi^{LL}\ p^{A}\ p^{B}\ r^{BA}\ r^{Ba}\ p^{LL}$	9	1.79	0.14
N. humilis	$\Psi^{A}\ \Psi^{BA}\ \Psi^{LL}\ p^{A}\ p^{B}\ r^{BA}\ r^{Ba}\ p^{LL}$	8	0.00	0.28
	$\Psi^{A}\ \Psi^{BA}\ \Psi^{LL}\ p^{A}\ p^{B}\ r^{BA}\ r^{Ba}$	7	0.37	0.23
	$\Psi^{A}\ \Psi^{BA}\ \Psi^{Ba}\ \Psi^{LL}\ p^{A}\ p^{B}\ r^{BA}\ r^{Ba}$	8	1.76	0.12
	$\Psi^{A}\ \Psi^{BA}\ \Psi^{Ba}\ \Psi^{LL}\ p^{A}\ p^{B}\ r^{BA}\ r^{Ba}\ p^{LL}$	9	1.84	0.11

Table 4. Model-averaged coefficient values (β), unconditional standard error (SE), and parameter weights (w_p) generated by averaging 42 co-occurrence models for three vertebrate species (*Craugastor bransfordii*, *Oophaga pumilio*, *Norops humilis*) and ctenid spider predators at La Selva, Costa Rica. See Table 1 for explanations of model parameters. Parameter weights were not provided for Ψ^{A} and Ψ^{BA} because these parameters were included in all models (w_p = 1.00).

	Occupancy							
Species	Intercept – Ψ^{A}	Ψ^{BA}	Ψ^{Ba}		Ψ^{LL}		$\Psi^{Arthropods}$	
	β (SE)	β (SE)	β (SE)	*w*	β (SE)	*w*	β (SE)	*w*
C. bransfordii	–3.41 (0.66)	0.18 (0.32)	9.19 (1.77)	0.99	1.14 (0.21)	0.98	0.003 (0.001)	0.01
O. pumilio	–2.86 (0.92)	–2.29 (0.39)	3.44 (0.76)	0.99	1.03 (0.25)	0.97	0.00 (0.00)	0.00
N. humilis	–2.97 (1.39)	3.27 (3.82)	–2.64 (1.51)	0.31	1.23 (0.53)	0.89	0.00 (0.00)	0.00

Table 5. Model-averaged coefficient values (β), unconditional standard error (SE), and Akaike parameter weights (w_p) generated by averaging 42 co-occurrence models describing patterns of detection for three vertebrate species (*Craugastor bransfordii*, *Oophaga pumilio*, *Norops humilis*) and predatory ctenid spiders at La Selva, Costa Rica. Parameter weights were not provided for p^{A} and p^{B}, because they were included in all models (w_p = 1.00).

	Detection									
Species	Intercept – p^{A}	p^{B}	r^{BA}		r^{Ba}		p^{LL}		$p^{Arthropods}$	
	β (SE)	β (SE)	β (SE)	w_p	β (SE)	w_p	β (SE)	w_p	β (SE)	w_p
C. bransfordii	–2.12 (0.24)	1.29 (0.16)	0.70 (0.14)	0.99	0.09 (0.14)	0.41	–0.02 (0.02)	0.30	–0.002 (0.00)	0.01
O. pumilio	–2.08 (0.41)	0.85 (0.22)	0.70 (0.19)	0.99	–0.20 (0.09)	0.48	0.04 (0.10)	0.32	0.00 (0.00)	0.00
N. humilis	–2.98 (0.98)	–0.53 (0.40)	0.33 (0.41)	0.87	–0.68 (0.15)	0.79	0.25 (0.27)	0.60	0.00 (0.00)	0.00

Figure legends

Figure 1. Three species of abundant terrestrial frogs and lizards and a predatory spider (Ctenidae) from lowland rain forests of Costa Rica: (A) *Craugastor bransfordii*, (B) *Oophaga pumilio*, (C) *Norops humilis*, and (D) *Ctenus curvipes*, consuming an individual of *Norops humilis*.

Figure 2. Site occupancy of *Craugastor bransfordii* (A), *Oophaga pumilio* (B), and *Norops humilis* (C) as a function of leaf-litter mass at sites conditionally occupied (Ψ^{BA}) and unoccupied (Ψ^{Ba}) by predatory spiders (Ctenidae). Ψ^{A} is the occupancy of spiders. The black arrow indicates the median value of leaf-litter mass. Results were model-averaged across a balanced design of 42 models (Appendix B).

Figure 3. Species interaction factors (SIF) between predatory spiders (Ctenidae) and *Craugastor bransfordii* (A) and *Oophaga pumilio* (B) in relation to leaf-litter mass in forest plots at La Selva, Costa Rica. Ctenid spiders are assumed to be dominant over prey frogs. SIF values < 1.0 indicate avoidance of the subordinate species, values > 1.0 indicate aggregated with dominate species, and values ~ 1.0 (grey dotted line) indicates independent patterns of co-occupancy between spiders and frogs. The black arrow indicates the median value of leaf-litter mass.

Figure 4. Conditional detection probability of predatory spiders (dominant species; *Ctenus* sps.) and prey frogs and lizards (subordinate species; A – *Craugastor bransfordii*, B – *Oophaga pumilio*, C – *Norops humilis*) in terrestrial habitats at La Selva, Costa Rica. p^{A} – detection probability of dominant species, given the subordinate species is absent; p^{B} – detection of the subordinate species, given the dominant species is absent; r^{BA} – detection of subordinate species, given the dominant species is present and detected; r^{Ba} – detection of the subordinate species, given the dominant species is present but not detected.

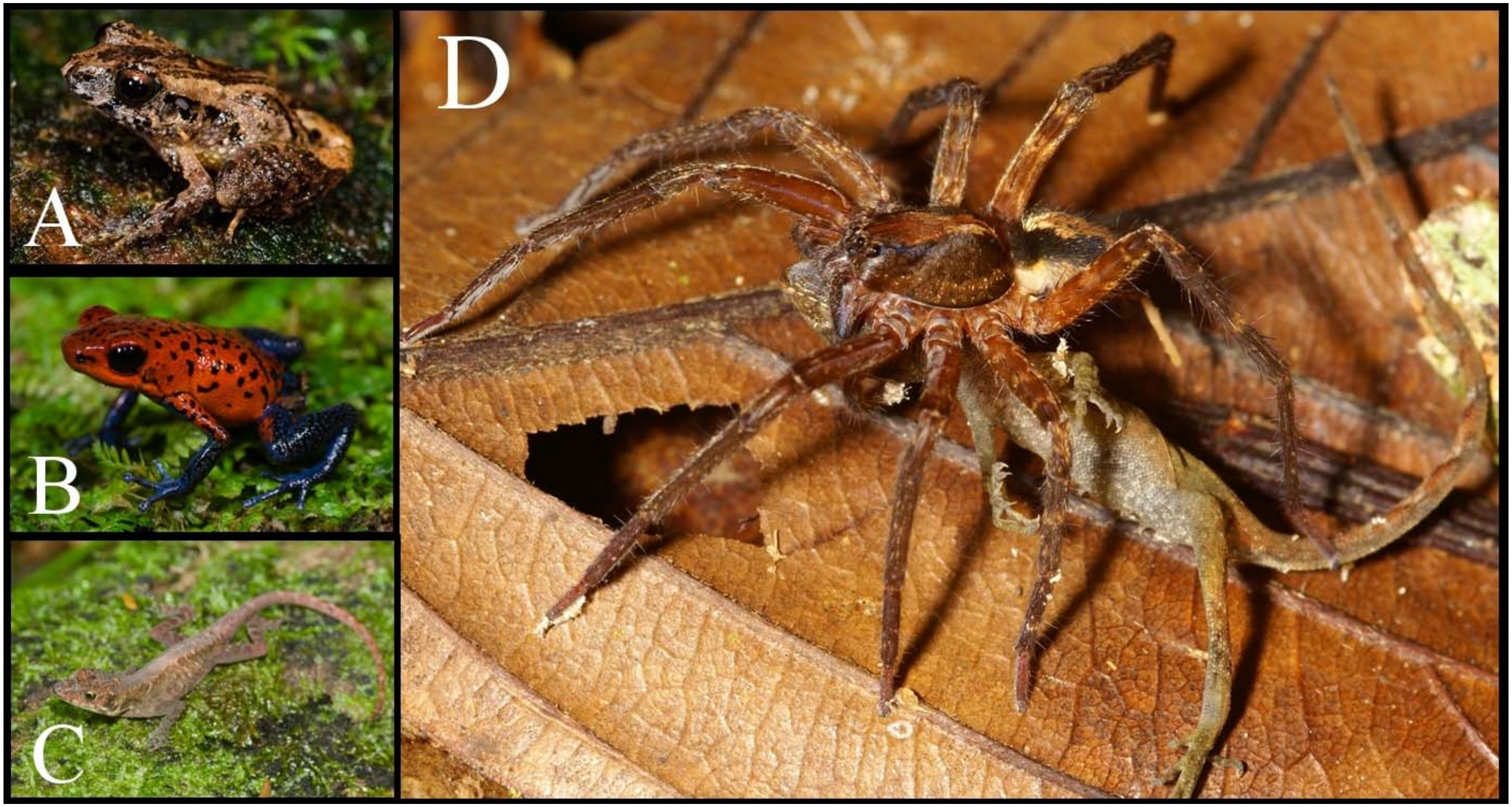


Figure 1

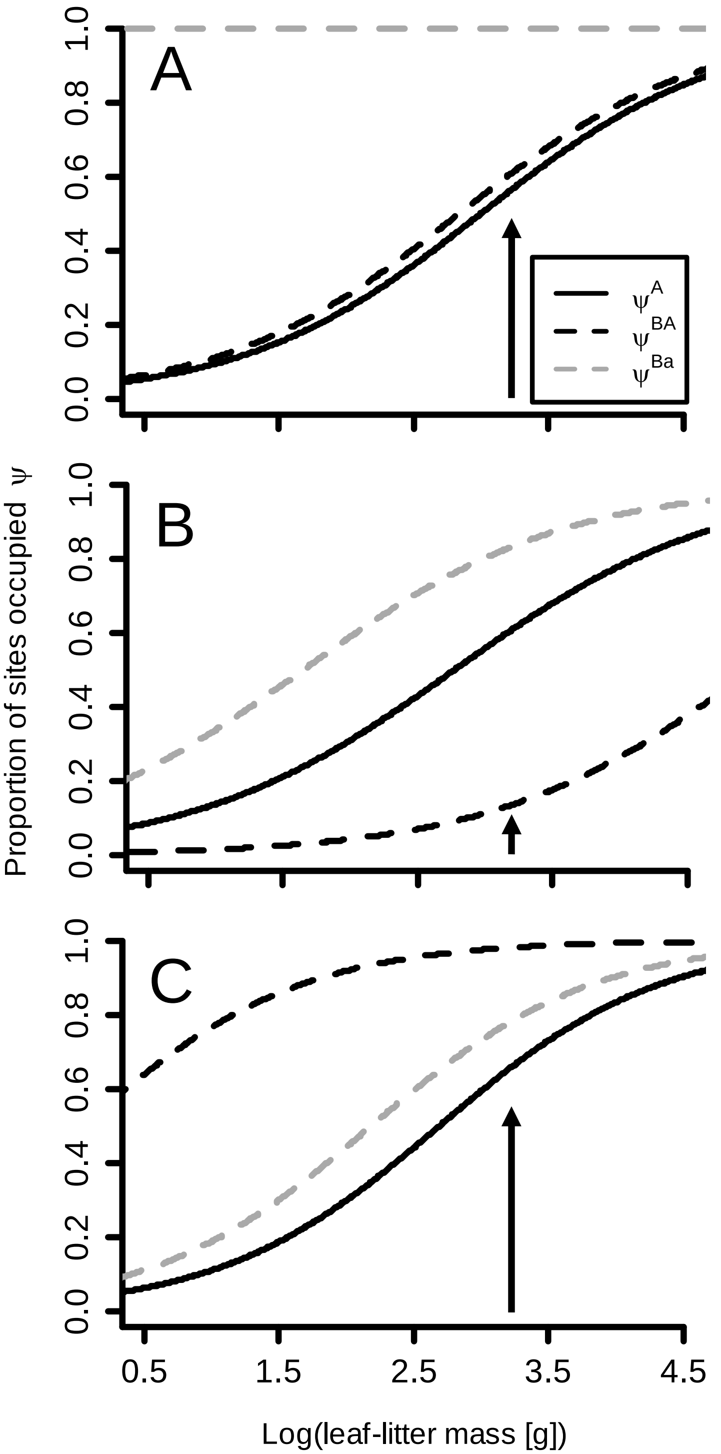

A
B
C
ψ^A
ψ^BA
ψ^Ba
Proportion of sites occupied ψ
Log(leaf-litter mass [g])
0.0
0.2
0.4
0.6
0.8
1.0
0.5
1.5
2.5
3.5
4.5

Figure 2

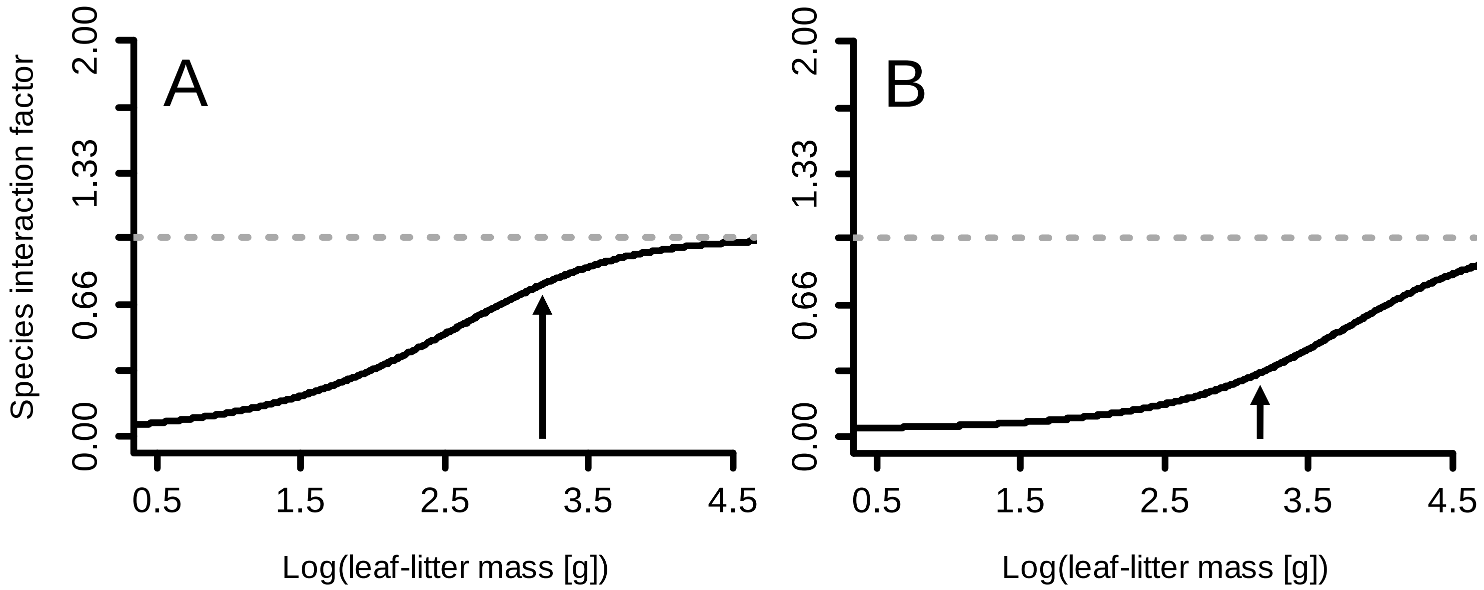
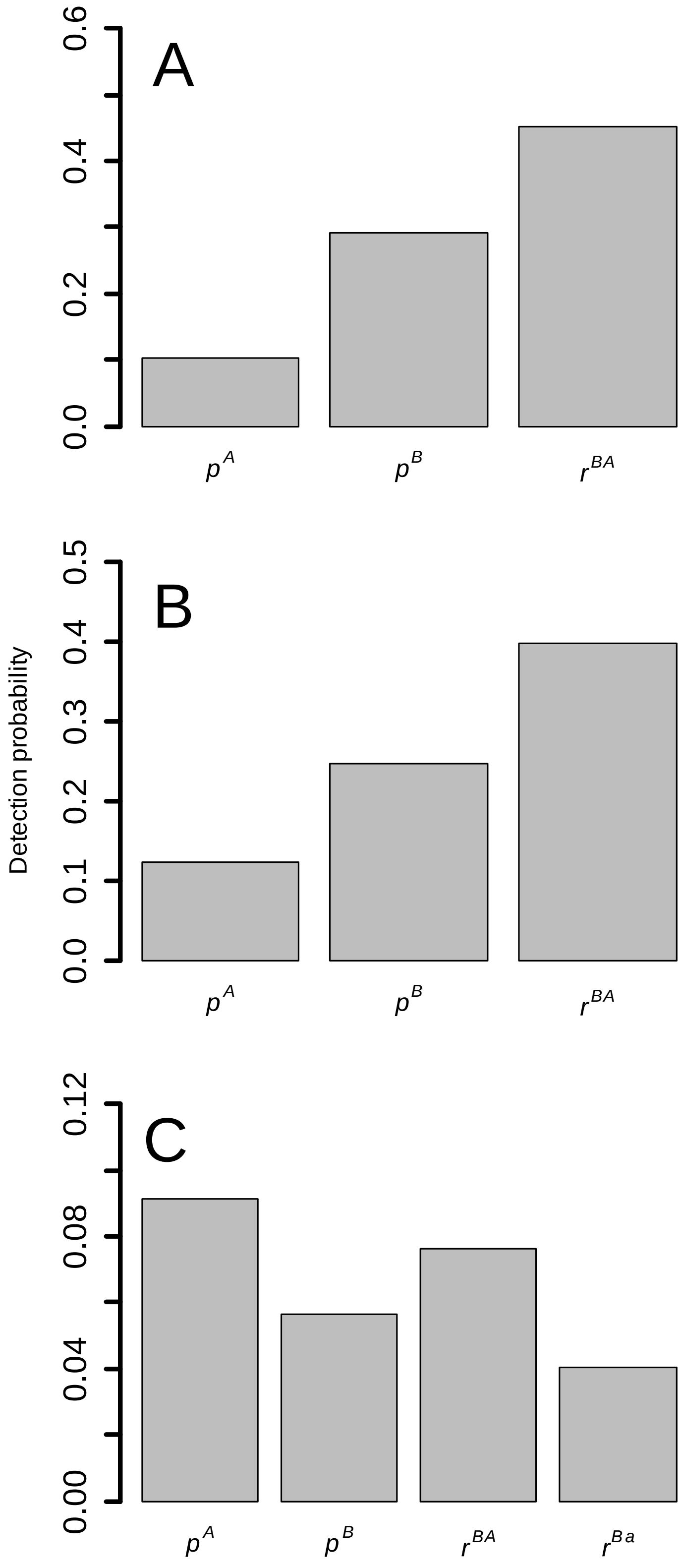

A
B
Species interaction factor
2.00
1.33
0.66
0.00
0.5
1.5
2.5
3.5
4.5
Log(leaf-litter mass [g])

Figure 3



A
0.0
0.2
0.4
0.6
p^A
p^B
r^{BA}
B
Detection probability
0.0
0.1
0.2
0.3
0.4
0.5
p^A
p^B
r^{BA}
C
0.00
0.04
0.08
0.12
p^A
p^B
r^{BA}
r^{Ba}

Figure 4

Appendix A. Taxonomic groups of invertebrates identified and quantified from leaf-litter samples in plots at La Selva, Costa Rica.

Phylum	Subphylum	Class	Order	Family	Museum numbers
Arthopoda	Chelicerata	Arachnida	Araneae		AUMS 17701–18730
Arthropoda	Chelicerata	Arachnida	Parasitiformes		AUMS 17948–17949
Arthopoda	Chelicerata	Arachnida	Opiliones		AUMS 17950–18075
Arthopoda	Chelicerata	Arachnida	Pseudoscorpiones		AUMS 18076–18215
Arthopoda	Chelicerata	Arachnida	Ricinulei		AUMS 18216–18221
Arthopoda	Chelicerata	Arachnida	Acariformes		AUMS 18222–18532
Arthopoda	Myriapoda	Chilopoda			AUMS 18533–18565
Arthopoda	Myriapoda	Diplopoda			AUMS 18566–18731
Arthopoda	Hexapoda	Entognatha	Collembola		AUMI 129401–129708
Arthopoda	Hexapoda	Insecta	Coleoptera		AUMI 129709–129945, 129965
Arthopoda	Hexapoda	Insecta	Dermaptera		AUMI 129946–129958
Arthopoda	Hexapoda	Insecta	Blattodea		AUMI 129967–130019
Arthopoda	Hexapoda	Insecta	Mantodea		AUMI 130020–130021
Arthopoda	Hexapoda	Insecta	Diptera		AUMI 130022–130264
Arthopoda	Hexapoda	Insecta	Hymenoptera	Formicidae	AUMI 130265–130550
Arthopoda	Hexapoda	Insecta	Lepidoptera		AUMI 130583, 130585, 130586
Arthopoda	Hexapoda	Insecta	Thysanoptera		AUMI 130587–130705
Arthopoda	Hexapoda	Insecta	Hemiptera		AUMI 130706–130799
Arthopoda	Hexapoda	Insecta	Orthoptera		AUMI 129964, 130800–130866
Arthropoda		Malacostraca	Isopoda		AUMI 41161–41362
Mollusca		Gastropoda			AUMI 41093–41155
Onycophora				Peripatidae	AUMI 41156–41160
Annelida		Clitellata	Hirudinea		AUMI 41373–41439

Appendix B. Complete model set examining the effects of predators and resources (leaf litter, arthropods) on occupancy and detection probability of *Craugastor bransfordii*, *Oophaga pumilio*, and *Norops humilis* in forest habitat at La Selva, Costa Rica. Arthropods were modeled specific to the favored prey of each vertebrate species: *C. bransfordii* – Acari, Araneae, Coleoptera, and Isopoda; *O. pumilio* – Acari and Formicidae; *N. humilis* – Araneae and Isopoda.

Model	Occupancy parameters	Detection parameters
1	$\Psi^{A}+\Psi^{BA}$	$p^{A}+p^{B}$
2	$\Psi^{A}+\Psi^{BA}$	$p^{A}+p^{B}+r^{BA}$
3	$\Psi^{A}+\Psi^{BA}$	$p^{A}+p^{B}+r^{BA}+r^{Ba}$
4	$\Psi^{A}+\Psi^{BA}+\Psi^{Ba}$	$p^{A}+p^{B}$
5	$\Psi^{A}+\Psi^{BA}+\Psi^{Ba}$	$p^{A}+p^{B}+r^{BA}$
6	$\Psi^{A}+\Psi^{BA}+\Psi^{Ba}$	$p^{A}+p^{B}+r^{BA}+r^{Ba}$
7	$\Psi^{A}+\Psi^{BA}+\Psi^{LL}$	$p^{A}+p^{B}$
8	$\Psi^{A}+\Psi^{BA}+\Psi^{LL}$	$p^{A}+p^{B}+r^{BA}$
9	$\Psi^{A}+\Psi^{BA}+\Psi^{LL}$	$p^{A}+p^{B}+r^{BA}+r^{Ba}$
10	$\Psi^{A}+\Psi^{BA}$	$p^{A}+p^{B}+p^{LL}$
11	$\Psi^{A}+\Psi^{BA}$	$p^{A}+p^{B}+r^{BA}+p^{LL}$
12	$\Psi^{A}+\Psi^{BA}$	$p^{A}+p^{B}+r^{BA}+r^{Ba}+p^{LL}$
13	$\Psi^{A}+\Psi^{BA}+\Psi^{LL}$	$p^{A}+p^{B}+p^{LL}$
14	$\Psi^{A}+\Psi^{BA}+\Psi^{LL}$	$p^{A}+p^{B}+r^{BA}+p^{LL}$
15	$\Psi^{A}+\Psi^{BA}+\Psi^{LL}$	$p^{A}+p^{B}+r^{BA}+r^{Ba}+p^{LL}$
16	$\Psi^{A}+\Psi^{BA}+\Psi^{Ba}+\Psi^{LL}$	$p^{A}+p^{B}$
17	$\Psi^{A}+\Psi^{BA}+\Psi^{Ba}+\Psi^{LL}$	$p^{A}+p^{B}+r^{BA}$
18	$\Psi^{A}+\Psi^{BA}+\Psi^{Ba}+\Psi^{LL}$	$p^{A}+p^{B}+r^{BA}+r^{Ba}$
19	$\Psi^{A}+\Psi^{BA}+\Psi^{Ba}$	$p^{A}+p^{B}+p^{LL}$
20	$\Psi^{A}+\Psi^{BA}+\Psi^{Ba}$	$p^{A}+p^{B}+r^{BA}+p^{LL}$
21	$\Psi^{A}+\Psi^{BA}+\Psi^{Ba}$	$p^{A}+p^{B}+r^{BA}+r^{Ba}+p^{LL}$
22	$\Psi^{A}+\Psi^{BA}+\Psi^{Ba}+\Psi^{LL}$	$p^{A}+p^{B}+p^{LL}$
23	$\Psi^{A}+\Psi^{BA}+\Psi^{Ba}+\Psi^{LL}$	$p^{A}+p^{B}+r^{BA}+p^{LL}$
24	$\Psi^{A}+\Psi^{BA}+\Psi^{Ba}+\Psi^{LL}$	$p^{A}+p^{B}+r^{BA}+r^{Ba}+p^{LL}$
25	$\Psi^{A}+\Psi^{BA}+\Psi^{\text{Arthropods}}$	$p^{A}+p^{B}$
26	$\Psi^{A}+\Psi^{BA}+\Psi^{\text{Arthropods}}$	$p^{A}+p^{B}+r^{BA}$
27	$\Psi^{A}+\Psi^{BA}+\Psi^{\text{Arthropods}}$	$p^{A}+p^{B}+r^{BA}+r^{Ba}$
28	$\Psi^{A}+\Psi^{BA}$	$p^{A}+p^{B}+p^{\text{Arthropods}}$
29	$\Psi^{A}+\Psi^{BA}$	$p^{A}+p^{B}+r^{BA}+p^{\text{Arthropods}}$
30	$\Psi^{A}+\Psi^{BA}$	$p^{A}+p^{B}+r^{BA}+r^{Ba}+p^{\text{Arthropods}}$
31	$\Psi^{A}+\Psi^{BA}+\Psi^{\text{Arthropods}}$	$p^{A}+p^{B}+p^{\text{Arthropods}}$

32	$\Psi^{A}+\Psi^{BA}+\Psi^{Arthropods}$	$p^{A}+p^{B}+r^{BA}+p^{Arthropods}$
33	$\Psi^{A}+\Psi^{BA}+\Psi^{Arthropods}$	$p^{A}+p^{B}+r^{BA}+r^{Ba}+p^{Arthropods}$
34	$\Psi^{A}+\Psi^{BA}+\Psi^{Ba}+\Psi^{Arthropods}$	$p^{A}+p^{B}$
35	$\Psi^{A}+\Psi^{BA}+\Psi^{Ba}+\Psi^{Arthropods}$	$p^{A}+p^{B}+r^{BA}$
36	$\Psi^{A}+\Psi^{BA}+\Psi^{Ba}+\Psi^{Arthropods}$	$p^{A}+p^{B}+r^{BA}+r^{Ba}$
37	$\Psi^{A}+\Psi^{BA}+\Psi^{Ba}$	$p^{A}+p^{B}+p^{Arthropods}$
38	$\Psi^{A}+\Psi^{BA}+\Psi^{Ba}$	$p^{A}+p^{B}+r^{BA}+p^{Arthropods}$
39	$\Psi^{A}+\Psi^{BA}+\Psi^{Ba}$	$p^{A}+p^{B}+r^{BA}+r^{Ba}+p^{Arthropods}$
40	$\Psi^{A}+\Psi^{BA}+\Psi^{Ba}+\Psi^{Arthropods}$	$p^{A}+p^{B}+p^{Arthropods}$
41	$\Psi^{A}+\Psi^{BA}+\Psi^{Ba}+\Psi^{Arthropods}$	$p^{A}+p^{B}+r^{BA}+p^{Arthropods}$
42	$\Psi^{A}+\Psi^{BA}+\Psi^{Ba}+\Psi^{Arthropods}$	$p^{A}+p^{B}+r^{BA}+r^{Ba}+p^{Arthropods}$

Chapter 4

Spatial patterns of *Oophaga pumilio* in a homogeneous plantation system are consistent with conspecific attraction

Abstract. The conspecific attraction hypothesis predicts that individuals are attracted to conspecifics because they may be cues to quality habitat and/or colonists may benefit from living in aggregations. Poison frogs (Dendrobatidae) are brightly colored, territorial, and visually oriented, features which make dendrobatids an appropriate model to test for conspecific attraction. In the present study, I tested the conspecific attraction hypothesis using an extensive mark-recapture dataset of the strawberry poison frog (*Oophaga pumilio*) from La Selva Biological Station, Costa Rica. Data were collected from replicate populations in a relatively homogenous *Theobroma cacao* plantation, a unique opportunity to test how conspecifics influence spatial ecology of migrants in a controlled habitat with homogeneous structure. I predicted that (1) individuals entering a population would aggregate with resident adults, (2) migrants would share sites with residents at greater frequency than expected by chance, and (3) migrant home-ranges would have shorter nearest-neighbor distances (NND) to residents than expected by chance. The results were consistent with these three predictions: relative to random simulations, I observed significant aggregation, home-range overlap, and NND distribution functions in four, five, and six, respectively, of the six migrant-resident groups analyzed. Conspecific attraction may benefit migrant *O. pumilio* by providing cues to suitable home sites and/or increasing potential for social interactions with conspecifics; if true, these benefits should outweigh the negative effects of other factors associated with aggregation. My study is consistent with conspecific attraction in *O. pumilio* and provides rare support from a field setting that conspecific attraction may be a relevant mechanism for models of anuran spatial ecology.

Keywords: Colonization, habitat selection, nearest-neighbor analysis, Neotropics, spatial ecology.

INTRODUCTION

A controversial factor influencing habitat selection is the role that individuals play in shaping the distribution of conspecifics. A large body of literature posits that, because conspecifics are competitors, individual fitness should decline with increasing conspecific density (Brown 1969, Rosenzweig 1985, 1991, Muller et al. 1997). This theory predicts that, to minimize intraspecific competition, individuals seeking habitat should avoid areas with established conspecifics. However, a contrary line of evidence suggests that individuals can be attracted to conspecifics (conspecific attraction, Stamps 1988), because (1) conspecifics serve as cues of suitable habitat quality (conspecific cueing, Stamps 1987), (2) colonists may benefit from living in aggregations after territories are established because individuals in aggregations may better protect territories, reduce predation, and promote social interaction or attract mates (Stamps 1988, 1994, Muller et al. 1997, Boulinier and Danchin 1997), and/or (3) individuals may reduce costs associated with prospection (Reed et al. 1999). Conspecific attraction is particularly applicable to territorial species, because the presence of territorial residents may indicate that a habitat is of sufficient quality to justify occupancy and defense (Stamps 1987). In the conspecific attraction model, probability of settlement is increased in the presence of conspecifics (Donahue 2006). For conspecific attraction to be an adaptive strategy, fitness increases accrued from settlement with conspecifics must outweigh the energetic costs associated with higher densities and increased intraspecific competition. Thus, conspecific attraction predicts that individuals with little or no experience should be more attracted to habitat with higher density of conspecifics than other individuals already experienced with the habitat (Stamps 1988, Donahue 2006).

Despite much interest in conspecific attraction by population and conservation biologists (e.g., Lima and Zollner 1996, Ward and Schlossberg 2004, Fletcher 2006, Campomizzi et al. 2008), empirical studies of whether conspecific attraction influences selection are logistically challenging, because it can be difficult to control for habitat quality in natural heterogeneous landscapes (Stamps 1988). However, support for conspecific attraction has been found for invertebrates (Meadows and Campbell 1972, Crisp 1976, Muller 1998, Donahue 2006), fish (Sweatman 1985, 1988), amphibians (Gautier et al. 2006, Pizzatto et al. 2015), reptiles (Stamps 1987, 1988, Clark 2007), and birds (Muller et al. 1997, Danchin et al. 1998, Etterson 2003, Ward and Schlossberg 2004, Austin et al. 2016), and a recent review of vertebrate social behavior emphasizes the importance of and need for more studies of conspecific attraction (Doody et al. 2013).

Two recent tests of conspecific attraction in anurans suggested that visual cues may be more important in moderating conspecific attraction than chemical cues. The European frog *Pelophylax* (*Rana*) *perezi* does not discriminate between habitats with and without conspecific chemical cues; rather, individuals select habitat on the basis of the presence/absence of chemical cues of predators (Gonzalo et al. 2006). While juvenile *Litoria aurea* similarly do not use chemical conspecific cues to select habitat, this species discriminates by the physical presence of conspecific individuals (Pizzatto et al. 2015). While much research has focused on understanding the role of acoustic cues during amphibian mate choice and mating strategies (Ryan 1994), visual cues are also ecologically important traits for communication and mate choice of terrestrial frogs in the tropics (Lindquist and Hetherington 1996, Hödl and Amézquita 2001, Grafe and Wanger 2007). For example, *Oophaga pumilio* and *Allobates femoralis* are diurnal members of the family Dendrobatidae that both use visual and acoustic cues during mate choice (Summers et al. 1999, Narins et al. 2003, Reynolds and Fitzpatrick 2007). For *A. femoralis*, acoustic and visual cues must be coupled to initiate male aggression toward conspecific competitors (Narins et al. 2003). Further, *O. pumilio* is a highly territorial species: males vigorously defend areas with suitable sites for advertisement, courtship, and oviposition (Pröhl and Hödl 1999), and male abundance is limited by available tadpole-rearing sites in bromeliads (Donnelly 1989a). Females have also been recorded to be territorial at one site in Costa Rica – where they defended feeding areas against other females, although this territoriality was to a lesser extent than that observed regularly in males (Meuche et al. 2011). Thus, given the species' relatively high abundance (Lieberman 1986), territoriality, and known use of visual-cues during mate choice (Summers et al. 1999), these features make *O. pumilio* an appropriate model organism to test whether conspecific attraction influences habitat selection of terrestrial frogs in diverse lowland Neotropical forests.

The conspecific attraction hypothesis predicts that, across habitats of equivalent quality, naïve juveniles and migrating adults will preferentially colonize and associate in space with pre-established adults more frequently than expected by chance. Here, I tested this prediction using a large mark-recapture dataset of *O. pumilio* at La Selva Biological Station, Costa Rica, collected from replicate plots within an abandoned *Theobroma cacao* plantation. I used the cacao plantation system because leaf litter, the primary terrestrial environment generating an arthropod food base, was relatively homogenous and trees, the primary substrate for bromeliads used as nesting habitat, were uniformly distributed, features which allowed us to establish replicate plots for this and other studies (Guyer 1988a, b, Donnelly 1989a, b). I made three predictions about the spatial distribution of *O. pumilio*, given the conspecific attraction hypothesis: (1) individuals entering a population (i.e., = recruitment from births [juveniles] or migrating adults; hereafter, collectively 'migrants) would aggregate around resident adults rather than distributing themselves in a random or uniform distribution relative to residents, (2) migrants would share sites with residents at a higher frequency than expected by chance, and (3) home-range centroids of migrants and residents would have nearest-neighbor distance distribution functions consistent with aggregation.

METHODS

Study site and species

La Selva Biological Station (hereafter, La Selva) is a private reserve owned by the Organization for Tropical Studies (OTS) in the Caribbean lowlands of northeastern Costa Rica, ca. 3 km south of Puerto Viejo de Sarapiquí, Heredia Province (10.42˚N, 84.02˚W). Elevation at La Selva ranges from 30–130 m asl. The site is characterized by an average temperature of 25.8˚C, receives ca. 4 m of precipitation per year (Sanford et al. 1994), and is classified within Holdridge's Tropical Wet Forest life zone (McDade and Hartshorn 1994). Rainfall is seasonal with most rain occurring during the wet season (May–December), relative to the dry season (January–April).

Oophaga pumilio (strawberry poison frog) is an abundant species of poison frog (family Dendrobatidae) occupying terrestrial habitats in lowland Caribbean forests from Nicaragua to Panama. The species is a dietary specialist consuming ants and mites (Lieberman 1986, Donnelly 1991); these taxa, which compose >80% of its diet, are sources of alkaloid compounds that are sequestered into poison glands in the frog's skin (Saporito et al. 2004, 2007a), providing a chemical defense from predators (e.g., Stynoski et al. 2014). Across its geographic distribution, the species is brightly colored, which is an aposematic signal to predators (Saporito et al. 2007b). Both sexes provide parental care. Fathers guard and hydrate fertilized eggs in leaf litter, and mothers transport hatched tadpoles to rearing sites in bromeliads (Weygoldt 1980). Tadpole-rearing sites are repeatedly revisited by mothers to provision tadpoles with unfertilized eggs (Brust 1993) which provide nutrition for growth and alkaloids for chemical defense (Stynoski et al. 2014). Both sexes can be territorial: whereas females have been found to defend foraging areas (Meuche et al. 2011), males are more strongly territorial, defending areas with suitable sites for advertisement, courtship, and oviposition (Pröhl and Hödl 1999). Bromeliad availability has also been experimentally demonstrated as a limited resource defended by males (Donnelly 1989a). Territorial males attempt to attract females by perching in elevated sites and advertising with vocalizations; these individuals usually are large and can produce calls with low dominant frequencies to deter rivals (Meuche et al. 2012). However, some males use alternative, non-calling mating tactics to parasitize advertising territorial males (i.e., satellite males; Meuche and Pröhl 2011). Home-range size of females is larger than that of males (Donnelly 1989b, Pröhl and Hödl 1999, Savage 2002), is independent of density (Donnelly 1989b), and may, in part, provide females access to bromeliads and mates (Murasaki 2010). The species' mating system has been described as sequential polygamy comprising sequential and simultaneous polygyny and sequential polyandry (Pröhl and Hödl 1999).

Data collection

The study site was an abandoned *Theobroma cacao* (hereafter, cacao) plantation system at La Selva. The plantation was dominated by cacao, but also contained *Bactris gasipaes* (pejibaye) and *Cordia alliodora* (laurel) interspersed at regular intervals. The cacao trees were spaced at regular, 3 m intervals at planting, and created a simple and regular environment, even with intermittent taller laurel and pejibaye penetrating the cacao canopy. The plantation activities ended in 1963 when the Organization for Tropical Studies (OTS) acquired the property. I used the cacao system here because plantations generate homogenous terrestrial habitats which provide environmental controls that cannot be found in natural forests (Boucher et al. 1983). Thus, my rationale for using this site was similar to others, who sought to take advantage of the relatively simple understory and homogeneity of the cacao-dominated environment to control for habitat variability while examining how other features influence population ecology of terrestrial vertebrates (e.g., Guyer 1988a, b, Donnelly 1989a, b).

To this end, I established four spatially independent gridded plots (12 m x 9 m) within the cacao system, with individual cacao trees providing a symmetrical grid system of forty-eight individually identifiable 1.5 m x 1.5 m cells within each plot. From February 1982–August 1983, *O. pumilio* were surveyed diurnally in each plot 2–10 times per month (mean = 3.5) using capture-mark-recapture techniques (Donnelly and Guyer 1994). Plots were surveyed by walking in a zig-zag pattern through tree rows, searching for individuals active on the surface of leaf-litter or understory vegetation up to 2 m above the ground. Captured individuals were measured for snout-vent length (SVL; mm) and mass (g), and were classified into two age-class groups: juveniles (< 19 mm snout-vent length [SVL]) and adults (≥ 19 mm SVL). Adults were further identified as male (presence of a darkly pigmented gular sac) or female (possessing red throat coloration; Bunnell 1973, Donnelly 1989c), and capture location was recorded as within a particular grid cell. Each individual was assigned a unique combination of toe clips and marked accordingly to facilitate individual identification during recaptures. When juveniles were recaptured and measured to a size of ≥ 19 mm SVL, individuals were considered to have matured and were categorized as male or female. Each plot was surveyed ten times in April 1982 to obtain a relatively accurate estimate of the number of individuals present in plots; in most other months, plots were surveyed 3–4 times/mo. The study period encompassed seasonal replication of dry and wet seasons (N = 2, respectively); however, weather was characterized by an El Niño event, such that weather conditions were more strongly seasonal than usual for La Selva (e.g., see Guyer 1988a).

Statistical analysis

Capture histories were combined into three–four month intervals throughout the sampling period. Months were pooled to capture seasonal variation in climate and rainfall: the dry season in 1982 (February–May), the first and second half of the wet season spanning 1982 into 1983 (June–September; October–January), the dry season in 1983 (February–May), and the start of the wet season in 1983 (June–August). Individuals were classified as migrants or residents within each plot on the basis of size (an estimate of age), and apparent duration of their presence in a given plot. For adults, I classified individuals as residents if they had been observed in a given plot during the previous season. All juveniles were classified as migrants because they were recently born into the population and had relatively little experience in the habitat they occupied, features similar to individuals migrating to novel habitat. Upon reaching maturity and transitioning to the adult stage class, individuals were classified as residents if they remained within the same plot. This classification system resulted in individuals being labeled as resident adults (resident females [RF], resident males [RM]), recently migrated adults (migrant females [MF], migrant males [MM]), and juveniles (J). As my criteria for classifying migrants and residents was unable to determine the status of adults in the first season, all adults were classified as residents.

We used two versions of the dataset in the analyses: (1) a dataset including all observations of every individual recorded in the four plots (hereafter, full dataset), and (2) a dataset restricted to include individuals captured ≥ 3 times (hereafter, subsetted dataset). The subsetted dataset was used to remove individuals whose tenure in plots was brief (i.e., temporary, non-resident visitors) and was used to elucidate spatial distribution among migrating individuals and residents.

We described seasonal variation in abundance by measuring population structure of *O. pumilio*, and I used the subsetted dataset to calculate the mean number of observed juveniles, females, and males across each plot. I developed five *a priori* candidate models to explain variation in abundance: (1) null model, (2) seasonal variation, (3) variation by age-sex classes (juvenile, female, male groups), (4) group and seasonal variation, and (5) a saturated (full) model with variation by group, season, and a group-season interaction. I used the candidate models to guide construction of linear mixed-effects models explaining variation in observed abundance, with plot assigned as a random effect. I ranked models using Akaike's Information Criterion adjusted for small sample sizes (AIC_c; Hurvich and Tsai 1989), and I used model weight statistics to measure the probability a given model represented the true best model among all candidates (Burnham and Anderson 2002).

To test predictions of the conspecific attraction hypothesis, I first used the subsetted dataset and averaged the two-dimensional capture coordinates for each individual to estimate a mean centroid of space use during each season. I then calculated Clark and Evan's (1954) *R*-value, an index of spatial dispersion that measures the degree to which individuals exhibit a clumped ($R < 1.00$), random ($R \sim 1.00$), or uniform ($R > 1.00$) distribution (Clark and Evans 1954; Krebs 1999) at the seasonal scale. I measured the *R*-value with border correction (Donnelly 1978) for juveniles, migrating females, and migrating males relative to resident females and resident males during each season in each plot.

Next, I sought to analyze space use and co-occurrence patterns at shorter intervals by measuring shared sites between age-sex groups. I estimated the observed proportion of shared sites (1.5 m x 1.5 m grid cells) by dividing the number of sites occupied by ≥ 2 individuals of different migrant-resident classes during each survey by the total number of sites occupied. The proportion of shared sites was measured for the same groups as in the *R*-value analysis using both the full and subsetted datasets.

Last, I sought to examine nearest-neighbor distances (NND; Clark and Evans 1954) among individuals of the migrant-resident groups. Because classic NND can be confounded when true nearest neighbors do not occur within the study area and/or when the study area is irregular in geometry (Cressie 1991), I used an analysis which accounts for edge effects and irregular geometry, the nearest-neighbor distance distribution function $G(r)$ (Cressie 1991). $G(r)$ estimates how density of a static point process increases with distance from a focal point, given complete spatial randomness (CSR), and then compares the random pattern to that of an observed NND distribution function, $\hat{G}(r)$. Analyses where $\hat{G}(r) > G(r)$ indicate that nearest neighbor distances in the observed pattern are shorter than predicted by a random process and suggest clustering. Conversely, $\hat{G}(r) < G(r)$ indicates greater distances among points than expected by random, a uniform pattern. I derived a mean centroid of space use for all individuals in each pooled sample of months using the subsetted dataset, and estimated $G(r)$ and $\hat{G}(r)$ for the same migrant-resident classes as in the *R*-value analysis. Border correction was implemented using the spatial Kaplan-Meier estimator (Baddeley and Gill 1997). To analyze whether individuals exhibited aggregation in all seasons and plots, I performed the Maximum Absolute Deviation test (MAD test; Diggle 1986, Cressie 1991, Loosmore and Ford 2006) with one tail, and used the MAD test statistic as a proxy for aggregation among individuals.

To determine if observed spatial distribution patterns deviated from those expected by CSR, I estimated *R*-values, proportion of shared sites, and $G(r)$ for randomly generated distributions of individuals. Simulated distributions were generated using the same density of migrant-resident classes observed in plots during each sampling unit (season for *R*-values and $G(r)$; individual surveys for proportion of shared sites). Because mean random values varied among simulations, I performed replicate simulations (N = 10) to better approximate true random means. I tested if observed patterns differed from those expected by chance using a paired linear mixed-effect models; to account for some seasonal differences in abundance, season was nested within plot as a random effect in all mixed-effect models. I used the statistical program R

(Program R; R Core Team 2015) for analyses, using functions in the packages *spatstat* (Baddeley et al. 2015) and *nlme* (Pinheiro et al. 2016) and with $\alpha = 0.05$.

My data were collected using a mark-recapture (MR) framework, and my analysis made use of those MR data by inferring the tenure of individuals residency in plots. While this may seem like a limited use relative to more complicated MR analyses which account for imperfect detection to estimate abundance, my primary objectives were not directly focused on estimating abundance, but rather involved modeling spatial distributions. While recent analytical advances have developed spatially-explicit MR analyses (e.g., Efford and Fewster 2013) to estimate density, these models cannot use detection probability to infer individual location and thus do not provide added benefit to the current project. Therefore, I analyzed observed spatial distributions, but I acknowledge that the results may be biased toward describing spatial patterns among individuals or groups within the population characterized by greater detection probability.

RESULTS

The full dataset included 1661 observations of 463 individuals made during the study. Of this total, 189 individuals were captured ≥ 3 times (total capture = 1297); these individuals composed the subsetted dataset. Population structure was generally consistent across seasons and was characterized by strongly female-biased sex ratios (Figure 1). The most well-supported model identified by the model-ranking procedure ($\Delta AIC_c = 0.00$; model weight = 1.00) described abundance as a function of age-sex groups, season, and an interaction age-sex group and season (saturated model; Appendix I). The model described two significant patterns: (1) juveniles and males did not differ in abundance ($P = 0.18$), whereas females were more abundant than both juveniles and males ($P < 0.001$), and (2) female and male abundance decreased in the second half of the 1982 wet season ($P < 0.001$, $P < 0.001$, respectively; Figure 1), whereas juvenile abundance increased in that season ($P = 0.027$; Figure 1).

We observed a significantly clumped spatial distribution in four of the six migrant-resident groups examined (Figure 2). Observed *R*-values for juveniles with resident females (0.81 ± 0.04 S.E.) and resident males (0.86 ± 0.05 S.E.) were both more clumped than that expected by chance ($P < 0.001$, $P = 0.032$, respectively). Migrant females and migrant males were clumped with resident females (0.81 ± 0.04, $P = 0.006$; 0.82 ± 0.04, $P < 0.001$; respectively), whereas both migrant females and migrant males did not clump with resident males (0.87 ± 0.07, $P = 0.12$; 0.93 ± 0.08, $P = 0.55$; respectively; Figure 2). An overall test for differences in *R*-values among the six groups was not significant ($F_{5,107} = 0.71$, $P = 0.62$).

Significant variation in the proportion of shared sites was observed among different migrant-resident classes (Figure 3). Juveniles shared sites with resident females and males more frequently than expected by chance ($P < 0.001$, $P < 0.001$, respectively). Migrant females shared sites with resident females more frequently than expected by chance ($P < 0.001$), but the proportion of shared sites with resident males did not differ from random ($P = 0.052$). Migrant males overlapped more frequently with both resident females and resident males than expected by random ($P < 0.001$, $P < 0.001$, respectively). An overall model testing for differences in proportion of shared sites among the six age-sex groups was highly significant ($F_{5,1138} = 17.60$, $P < 0.001$). Overlap of migrant and resident males was significantly higher than all the other groups ($P < 0.0001$ in each case); in contrast, migrant and resident females overlapped less than all other groups (J-RF, $P = 0.001$; J-RM, $P = 0.002$; MF-RF, $P = 0.013$; MM-RM, $P < 0.0001$), except for migrant males and resident females ($P = 0.076$).

Maximum Absolute Deviation (MAD) tests of $\hat{G}(r)$ and $G(r)$ indicated that the statistical distribution of $\hat{G}(r)$ tended toward clustered nearest-neighbor distances relative to that expected by random (Figure 4) for each of the six migrant-resident groups (J-RF, P = 0.0015; J-RM, P < 0.0001; MF-RF, P = 0.0023; MF-RM, P = 0.001; MM-RF, P = 0.0031; MM-RM, P = 0.0066).

DISCUSSION

The conspecific attraction hypothesis predicts that, across habitats of equivalent quality, naïve juveniles and migrating adults will preferentially colonize and associate in space with pre-established adults to a greater degree than expected by chance. Thus, if *O. pumilio* are attracted to conspecifics, I predicted that, relative to random spatial patterns, migrants entering populations in a relatively homogeneous cacao habitat would (1) be clumped in space with residents, (2) share sites with residents more frequently, and (3) have shorter nearest-neighbor distances to residents. I suggest the results presented here provide evidence consistent with the predictions of the conspecific attraction hypothesis. For the six migrant-resident groups I analyzed, my spatial analyses described significant clumping, increased home-range overlap, and nearest-neighbor distances in four, five, and six of the respective groups considered.

Two non-mutually exclusive hypotheses may explain why *O. pumilio* migrating into a population as juveniles or adults may benefit from close occurrence with established resident adult females and males. First, individuals may perceive conspecifics as cues to habitat characterized by increased resources or home sites of sufficient quality to justify a migrant's propensity to invade a site and/or a resident's propensity to defend a site (conspecific cueing; Stamps 1987). Here, migrating individuals may perceive resident females as cues to areas with access to resources sufficient for survival. In this scenario, spatial association of migrants with residents could confer potential advantages in fitness relative to migrants occupying areas of unknown quality. Whether individuals use conspecifics as strict cues when selecting habitat merits further testing in a more rigorous experimental design (e.g., Stamps 1987); if so, then individuals are predicted to select habitat previously occupied by a conspecific over comparable unoccupied habitat without conspecific cues.

A second hypothesis explaining why migrating *O. pumilio* are attracted to conspecifics is that attraction to conspecifics facilitates social interactions among individuals. Weygoldt (1980) was the first to describe larval provisioning by adult *O. pumilio*, and Brust (1993) described this behavior in detail and determined that larvae are obligatorily oophagous in the field. Pröhl and Hödl (1999) found that maternal investment of *O. pumilio* is generally higher in females than males, that females are selective when choosing mates, and that there is significant variance in reproductive success of males (Pröhl and Hödl 1999); together, these observations suggest that female mate choice is an important factor influencing fitness. Females also have larger home ranges than males (Donnelly 1989b, Pröhl and Hödl 1999), which may increase access to males when selecting mates (Murasaki 2010). If social interactions such as female mate choice are important factors influencing the fitness of *O. pumilio*, then females with behavioral phenotypes that associate more and interact better with neighboring individuals may have greater fitness relative to individuals lacking these traits or exhibiting them to a lesser degree.

Whereas most of the migrant-resident groups analyzed showed results consistent with aggregation, such non-random patterns did not always manifest for migrant males+resident males or migrant females+resident males. Males are the territorial sex at La Selva (Bunnell 1973, Donnelly 1989a), so migrant males may be forced to establish home ranges that avoid aggregation with resident males, an effect that might generate observed random spatial distribution patterns between those groups (Figure 2, Figure 4). However, migrant males shared sites with resident males at a significantly high rate (Figure 3). While males vigorously defend their territories by wrestling other males that enter and call within the territory, non-vocal males are not attacked, and a recent study found evidence for a satellite tactic in which non-calling males parasitize the territories of calling males (Meuche and Pröhl 2011). Therefore, conspecific attraction and satellite mating tactics may explain the high proportion of shared sites observed between migrant and resident males.

Non-random patterns of migrant females and resident males may be driven by mate choice. Female mate choice is a hypothesized mechanism driving the larger home-range size of females (Donnelly 1989b, Murasaki 2010), so migrant females may space themselves more uniformly than relative to resident males. In this scenario, greater spacing relative to males would allow access to more individuals from which to choose during reproduction. This appears to the case in my study, because spatial patterns of migrant females relative to resident males were best characterized by random in all three analyses.

Two studies to date have tested whether conspecific attraction is a viable model explaining habitat selection of frogs. Using chemical cues from predators and conspecifics, Gonzalo et al. (2006) found no evidence that *Pelophylax perezi* respond to chemical cues of conspecifics when selecting habitat; instead they found individuals avoided chemical cues from predators. Similarly, experimental trials of juvenile *Litoria aurea* did not document an effect of chemical conspecific cues on habitat selection, but instead found a significant effect of conspecific presence on habitat selection (Pizzatto et al. 2015). These studies suggest that conspecific attraction in frogs may be driven, at least in part, by visually mediated conspecific cues, more than chemical cues. Because *Oophaga pumilio* use visual cues during mate choice (Summers et al. 1999), visual cues from conspecifics also may provide information for individuals when selecting habitat, particularly for females who do not advertise their presence with vocalization.

Because habitat was relatively homogeneous in the plots we sampled, I assume that the observed signatures of aggregation resulted from conspecific attraction rather than habitat selection for resources. While I acknowledge that, as with any field study, variables which I did not measure may have influenced the observed patterns (e.g., spatial variance in food resources, oviposition sites, or tadpole rearing sites), attributes of the cacao system and the ecology of *O. pumilio* allow us to assume limited effects of confounding variables. Specifically, a predictable pattern of cacao leaf abscission and regular arrangement of trees generated seasonally homogeneous leaf-litter environment in plots, from which I can assume low variance of frog oviposition sites and foraging areas. I did not measure variance in bromeliad abundance, which may have influenced frog space use around tadpole rearing sites (Donnelly 1989a); however, the cacao trees were all planted at the same time plantation, such that I can assume the colonization of primarily epiphytic bromeliads was constrained to be uniform through plots in cacao trees. If individuals metamorphose and enter the landscape within or near parental home ranges, then juvenile settlement might be influenced by parent recognition, either visually as a result of shared experiences during maternal provisioning or chemically through the MHC complex (Brown and Eklund 1994, Villinger and Waldman 2012, Pizzatto et al. 2015). If kin recognition occurs, then juveniles might exhibit preference toward settling into habitat near related individuals, which might partially confound patterns observed in this study. However, mothers are unable to directly discriminate between offspring and unrelated young during maternal provisioning (Stynoski 2009), which suggests that kin recognition is absent in *O. pumilio* and did not influence settlement patterns of juveniles in my study.

Thus, with study limitations in mind, I still interpret my results from as preliminary support for conspecific attraction in *O. pumilio*. I believe my results represent necessary conditions of conspecific attraction; if these patterns had not been observed, I would have been able to reject the hypothesis. However, my analysis does not provide provide a sufficient demonstration of conspecific attraction. I contend my study is a productive exercise in science, but a future experimental approach with rigorous controls is needed to provide a sufficient test of conspecific attraction in *O. pumilio* (e.g., Stamps 1987).

CONCLUSION

The conspecific attraction hypothesis predicts that, across habitats of equivalent quality, naïve juveniles and migrating adults will preferentially colonize and associate in space with pre-established adults to a greater degree than expected by chance. Here I use a large spatially and temporally replicated dataset to from homogenous cacao plantations at La Selva to demonstrate that juvenile and migrating adult *O. pumilio* exhibited home-range centroids, home-range overlap, and nearest-neighbor distances that are consistent with necessary predictions of conspecific attraction in a field setting. Conspecific attraction may benefit migrants by providing cues to suitable home sites, reducing costs associated with prospection, and increasing potential for social interactions with conspecifics; these benefits should outweigh the negative effects of other factors associated with aggregation, such as resource competition, predator attraction, and/or pathogen transmission. This study provides support for conspecific attraction in a field setting, and underscores that conspecific attraction may be a relevant mechanism for models of anuran population ecology in the Neotropics.

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Figure 1. Seasonal variation in population structure of *Oophaga pumilio* in replicate plots (N = 4) of *Theobroma cacao* (cacao) plantations at La Selva Biological Station, Costa Rica. Histograms represent mean (± 1 S.E.) abundances of individuals observed ≥3 times. Apparent population structure was consistent across plots, with female-dominated adult sex ratios and comparable abundance of juveniles and adult males.

Figure 2. Spatial arrangement of migrant and resident *Oophaga pumilio*, as described by Clark and Evan's (1954) *R*-value (mean ± S.E.) with border correction, in a cacao plantation environment at La Selva, Costa Rica. Values < 1.00 indicate a clumped distribution pattern (bottom gray hash), values ~ 1.00 indicate a random distribution (complete spatial randomness [CSR] – black hash), and values > 1.00 indicate a uniform distribution pattern (top gray hash). Groups are juveniles with resident females (J-RF) and resident males (J-RM), migrant females with resident females (MF-RF) and resident males (MF-RM), and migrant males with resident females (MM-RF) and resident males (MM-RM). Asterisks (*) indicate groups that deviated significantly from complete spatial randomness (CSR; black hashed line).

Figure 3. Home-range overlap as measured by the proportion of shared sites by two or more individuals of migrant and resident *Oophaga pumilio* in a cacao plantation at La Selva, Costa Rica. Asterisks (*) indicate groups that deviated significantly from random. Groups defined as in Figure 2.

Figure 4. Maximum Absolute Deviance (MAD) test statistics from nearest-neighbor distance distribution functions *G(r)* among (1) migrant and resident individuals of *Oophaga pumilio* observed in cacao plantations at La Selva Biological Station Costa Rica, and (2) those generated

by random. Asterisks (*) indicate when observed MAD statistics (dark grey) deviated significantly from randomly simulated data (light grey). Groups defined as in Figure 2.

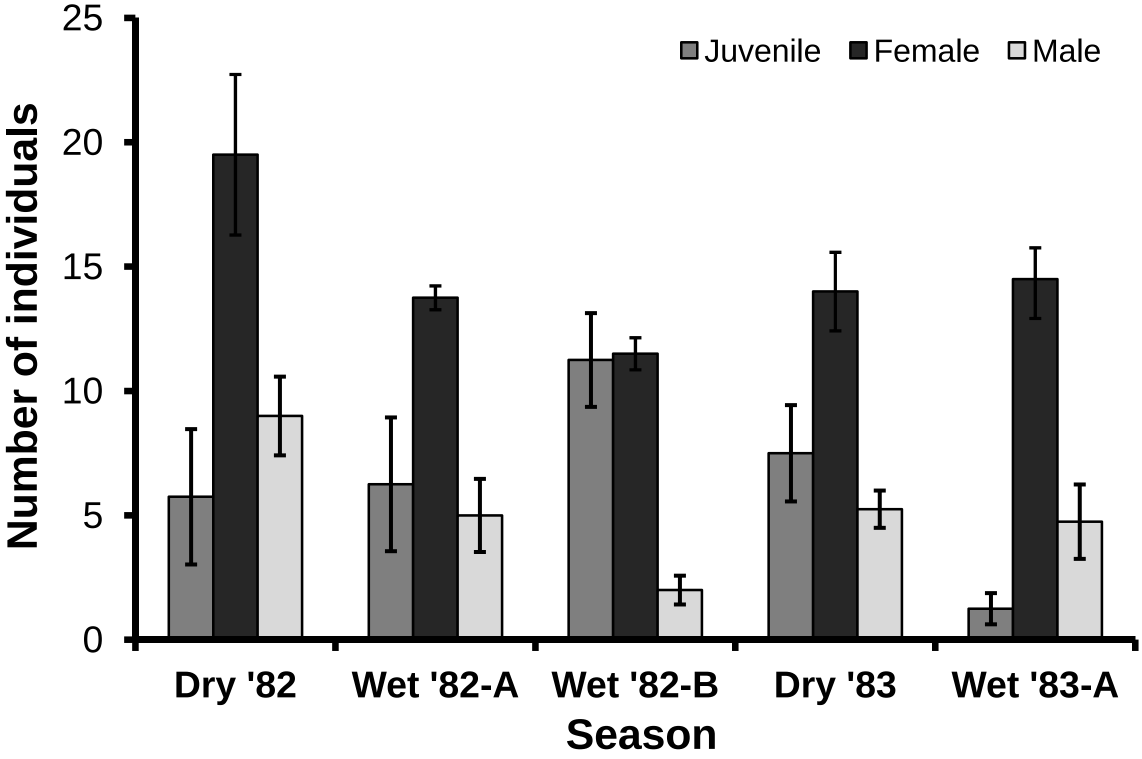
25
20
15
10
5
0
Number of individuals
Juvenile
Female
Male
Dry '82
Wet '82-A
Wet '82-B
Dry '83
Wet '83-A
Season

Figure 1

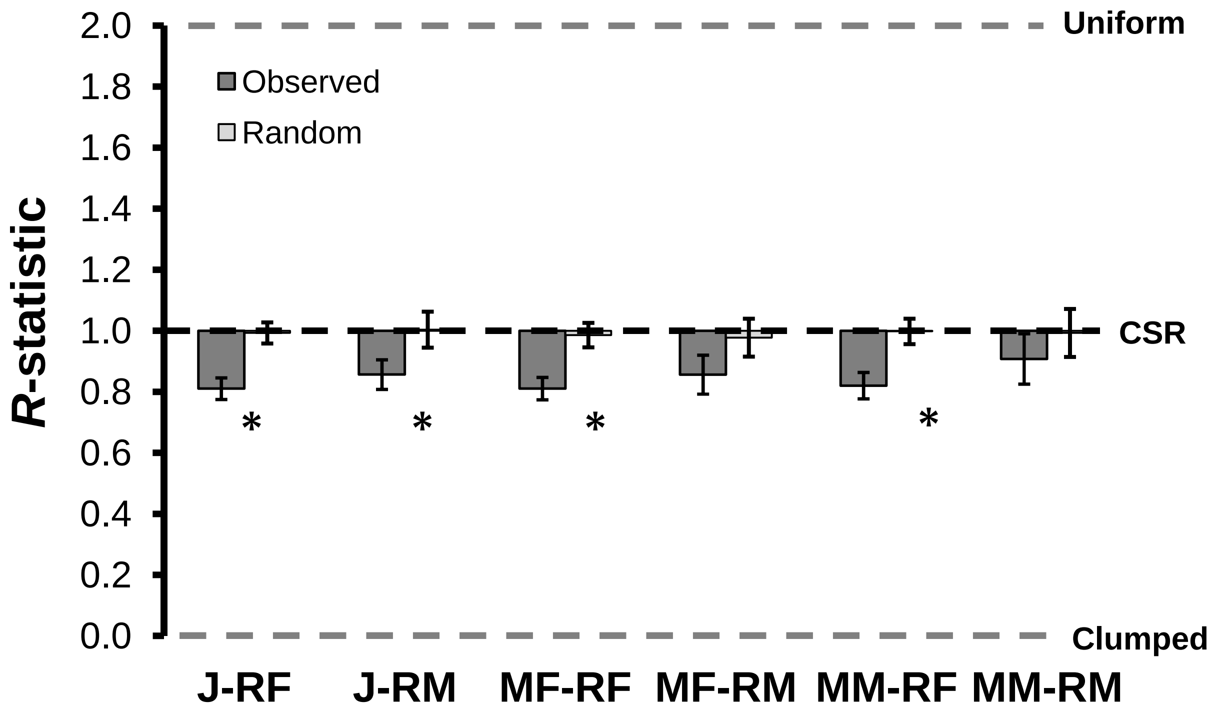
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
R-statistic
Uniform
CSR
Clumped
Observed
Random
*
*
*
*
J-RF
J-RM
MF-RF
MF-RM
MM-RF
MM-RM

Figure 2

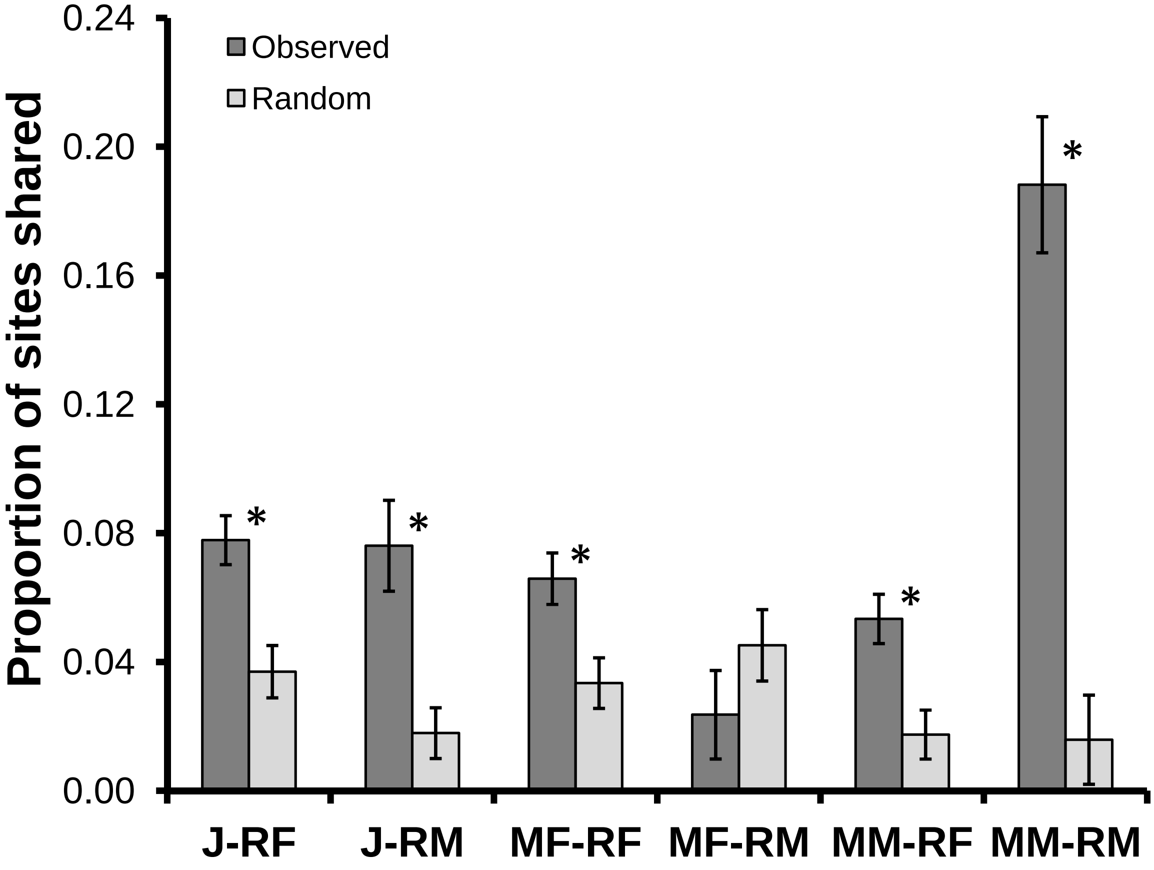
0.24
0.20
0.16
0.12
0.08
0.04
0.00
Proportion of sites shared
▨ Observed
☐ Random
*
*
*
*
*
J-RF
J-RM
MF-RF
MF-RM
MM-RF
MM-RM

Figure 3

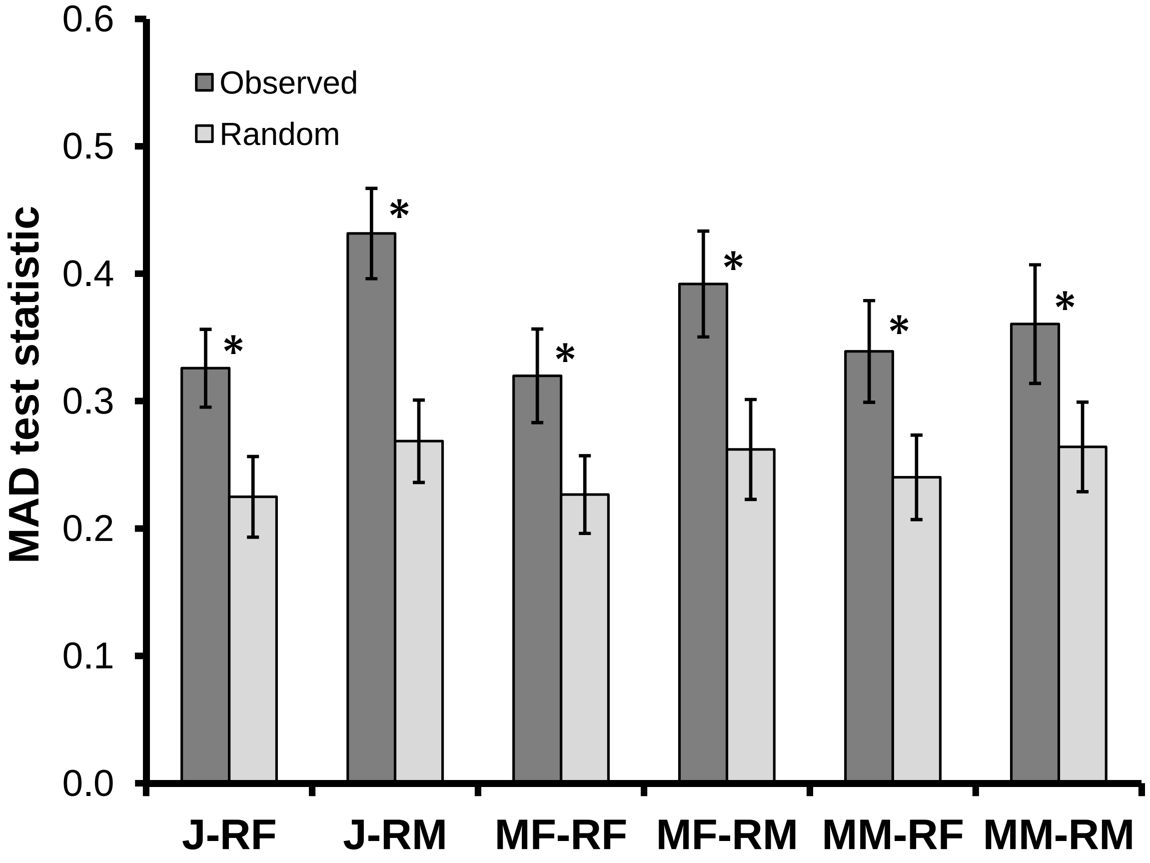
0.6
0.5
0.4
0.3
0.2
0.1
0.0
MAD test statistic
Observed
Random
*
J-RF
J-RM
MF-RF
MF-RM
MM-RF
MM-RM

Figure 4

Appendix I. Candidate linear mixed-effects models explaining variation in observed abundance of *Oophaga pumilio* in cacao plantations at La Selva Biological Station, Costa Rica. The most well-supported model ($\Delta AIC_c = 0.00$; model weight = 1.00) described abundance varying as a function of age-sex groups (juvenile, female, male), season, and a group-season interaction.

Model	K	AIC_c	ΔAIC_c	Model weight	Log-likelihood
Group + Season + Group*Season	17	308.60	0.00	1.00	-130.02
Group+Season	9	336.53	27.93	0.00	-157.46
Group	5	344.44	35.84	0.00	-166.67
Season	7	379.85	71.25	0.00	-181.85
Null	3	387.21	78.61	0.00	-190.39

Chapter 5

Conclusion

In this dissertation, I evaluated three hypothetical models of population regulation for three frog and lizard species which occur on the forest floor at La Selva Biological Station and other lowland wet tropical forests in Central America. In particular, my conceptual framework tried to reconcile and integrate these three hypothetical mechanisms – bottom-up limitation by resources, top-down limitation by predators, and parallel regulation through conspecific attraction (Hunter and Price 1992, Laundré et al. 2014).

First, I performed an experimental study to test the litter-mosaic hypothesis, a conceptual model where frog and lizard abundance is bottom-up regulated by leaf abscission of deciduous trees, mediated by tree-driven seasonal variance in microhabitat and food resources (Guyer 1988). I tested the litter-mosaic hypothesis by studying the seasonal abundance of leaf litter, terrestrial arthropods, frogs (*Craugastor bransfordii*, *Oophaga pumilio*), and lizards (*Norops humilis*) beneath two tree species with different patterns of leaf-drop abscission, *Castilla elastica*, *Dipteryx panamensis*. I also experimentally manipulated leaf abscission beneath *C. elastica* with litter supplementation. I observed strong seasonal patterns of leaf litter, arthropods, and vertebrate abundance beneath trees in forest, but these patterns did not vary by tree species in ways anticipated by the litter-mosaic hypothesis. Seasonal abundance of vertebrates also did not correlate strongly with seasonal patterns of terrestrial litter. Experimental supplementation of litter was consistent with the litter-mosaic hypothesis by driving elevated abundance of the anole *N. humilis* in manipulated *C. elastica* plots relative to controls, due to demographic shifts in either apparent survival, immigration, or recruitment; however, the frogs *C. bransfordii* and *O.*

pumilio did not respond similarly. Thus, my experimental results suggested the litter-mosaic hypothesis can be refined and restricted to describing spatiotemporal variance of terrestrial anoles, while excluding frogs.

Second, I evaluated whether an assemblage of predatory spiders (Ctenidae) exerted predictable effects on prey frogs and lizards, again using *C. bransfordii*, *O. pumilio*, and *N. humilis*. In particular, I provided an explicit test of the mainland-island model of anole population regulation (Andrews 1979), which predicts the anole populations – and, by extension, frogs – are more strongly regulated by predators than food resources in Central America. By modeling the relative contribution of food, microhabitat, and predatory spiders to frog and anole occupancy, I found frog occupancy was most strongly influenced by predators, an effect which increased at lower levels of leaf litter. However, anoles occupied sites independent of predators, an observation inconsistent with the mainland-island model. All species were positively associated with leaf litter and had elevated detection probability when predators were present; the latter effect was also inconsistent with predictions of the mainland-island model. My modeling results joined those of two experiments demonstrating food limitation of mainland anoles and predator limitation of island anoles (Guyer 1988, Schoener et al. 2002) which are also inconsistent with the mainland-island model. Thus, my results added to persistent evidence rejecting the mainland-island model of anole population regulation, which suggests that mainland and island systems may be regulated more similarly than previously acknowledged. I hypothesized that behavioral decisions by mainland anoles may be effective at reducing predation pressure from predatory spiders, until other resources become limiting.

Third, in an attempt to understand how interspecific interactions influence population ecology of the leaf-litter frog and lizard assemblage, I tested whether patterns of spatial dispersion among migrant and resident *O. pumilio* were consistent with predictions of the conspecific attraction hypothesis (Stamps 1988). I used eighteen months of mark-recapture observations from a homogenous, fallow cacao plantation, a habitat characterized by relatively equivocal habitat quality which served as an environmental control. Using three measures of spatial association across two temporal time scales, I found that juveniles and migrant adults exhibited spatial patterns of association with resident adults in ways consistent with necessary predictions of conspecific attraction. Conspecific attraction may benefit migrant *O. pumilio* by providing cues to suitable home sites and/or increasing potential for social interactions with conspecifics; if true, these benefits should outweigh the negative effects of other factors associated with aggregation. My study is consistent with conspecific attraction in *O. pumilio* and provides rare support from a field setting that conspecific attraction may be a relevant mechanism for models of anuran spatial ecology. Future work should provide experimental tests of the conspecific attraction model in Central American forests, using both anuran and anole species. Because the conspecific attraction hypothesis was generated from studies of the island anole *Dactyloa aenea*, the model may be particularly applicable to anoles in this ecosystem.

Predator-prey models described an effect where the spider-frog interactions decreased with increasing leaf-litter depth, and this effect has consequences for understanding models of amphibian abundance in a few ways. First, because the abundance of terrestrial leaf litter is strongly seasonal in lowland Caribbean wet forests, the relationship between litter and predator-prey interactions also has implications for understanding seasonal abundance cycles at La Selva. Because models suggested that predator-prey interactions vary across a gradient of leaf-litter abundance, ctenid spiders may exert greater effects on terrestrial frogs during periods of low leaf litter during the wet season, potentially when frogs have fewer escape retreats in litter. Thus, predator-prey interactions can be incorporated into the litter-mosaic model (Guyer 1988). Second, because terrestrial frog populations have declined by 75% over the last four decades at La Selva Biological Station, a decline which has been linked to climate-driven decreases in standing leaf litter (Whitfield et al. 2007), my results also implicate predator-prey interactions as a potential mechanism involved in amphibian declines at La Selva and other similar sites in Central America. Models of resource-driven amphibian declines (Whitfield et al. 2016) should consider how altered predator-prey relationships may influence population and community dynamics in such ecosystems. Last, and perhaps most significantly, predator-prey modeling results provided an explicit test of predator effects on terrestrial frogs and lizards, while also integrating conceptual models of bottom-up and top-down regulation for frogs at La Selva for the first time.

A previous 16-mo experimental manipulation of leaf litter at La Selva Biological Station found leaf litter to regulate *C. bransfordii*, *O. pumilio*, and *N. humilis* (Whitfield et al. 2014), but my experimental supplementation of litter beneath *C. elastica* trees only regulated abundance of *N. humilis*. My results may have differed from those of Whitfield et al. (2014) because of the differing temporal scale of litter manipulation. While Whitfield et al. (2014) manipulated litter continually over a 16-mo period, I supplemented litter in a pulse that had an approximately 3-mo effect on the terrestrial litter layer (Chapter 2); this was meant to simulate leaf abscission from single canopy trees in an explicit test of the litter-mosaic hypothesis (Guyer 1988). However, comparison of my design and results to those of Whitfield et al. (2014) refines our understanding of leaf-litter regulation of the terrestrial frog and lizard assemblage. Specifically, the differences between these two litter manipulation experiments suggest that the regulatory effects of leaf litter vary at a temporal scale, such that short temporal increases in leaf litter due to the leaf abscission of single-canopy trees may not represent strong enough pulses of resources to increase the abundance of the frogs *C. bransfordii* and *O. pumilio*.

My results from Chapter 2 supported the importance of leaf litter and leaf-drop phenology in regulating populations of the anole *N. humilis*, but not necessarily because of increased food resources for *N. humilis*. Monthly variation in population growth was best explained by seasonality and was not strongly correlated with seasonal abundance of leaf litter or arthropod food resources. Experimental supplementation of litter beneath *C. elastica* drove elevated leaf litter, arthropods, and *N. humilis*; thus, increases in anoles may have been driven by litter, arthropods, or both. When Guyer (1988) supplemented food for *N. humilis*, he observed a doubling of population size in food supplemented populations relative to controls; however, both treatment groups experienced significant seasonal variation in anole abundance, similar to that observed here (Chapter 2). Thus, seasonality appears to be contributing to variation in abundance of *N. humilis* in ways that remain poorly understood.

In Chapter 2, I observed strongly seasonal variation of terrestrial leaf litter which did not correlate with abundance of entire frog and anole populations in plots (192 m^2) around trees, a result which ostensibly runs counter to a large literature describing a positive relationship between litter and abundance of terrestrial herpetofauna (see Whitfield et al. 2014, and citations therein). However, I did recover a positive relationship between litter and abundance of all three focal vertebrates in Chapter 3, where site occupancy in individual grid cells (9 m^2) was positively related to litter abundance. My interpretation of the disparity between these results is as follows. In Chapter 2, abundance of populations in plots may have been characterized by significant spatial heterogeneity, which may have been driven by strong heterogeneity of leaf litter; however, my analysis assumed that plots were characterized by a relatively homogeneous terrestrial environment and did not account for potential heterogeneity. Alternatively, in Chapter 3, I estimated abundance of focal vertebrates at a much more local scale, by estimating site occupancy in individual grid cells within plots around trees. My analysis in Chapter 3 was much less likely to be characterized by strongly heterogeneous litter profiles, and observations of site occupancy were paired directly with measures of leaf-litter abundance. Because paired data are much stronger at resolving true relationships between variables relative to unpaired data, I believe the positive relationship observed between litter and vertebrate site occupancy observed in Chapter 3 reflects the true positive relationship between those variables that Chapter 2 was unable to recover. Thus, I point toward the results from Chapter 3 as being consistent with the large literature describing the positive relationship between leaf litter and abundance of terrestrial frogs and lizards in Neotropical wet forests.

In conclusion, my results contribute to our understanding of population regulation and patch dynamics for terrestrial frogs and lizards in Neotropical wet forests. My experimental results suggest that *N. humilis* populations respond to pulses of terrestrial litter in ways consistent with the litter-mosaic hypothesis, but the *O. pumilio* and *C. bransfordii* did not. Dispersal of *O. pumilio* through the landscape may be driven in part by conspecific attraction; because other studies have demonstrated conspecific attraction for anoles in Caribbean islands, future studies should test whether that mechanism is relevant for mainland anoles as well. Because predatory spiders exerted stronger effects on the occupancy of terrestrial frogs at low levels of terrestrial litter, seasonal declines in frog abundance during the wet season may be driven in part by elevated predation interactions when leaf litter is scarce. Predator-prey models reject a large literature invoking predation as the dominant force shaping ecology of diverse mainland anoles, and suggested similar mechanism may regulate the ecology and evolution of mainland and island anoles.

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Vita

Brian Patrick Folt was born on 20 November 1988 in Akron, Ohio, and grew up living in Rochester Hills, Michigan and northeastern Ohio. After graduating from Hudson High School in 2007, he enrolled at Ohio University, where he was supported in part by a Gateway Excellence Scholarship. He spent the summer of 2010 studying tropical ecology at La Selva Biological Station, Costa Rica, with an emphasis on amphibians and reptiles; that experience was particularly formative. After graduating from Ohio University in 2011 (B.S., Biological Sciences, *cum laude*), he enrolled in graduate school at Auburn University, where he continued studying ecology. After graduate school, he hopes to continue learning about the natural history of tropical and temperate organisms.