ORIGINAL PAPER

Leaf-litter herpetofaunal richness, abundance, and community assembly in mono-dominant plantations and primary forest of northeastern Costa Rica

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Abstract Given current deforestation and land-use change in species-rich tropical forests, a pressing need in conservation biology is to understand how converted, human-modified landscapes support biodiversity. Here, we measured the species richness, abundance, and community composition of amphibians and reptiles in reference primary forest and mono-dominant plantations of three native tree species (*Pentaclethra macroloba*, *Virola koschnyi*, *Vochysia guatemalensis*) at La Selva Biological Station in the Caribbean lowlands of northern Costa Rica. Because these plantation species generate markedly different forest-floor habitats, we hypothesized that tree species would support different assemblages of leaf-litter herpetofauna. Primary forest, *Virola*, and *Vochysia* supported greater richness of frogs than *Pentaclethra*. Frog densities were significantly lower in *Pentaclethra* and *Vochysia* than in nearby primary forest. Using non-metric multidimensional scaling and permutational multivariate analysis of variance, we found *Pentaclethra* to support significantly different assemblages of frogs and lizards than primary forest reference sites, while *Vochysia* supported a unique assemblage of frogs. Our results suggest that some tree species plantations can support herpetofaunal assemblages comparable to primary forest in richness, community assembly, and abundance. While herpetofaunal community ecology varies among plantation species, our study provides a compelling example of how plantation landscapes can facilitate the restoration of native fauna on degraded landscapes.

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Introduction

Current changes in tropical forests are an alarming concern for the maintenance of high tropical species richness (Bradshaw et al. 2009; Bickford et al. 2010). Tropical forests have undergone enormous deforestation in the last century (Sodhi et al. 2010), with the rate of tropical deforestation higher in Central and South American than anywhere else (Bradshaw et al. 2009). With intact tropical forests rapidly shrinking due to anthropogenic pressures, a pressing question in conservation biology asks how species respond to increasingly disconnected, human-modified landscapes, such as urban or agricultural areas (Bawa and Seidler 1998; Chazdon et al. 2009; Gardner et al. 2009).

Tropical land use in the form of plantations grew by a factor of four throughout the 1980s (Lugo 1997), and plantations have emerged as an increasingly important component of tropical forest cover. While plantations provide economic benefits such as lumber and pulp, they also generate beneficial ecosystem services by storing atmospheric carbon, reforesting degraded areas, creating buffer zones between natural forests and non-forest areas, and decreasing fragmentation among forest patches (providing important dispersal corridors) (Hartley 2002). Therefore, plantations can support local fauna and conserve tropical biodiversity, yet the degree to which certain plantation types support a fauna is variable. Given trends in deforestation and fragmentation, future tropical landscapes will likely comprise highly fragmented mosaics with a significant proportion of plantations. Thus, understanding how different plantations support regional biodiversity has strong implications for the sustainable conservation of diverse tropical faunas (Hartley 2002; Gardner et al. 2007a; Bhagwat et al. 2008).

Amphibians are currently one of the most imperiled vertebrate groups on the planet with over 43 percent of species in decline (Stuart et al. 2004). Because habitat loss is the major factor contributing to declines in the tropics (Alford and Richards 1999; Blaustein and Kiesecker 2002; Collins and Storfer 2003; Cushmann 2006; Gardner et al. 2007a), understanding how converted landscapes such as plantations support amphibian diversity is vital for the conservation of amphibians. Most studies in temperate and sub-tropical systems have found plantations to support fewer amphibians and reptiles species than nearby primary forest controls (Gardner et al. 2007a), yet most of the studies cited (5/7) focus on non-native tree species. Conversely, half of the studies of native-species plantations (2/4) found plantations to support an equal or greater richness than nearby reference sites. These studies suggest that native tree species plantations may support more species-rich amphibian and reptile assemblages than non-native ones, a disparity that has been noted in general for other taxa (Hartley 2002). However, few studies have addressed herpetofaunal ecology on native tree species plantations; thus, more work is needed to understand the relative value of native and exotic plantation species for the conservation of imperiled tropical amphibians and reptiles.

Within this study, we used a randomized block design of native tree species monocultures and a reference primary forest to analyze amphibian and reptile ecology and conservation in plantation habitats in the Caribbean lowlands of northern Costa Rica. We compared species richness, abundance, and measures of community composition to

examine how leaf-litter herpetofaunal assemblages varied in reference forest and mono-culture plantations of three tree species: *Pentaclethra macroloba* (Fabaceae), *Virola koschnyi* (Myristicaceae), and *Vochysia guatemalensis* (Vochysiaceae). We hypothesized that plantation tree species would support different assemblages of leaf-litter herpetofauna, because these tree species differ in the mass, chemical composition, and dynamics of forest-floor leaf litter (Raich et al. 2007; Russell and Raich 2012) and in the quantity and chemical composition of soil organic carbon (Russell et al. 2007), important microhabitat factors for herpetofauna (Watling 2005; Whitfield and Donnelly 2006). We used herpe-tofaunal community assembly to make inferences about faunal restoration, ecosystem function, and the relative conservation value of tree species monocultures—alone or as mosaics—for the conservation of tropical amphibians and reptiles.

Materials and methods

Study sites

La Selva Biological Station (hereafter La Selva) is a private reserve owned by the Orga-nization for Tropical Studies (OTS; 10.42°N, 84.02°W). La Selva is located in the Caribbean lowlands of northeastern Costa Rica. Elevation ranges from 30 to 135 m asl. La Selva has an average temperature of 25.8 °C, receives approximately 4,000 mm of rainfall annually (Sanford et al. 1994), and falls within Holdridge's Tropical Wet Forest life zone (McDade and Hartshorn 1994). La Selva is 1,600 hectares in area, of which 1,170 are old growth. Single hectare plots in primary forest can have 79–107 tree species. The under-story is dominated by palms (Hartshorn 1972, 1983; Lieberman and Lieberman 2007). La Selva is surrounded on three sides by a highly fragmented landscape, including secondary forest, pasture, and banana, pineapple, and tree plantations (Bell and Donnelly 2006).

In 1988, experimental plantations were planted on grazed pastureland that OTS acquired adjacent to the La Selva reserve (ECOS project; Russell et al. 2007). Four replicate blocks were subdivided into eleven 50 m × 50 m treatment plots of tree species monocultures plus one plot left as an unplanted control. A nearby control block of primary forest was also divided into 12 equivalently sized plots that have been used as reference sites for comparison to the plantations. Each of the five blocks are situated <100 m from each other and the Río Peje, and <200 m from primary forest. Regeneration within the treatments was allowed to occur naturally after overstory canopy closure was achieved at 3–4 years (A.E. Russell, pers. comm.). Because diverse flora have colonized the planta-tions but the treatments are still dominated by a single tree species, we refer to the treatments as mono-dominant plantations hereafter. The soil type is classified as Mixed Haplic Haploperox on all five blocks (Kleber et al. 2007); it is acidic and highly leached but also contains a relatively high amount of organic matter (Russell et al. 2007).

Study species

The three study tree species are *Pentaclethra macroloba*, *Virola koschnyi*, *Vochysia guatemalensis*; each species is hereafter referred to by its genus name. All three species are evergreen angiosperms that extend into the upper canopy of lowland forests upon matu-ration. The species vary in their respective abundances in La Selva. *Pentaclethra*, an N_2-fixing species (Hartshorn 1972), is the most common tree species at La Selva, which is particularly dominant on old alluvial soil, residual soils derived from basalt, and in swamps

(Lieberman and Lieberman 2007). *Vochysia* and *Virola* occur on flat alluvial terraces, older oxisol plateaus, and older oxisol slopes at La Selva, the former being two to three times more abundant than the latter (O. Vargas, pers. comm.). *Pentaclethra* and *Virola* have no significant leaf-drop event throughout the year (Frankie et al. 1974); similar phenology data are not available for *Vochysia* to our knowledge.

Sampling methods

From 28 June 2010 to 27 July 2010, we used modified diurnal visual encounter surveys (VES; Crump and Scott 1994, sensu von May et al. 2010, classical transects sensu Lovich et al. 2012) to survey plots for reptiles and amphibians. Samples were taken between 0800 and 1500 h. Transect samples were taken within 36 m × 36 m subplots in the center of each tree plot to control for edge effects. Two surveyors walked slowly along each side of three pre-determined 108 m transect lines (432 m^2 per transect) in a given sub-plot. The VES transects were both area- (4 m × 108 m) and time-constrained to a minimum of 1 h per transect. The two observers sampled 2 m to either side of a transect line and on any substrate up to 2 m off the ground. We recorded and attempted to capture all animals encountered, with the exception of venomous snakes. We identified all captures with respect to species, location, sex, perch type, perch height, and snout-vent length. We marked animals during the first sampling block; mark-recapture rates were low in adjacent transects (<1 %); therefore, transects were considered independent of each other and pseudoreplication was avoided. Block and transect sampling order were randomly generated using a Random Number Table (in Heyer et al. 1994). As a result of extreme topographic variation, sampling in the *Pentaclethra* treatments of Blocks 2 and 3 were limited to two transects instead of three.

Diurnal visual encounter surveys are an effective method to sample leaf-litter herpetofauna, such as Craugastoridae and Dactyloidae, given time and labor constraints (Doan 2003; Crump and Scott 1994; Pearman et al. 1995). Because amphibians and reptiles are often characterized by low detection probabilities (Mazerolle et al. 2007), it is highly unlikely that this sampling method provided absolute estimates of abundance. While it would have been desirable to better understand the extent to which our method estimated abundance relative to true values, such "hard" validation methods are destructive (e.g. fenced leaf-litter quadrat sampling; Rodda and Campbell 2002; Heatwole 2012), and we wanted to avoid disturbing ongoing long-term studies occurring in the ECOS plantations (e.g. Russell and Raich 2012). However, because we used the same sampling method on all study plots and any sampling biases were conserved throughout, we believe our methods collected sufficient data to evaluate our goals.

Statistical analyses

Because leaf-litter amphibians and reptiles have distinct life-history strategies (Gibbons et al. 2000), we performed separate statistical analyses for these taxa (sensu Gardner et al. 2007a). We compared species richness with the number of species observed by calculating an estimated total richness—Chao1, an abundance-based nonparametric estimator. We assessed sampling completeness by calculating the number of species observed as a percent of the estimated total richness. The Chao1 species richness estimates were calculated using the program EstimateS (Gotelli and Colwell 2001; Colwell 2004).

We compared herpetofaunal densities using Kruskal–Wallis rank sum tests; pairwise post hoc comparisons of median density were performed using Wilcoxon rank-sum tests

with sequential Bonferroni correction of p-values (Rice 1989) to adjust for multiple comparisons. Kruskal–Wallis and Wilcoxon rank sum tests were performed in the statistical program R version 2.12.1 (R; R Development Core Team 2011).

To compare patterns of community assembly, we first plotted species rank-abundance curves. We identified indicator species by quantifying the fidelity and relative abundance of species within each treatment (Dufrêne and Legendre 1997). Statistical significance was determined with 1000 Monte Carlo simulations. We then used non-metric multidimensional scaling (NMDS) plots based on Jaccard's-shortest dissimilarity measure to visualize the similarity of assemblages on a non-metric scale. NMDS is an ordination technique that uses a dissimilarity measure to represent samples as points in low-dimensional space. To evaluate the accuracy of the ordination, we used a stress function ranging from 0 to 1, where values <0.20 suggest that ordination accurately represents the dissimilarity among samples. For each plantation treatment and primary forest, we plotted ordination ellipses based on the 95 % confidence intervals of each treatment's centroid. We used permutational multivariate analysis of variance (PERMANOVA) to evaluate dissimilarity of species presence/absence and abundance data. To determine the specific relationships between each treatment pair, we ran six pair-wise PERMANOVAs with sequential Bonferroni correction of P values (Rice 1989) for both frogs and lizards. Transects that recorded zero lizards were removed to facilitate analyses. The indicator species analysis, NMDS, and PERMANOVA were performed using the packages 'labdsv' and 'vegan' in R.

Results

Among three plantation types and the primary forest, 770 amphibians and reptiles were captured and identified representing 20 species. Total observed species richness ranged from 9 to 14 within treatments and primary forest (Table 1). In general, the Chao1 species richness estimator predicted *Vochysia* to support more species-rich assemblages of frogs and lizards than the other tree species and primary forest; conversely, Chao1 predicted *Pentaclethra* and *Virola* to support assemblages that were less species rich than *Vochysia* and primary forest. Because the observed species richness was >70 % of the Chao1 total richness estimates for frogs and lizards in the majority of our study treatments (Table 1), we considered our sampling methodologies to be a relatively accurate representation of these faunas. We captured few snakes, a group characterized by extremely low detection probability (Steen et al. 2012); thus, we did not include them as a separate group in the analyses.

The plantation treatments and primary forest differed significantly in median density of frogs (K = 14.024, df = 3, $P = 0.003$) and lizards (K = 9.448, df = 3, $P = 0.03$, Fig. 1). Frog median density in primary forest (mean ± SD: 19.6 ± 8.6 ind/100 m^2) was significantly higher than that for *Pentaclethra* (9.5 ± 7.2 ind/100 m^2; W = 15.5, $P = 0.004$) and *Vochysia* (10.7 ± 6.1 ind/100 m^2; W = 17.5, $P = 0.002$). Lizard median density in *Pentaclethra* (1.2 ± 1.1 ind/100 m^2) was significantly lower than that for *Vochysia* (3.9 ± 2.6 ind/100 m^2; W = 22, $P = 0.02$) and primary forest (3.9 ± 3.3 ind/100 m^2; W = 23.5, $P = 0.02$); however, after P value adjustment, these results were not significant. The overall herpetofaunal density recorded in primary forest samples (5.8 ± 2.6 ind/100 m^2) was similar to recent measures in a long-term study at La Selva which employed diurnal quadrats as the sampling method (ca. 4.75 ind/100 m^2; Whitfield et al. 2007).

Table 1 Species of amphibians and reptiles and number of individuals collected in each treatment (*PEMA Pentaclethra macroloba*, *VIKO Virola koschnyi*, *VOGU Vochysia guatemalensis*), primary forest, and the summed total

Taxa	PEMA	VIKO	VOGU	FOR	Total
Frogs					
Bufonidae					
Rhaebo haematiticus	0	3	1	2	6
Craugastoridae					
Craugastor bransfordii	19	93	38	136	286
Craugastor fitzingeri	0	1	0	0	1
Craugastor mimus	1	4	5	17	27
Craugastor noblei	0	0	1	0	1
Craugastor talamancae	0	1	0	5	6
Dendrobatidae					
Oophaga pumilio	71	66	71	69	277
Eleutherodactylidae					
Diasporus diastema	0	0	1	0	1
Hylidae					
Scinax boulengeri	0	0	0	1	1
Strabomantidae					
Pristimantis cerasinus	3	9	3	5	20
Pristimantis ridens	1	0	8	1	10
Number of species	5	7	8	8	11
Number of individuals	95	177	128	236	636
Chao1 richness	6	8	11	10	
Percent completeness	83.3	87.5	72.7	80.0	
Lizards					
Corytophanidae					
Corytophanes cristattus	0	0	0	1	1
Dactyloidae					
Norops carpenteri	1	0	1	0	2
Norops quaggulus	3	9	28	31	71
Norops limifrons	8	15	17	12	52
Teiidae					
Ameiva festiva	0	0	1	3	4
Number of species	3	2	4	4	5
Number of individuals	12	24	47	47	130
Choa1 richness	3	3	5	4.5	
Percent completeness	100.0	66.7	80.0	88.9	
Snakes					
Colubridae					
Pseustes poecilonotus	1	0	0	0	1
Dipsadidae					
Imantodes cenchoa	0	1	0	0	1
Rhadinaea decorata	0	0	0	1	1
Viperidae					

Table 1 continued

Taxa	PEMA	VIKO	VOGU	FOR	Total
Porthidium nasutum	0	0	1	1	2

Summaries including total species, total abundance, Chao1 richness estimates, and percent for frogs and lizards are provided for frogs and lizards below those sections. Chao1 richness was calculated with EstimateS (Colwell 2004)

We found differences in species abundance distributions among plantation treatments and primary forest, as illustrated by rank-abundance curves (Fig. 2). We found more abundant species (i.e. species with >10 individuals) in *Vochysia* and primary forest than in *Pentaclethra* and *Virola*. The two most abundant species in *Virola* and primary forest were *Craugastor bransfordii* and *Oophaga pumilio*, respectively; however, this order reversed in *Pentaclethra* and *Vochysia*. If the species rank abundance curves are used as a measure of community assembly, then the relatively uneven diversity distribution of *Pentaclethra* is distinct from the other treatments. Five species were found to be significantly characteristic of the study treatments. *Pristimantis ridens* was characteristic of *Vochysia* plots ($P = 0.018$), while *Craugastor bransfordii* ($P = 0.002$), *Craugastor mimus* ($P = 0.013$), *Craugastor talamancae* ($P = 0.042$), and *Norops quaggulus* ($P = 0.010$) were characteristic of reference primary forest plots.

We found that frog and lizard assemblages were dissimilar among treatments in this study, as 95 % confidence intervals of NMDS cluster centroids showed separation between *Pentaclethra* and primary forest (Fig. 3). The frog assemblages recorded a stress of 0.11 after 11 iterations at three dimensions, while the lizard assemblages reached a stress of 0.06 after 3 iterations at two dimensions. *Pentaclethra*, *Virola*, *Vochysia*, and primary forest differed significantly in community assembly of frogs and lizards (Table 2). Within frogs, pairwise PERMANOVAs revealed significantly different assemblages between *Pentaclethra* and *Virola*, *Pentaclethra* and primary forest, and *Vochysia* and primary forest; the frog assemblage of *Virola* was indistinguishable from that of reference primary forest. Pairwise comparison of lizards revealed that *Pentaclethra* supported a significantly different assemblage than primary forest; the lizard assemblages of *Virola* and *Vochysia* were indistinguishable from those of reference primary forest (Table 2).

Discussion

While the herpetofauna of La Selva is among the most well studied of any locality in the tropics, the amphibians and reptiles from the surrounding agricultural landscape are essentially unknown. To our knowledge, this is the first study to address the community ecology of amphibians and reptiles occurring in human-modified landscapes of the La Selva region. Our study supports the hypothesis that plantation tree species can support different assemblages of leaf-litter amphibians and reptiles. Previous studies have shown single plantation species to support herpetofaunal assemblages distinct from those of nearby reference forest (Pawar et al. 2004; Pineda and Halffter 2004; Gardner et al. 2007b). Our results support previous findings from plantations (Hartley 2002), which indicate that single plantation species do not aptly encompass the overall variation that exists among different plantation landscapes and only provide limited information about plantation ecology in general. While we appreciate all comparisons of plantations and reference

Fig. 1 Box-and-whisker plots of frog (**a**), lizard (**b**), and entire herpetofaunal (**c**) densities in primary forest (FOREST), *Pentaclethra macroloba* (PEMA), *Virola koschnyi* (VIKO), and *Vochysia guatemalensis* (VOGU). *Bold lines in each box* denote median densities; *top* and *bottom box edges* are the *upper* and *lower* quartiles, respectively. The results of the pairwise post hoc analysis are labeled above each treatment for frogs, but not for lizards (non-significant after adjustment for multiple comparisons) and entire herpetofauna (unpubl. data)
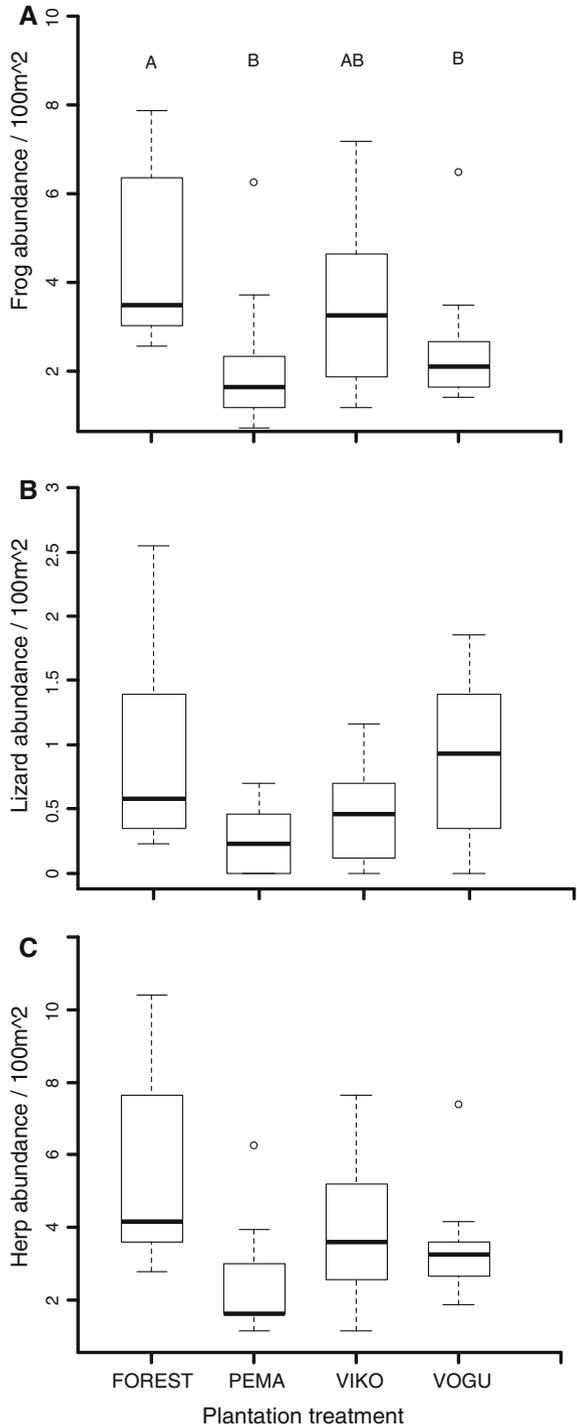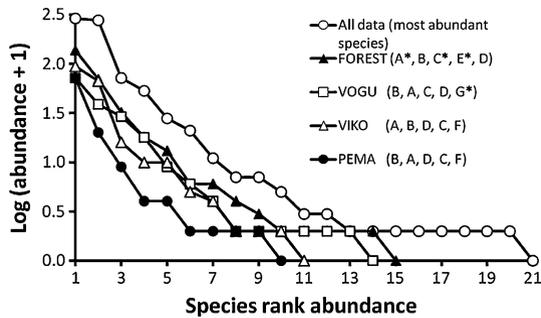
Fig. 2 Rank-abundance curves of species recorded in each plantation treatment, primary forest, and the combined samples. Tree species acronyms are as in Table 1. The rank-abundance curve for all combined data is shown on top of the individual curves for each treatment type. The seven most abundant species are labeled with letters in the curve for all data. For each treatment, the five most abundant species are listed in the legend in decreasing order. Species significantly characteristic of treatments according the indicator species analysis (P < 0.05) are marked with an *. The relative abundance was transformed to log (abundance + 1), where abundance is the number of individuals recorded in each forest type. Letter codes: *A Craugastor bransfordii, B Oophaga pumilio, C Norops quaggulus, D Norops limifrons, E Craugastor mimus, F Pristimantis cerasinus, G Pristimantis ridens*

habitats (e.g. Lieberman 1986; Heinen 1992), more than a single plantation type should be considered to make generalizations about the ecology or biodiversity conservation in plantation or "disturbed" habitats, because these habitat classifications possess more heterogeneity then previously recognized.

Plantations are largely thought to lack biodiversity relative to primary forest (Freedman et al. 1996), and a review of herpetofaunal studies, most of which focused on exotic tree species plantations, was generally consistent with this notion (Gardner et al. 2007a). We observed low species richness of frogs in *Pentaclethra*, but *Virola* and *Vochysia* supported faunas with comparable species richness to primary forest. These results provide important examples of native tree species plantations harboring biodiversity relative to primary forest and evidence that native species plantations may support greater richness than exotic ones (Hartley 2002).

The assemblage-level differences we observed may result from distinct microhabitat environments of each homogeneous plantation and the more heterogeneous primary forest. Other tropical studies have found a positive relationship between herpetofaunal abundance and leaf-litter depth (Scott 1976; Lieberman 1986; Heinen 1992; Whitfield et al. 2007). However, we measured the greatest abundance of the herpetofauna in *Virola*, a tree species that produces the lowest standing litter crop of the three study species (Raich et al. 2007). This result suggests that microhabitat aspects other than leaf-litter depth (e.g. moisture; Fauth et al. 1989; Vonesh 2001) may be more important in determining local abundances of the native herpetofauna. Microhabitat selection in moist litter is essential to maintaining hydration in terrestrial frogs (Seebacher and Alford 2002); because terrestrial lizards utilize the same microhabitats and prey as frogs (Lieberman 1986; Pounds and Crump 1994; Whitfield and Donnelly 2006), microhabitat selection is probably comparably important for lizards. While the focal plantation species in our study are all evergreen angiosperms with continual annual leaf production (Frankie et al. 1974), the species differ in leaf morphology and characteristics of litter mass and dynamics (Raich et al. 2007) which create markedly different leaf-litter habitats for the forest-floor fauna (Russell et al. 2010). In particular, *Pentaclethra* has a compound, highly dissected leaf morphology that seems

Fig. 3 Non-metric
multidimensional scaling
(NMDS) plots for frogs (**a**) and
lizards (**b**). Non-metric
multidimensional scaling
graphically visualizes
dissimilarity matrices of species
assemblages and abundances;
points more closely-situated are
more similar relative to distant
points. *Black ellipses* indicate
95 % confidence intervals for
clusters of each treatment. Stress
values indicate a measure of
distortion when multi-
dimensional ordinations are
plotted in a two-dimensional
plane. Species acronyms are as in
Table 1
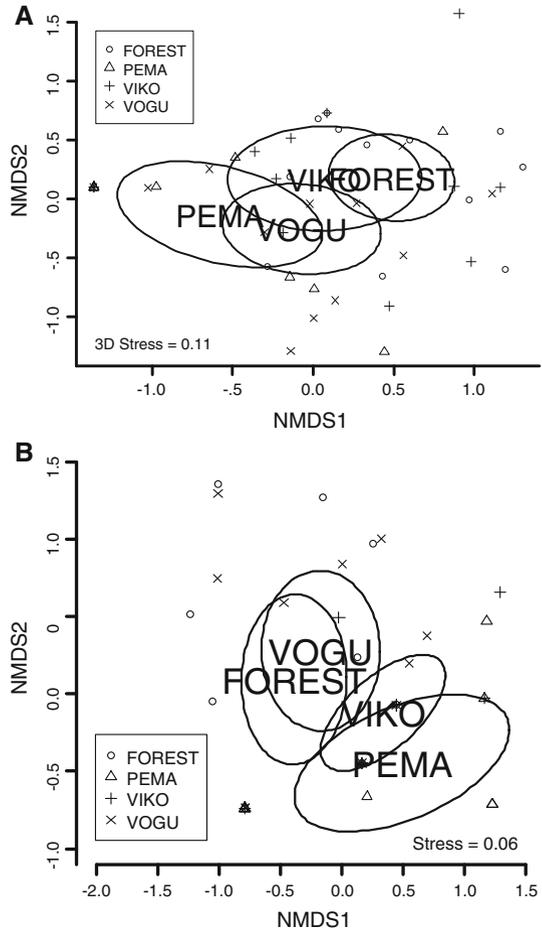
to create a drier litter microhabitat relative to those of the broad, simple leaf morphologies of *Virola* and *Vochysia* (BF pers. obs.). Because *Pentaclethra* supported the lowest abundance, it seems microhabitat attributes such as relative moisture may better explain differences in herpetofaunal abundance in these plantations than other classic factors (e.g. leaf-litter depth; see Reider et al. 2013 for a discussion of how deeper litter could decrease the fitness of terrestrial herpetofauna).

In addition to creating unique litter habitats at the scale of monoculture plantations (Russell et al. 2010), tree species effects may similarly influence herpetofauna in primary forest settings at the level of single canopy trees by generating unique forest-floor microhabitats. Using single forest trees as a spatial scale, Guyer (1988, 1994) hypothesized that tree species may mediate different cycles of leaf-litter reptile abundance through different leaf-drop phenologies in lowland tropical forest of Costa Rica. When scaled to the community level, this logic suggests that tree species may support different abundances of multiple species (i.e. assemblages) through time. We measured unique abundances and assemblages of amphibians and reptiles with respect to different tree species during a wet season "snap-shot" in time, a finding consistent with Guyer (1988, 1994). But, future

Table 2 *P* values associated with permutational multivariate analysis of variance (PERMANOVA) of frog and lizard assemblages

	PEMA	VIKO	VOGU	FOREST
Frogs:	$F = 2.153$, df $= 3$, $P = 0.006$			
PEMA	–			
VIKO	**0.030**	–		
VOGU	0.670	0.083	–	
FOREST	**0.002**	0.425	**0.007**	–
Lizards:	$F = 2.345$, df $= 3$, $P = 0.012$			
PEMA	–			
VIKO	0.228	–		
VOGU	0.013	0.120	–	
FOREST	**0.008**	0.068	0.623	–

Overall PERMANOVA results for frogs and lizards are listed adjacent to respective sub-headers; pairwise comparisons of assemblages between tree species are reported below. Species acronyms are in Table 1. Values in bold indicate significance at $P < 0.05$ after sequential Bonferroni correction

research should investigate whether the effect of tree phenology on the leaf-litter habitat yields consistent temporal patterns to herpetofaunal richness and abundance.

Mono-dominant plantations of the three tree species that we studied differ in value from a herpetological conservation perspective. *Virola* supports both frog and lizard assemblages indistinguishable from those of nearby primary forest, and, therefore, appears to have the highest conservation value. While *Vochysia* supports a low density and dissimilar assemblage of frogs relative to primary forest, it possesses a relatively dense, species rich, and similar lizard assemblage, and so is of intermediate conservation value. Lastly, because we observed no unique benefits to the use of *Pentaclethra*, it has the lowest conservation value from the perspective of herpetofaunal conservation.

Dr Leslie Holdridge was among the first to experiment with both monocultures and mixed plantations of laurel (*Cordia alliodora*), cacao (*Theobroma cacao*), pejibaye (*Bactris gasipaes*) in search of sustainable tropical land-use systems that conserve biodiversity in the 1950s (McDade and Hartshorn 1994). When the three plantation species from our study are considered as one group, the mosaic plantation landscape supports greater richness than any single plantation species, which is similar to studies that have found polycultures to support greater richness and abundance than monocultures (Hartley 2002). Similarly, Bell and Donnelly (2006) found small forest fragments in the La Selva region to support low richness; however, the summed fragments supported comparable richness to primary forest on a landscape scale. Because our plantation species are variable in the fauna they support, our results indicate that plantation mosaics may be the best option to conserve the species-rich leaf-litter amphibians and reptiles of lowland Caribbean Costa Rica.

Our study provides a powerful example of how plantation forests can facilitate the restoration of native faunas onto degraded lands. Pastures provide suboptimal habitat to support tropical amphibians (Urbina-Cardona et al. 2006), likely by increasing mortality through depredation and dessication (Rothermel and Semlitsch 2002). Thus, prior to the initiation of the ECOS project, we assume that the pasture landscape likely supported a depauperate herpetofauna relative to nearby primary forests. Given the close proximity of the primary forest to the ECOS plantations during plantation growth, the primary forest

likely provided a source pool of species, some of which dispersed and colonized suitable plantation habitat. Frog and lizard species turnover between the three plantations and primary forest is low (Table 1). Thus, the current plantation herpetofauna do not reflect a history of perturbation and negative land use, as the richness, abundance, and assemblages of frogs and lizards in many cases do not differ from nearby reference forest. Rather, we believe the comparable community ecology of amphibians and reptiles between plantations and primary forest suggest that these reforested, mono-dominant plantations possess aspects of ecosystems functioning at levels comparable to natural forests. Our study indicates that plantations may ultimately prove a valuable component of landscape mosaics to support and conserve diverse tropical faunas in a sustainable future.

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