
The Value of Primary, Secondary, and Plantation Forests for a Neotropical Herpetofauna

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Abstract: *Plantation forests and second-growth forests are becoming dominant components of many tropical forest landscapes. Yet there is little information available concerning the consequences of different forestry options for biodiversity conservation in the tropics. We sampled the leaf-litter herpetofauna of primary, secondary, and Eucalyptus plantation forests in the Jari River area of northeastern Brazilian Amazonia. We used four complementary sampling techniques, combined samples from 2 consecutive years, and collected 1739 leaf-litter amphibians (23 species) and 1937 lizards (30 species). We analyzed the data for differences among forest types regarding patterns of alpha and beta diversity, species-abundance distributions, and community structure. Primary rainforest harbored significantly more species, but supported a similar abundance of amphibians and lizards compared with adjacent areas of second-growth forest or plantations. Plantation forests were dominated by wide-ranging habitat generalists. Secondary forest faunas contained a number of species characteristic of primary forest habitat. Amphibian communities in secondary forests and Eucalyptus plantations formed a nested subset of primary forest species, whereas the species composition of the lizard community in plantations was distinct, and was dominated by open-area species. Although plantation forests are relatively impoverished, naturally regenerating forests can help mitigate some negative effects of deforestation for herpetofauna. Nevertheless, secondary forest does not provide a substitute for primary forest, and in the absence of further evidence from older successional stands, we caution against the optimistic claim that natural forest regeneration in abandoned lands will provide refuge for the many species that are currently threatened by deforestation.*

Keywords: amphibians, lizards, human-dominated landscapes, land-use change, primary forest, secondary forest, plantations

El Valor de la Biodiversidad de Bosques Primarios, Secundarios y Plantaciones para una Herpetofauna Neotropical

Resumen: *Los bosques de plantaciones y los bosques de vegetación secundaria se están convirtiendo en los componentes dominantes de muchos paisajes forestales tropicales. Sin embargo, se dispone de poca información sobre las consecuencias de diferentes opciones silvícolas para la conservación de la biodiversidad en los trópicos. Muestreamos la herpetofauna en la bojarasca de bosques primarios, secundarios y de plantaciones de Eucalyptus en el área del Río Jari en el noreste de la Amazonía Brasileña. Utilizamos cuatro técnicas de muestreo complementarias, combinando muestras de 2 años consecutivos, y recolectamos 1739 anfibios de la bojarasca (23 especies) y 1937 lagartijas (30 especies). Analizamos los datos para diferencias entre los tipos de bosque en relación con la diversidad alfa y beta, las distribuciones especies-abundancia y la estructura de la comunidad. El bosque primario albergó un número de especies significativamente mayor; pero soportó una abundancia de anfibios y lagartijas similar a la de áreas de vegetación secundaria o plantaciones adyacentes. Los bosques de plantaciones fueron dominados por generalistas con amplio rango de hábitats. Las faunas de*

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Paper submitted May 9, 2006; revised manuscript accepted October 19, 2006.

bosques secundarios contenían un número de especies característico del hábitat de bosque primario. Las comunidades de anfibios en bosques secundarios y plantaciones de eucalipto formaron un subconjunto anidado de especies de bosque primario, mientras que la composición de especies de la comunidad de lagartijas en las plantaciones fue diferente y fue dominada por especies de áreas abiertas. Aunque los bosques de plantaciones están relativamente empobrecidos, los bosques en regeneración natural pueden ayudar a mitigar algunos efectos negativos de la deforestación sobre la herpetofauna. Sin embargo, el bosque secundario no es un sustituto del bosque primario y, en ausencia de mayor evidencia en bosques secundarios más viejos, damos la voz de alarma contra la afirmación optimista de que la regeneración natural de bosques en tierras abandonadas proporcionará refugio a muchas especies que actualmente están amenazadas por la deforestación.

Palabras Clave: anfibios, bosque primario, bosque secundario, cambio en el uso de suelo, lagartijas, paisajes dominados por humanos, plantaciones

Introduction

Loss of native habitat through deforestation and degradation is currently the primary cause of species range declines and population extinctions worldwide (Mace et al. 2005), with approximately 15 million ha of forest destroyed each year during the 1990s, mostly in the tropics (FAO 2001). A consequence of this large-scale conversion of tropical forest landscapes has been the rapid expansion of, for example, degraded primary forests (e.g., through selective logging), secondary forests, and exotic tree plantations. Globally, tropical secondary forests have replaced one-sixth of all tropical primary forests that were felled during the 1990s (Wright 2005) and exceed the area covered by primary forest in many countries. Tropical forest plantations have increased from 18 million ha in 1980 to more than 70 million ha in 2000 (FAO 2001).

The inadequacy of the global protected-area networks means that the future of many tropical forest species will depend in part on their conservation in human-dominated landscapes (Daily 2001; Lindenmayer & Franklin 2002; Fischer et al. 2006). Nevertheless, current understanding of the conservation value of secondary forests (Dunn 2004; Gardner et al. 2007) and timber plantations (Hartley 2002; Lindenmayer & Hobbs 2004) is poor, which casts doubt on optimistic predictions (e.g., Wright & Muller-Landau 2006) regarding the future contribution of production and regenerating tropical landscapes to biodiversity conservation (Brook et al. 2006; Laurance 2007; Gardner et al. 2007).

There is a distinct absence of consensus among researchers as to the effects of habitat modification on species diversity in tropical forests, with results of individual studies showing positive and negative effects of modification with nearly equal frequency (e.g., butterflies, Hamer & Hill 2000; birds, Hill & Hamer 2004). Amphibians and reptiles are the most threatened groups of terrestrial vertebrates (Stuart et al. 2004; IUCN 2006), yet no available synthesis summarizes the consequences of tropical deforestation for these organisms. Although the importance of primary forest has been emphasized by a number of researchers (Lieberman 1986; Marsh & Pear-

man 1997; Vallan 2000, 2002; Tocher et al. 2002; Jenkins et al. 2003; Gillespie et al. 2005), this conclusion is not unanimous, and other studies of land-use change on tropical herpetofaunal diversity report no effect (Germano et al. 2003; Fredericksen & Fredericksen 2004; Vallan et al. 2004), a conditional effect (e.g., dependent upon assemblage subgroups (Inger 1980; Pearman 1997), or even a positive effect (Vonesh 2001; Fredericksen & Fredericksen 2002). Furthermore, the majority of studies address the conservation value of remnant or degraded areas of native habitat (reviewed in Bell & Donnelly 2006), and relatively few focus on sampling the surrounding landscape matrix (Vitt & Caldwell 2001; Gardner et al. 2007). In summary the conclusions of relevant studies are inadequate, and from a policy perspective, alarmingly ambiguous.

Part of the explanation behind the lack of consensus in these studies is the ubiquity of various methodological shortcomings and differences in analytical approach (Heyer et al. 1994). Typical limitations of studies concerned with the effect of habitat change on tropical herpetofauna include the lack of an undisturbed baseline, nonindependence among samples due to limitations in the spatial extent of the study, poor sample representation through low capture or trapping success, inappropriate analyses combined with a failure to recognize the limitations of certain methodologies, and the failure to account for any differences in the conservation value of individual species (Gardner et al. 2007).

We attempted to address the problems outlined above by making a comprehensive and robust evaluation of the value of primary, secondary, and plantation forests for a Neotropical herpetofauna. The Brazilian Amazon is a priority area for research on the effects of habitat change on amphibians and reptiles because the rate of deforestation is among the highest recorded in the world (Fearnside 2005); understanding of its diverse herpetofauna is largely restricted to a small number of well-studied areas of relatively pristine habitat (reviewed in Duellman 2005, but see Tocher et al. 2002); and knowledge of many species is limited to alpha taxonomy (Rodrigues 2005). Secondary forests are an increasingly dominant feature of the deforestation frontier of the Amazon, following rapid

abandonment of the land in the wake of large-scale land clearance (Houghton et al. 2000). In addition, a large expansion in the plantation forest estate is predicted during the coming decades in response to the burgeoning global demand for timber (FAO 2001), with much of the increase expected to occur in the Amazon (Fearnside 1998). By sampling a landscape created by a large-scale forestry project, we minimized the confounding influence of edge effects and habitat fragmentation and maximized the spatial independence among sites of each forest type. To evaluate the biodiversity consequences of clearing areas of native forest for tree plantations and the potential for faunal recovery through natural regeneration, we examined patterns of alpha and beta diversity for lizards and leaf-litter amphibians among the three forest types and compared species-abundance distributions and patterns of community structure in each habitat, identifying the key species characteristic of each level of disturbance. We also examined why many other researchers found no significant or counterintuitive effects of habitat degradation. Finally, we considered our results in the context of integrated management of human-dominated tropical forest landscapes.

Methods

Study Area and Site Selection

Sampling was conducted within the Jari Celulose/Grupo Orsa landholding on the Jari River in northeastern Brazilian Amazonia ($00^{\circ}27'00''-01^{\circ}30'00''\text{S}$, $51^{\circ}40'00''-53^{\circ}20'00''\text{W}$). About 10% of the area was cleared and

planted with exotic trees during the late 1960s and 1970s. Today the landholding is characterized by a complex mosaic of fast growing (5- to 6-year rotation) *Eucalyptus* plantations, interspersed with areas of secondary forest fallow land, and surrounded by over 1 million ha of primary forest subject to minimal levels of disturbance (light subsistence hunting and extraction of nontimber forest products) (Fig. 1).

We established 15 study sites within this landscape that included the three major forest types: (1) mature primary rainforest, (2) "mature" *Eucalyptus* plantations (4–5 years old), and (3) even-aged secondary forest (14–19 years since abandonment) (Fig. 1). The scale of the landscape allowed us to select study sites ($n = 5$ in each forest type) that were both spatially independent (average distance between primary, secondary, and *Eucalyptus* sites was 30 km [range 14–67], 9 km [4–44], and 11 km [7–50], respectively) and of sufficient size (average size of *Eucalyptus* and secondary forest blocks was 1687 ha [range 574–3910] and 2682 ha [1079–3508], respectively) to minimize problems of pseudoreplication and edge effects. Moreover, *Eucalyptus* and secondary forest sites were located similar distances from the nearest areas of continuous primary forest (average 1124 m [range 550–2300] and 1316 m [650–2800], respectively). To our knowledge no other landscape exists within the Amazon basin that would allow a comparable sampling design. Within each site we cut a 1.5-km line transect (2 m wide), starting at least 500 m from the edge in all sites (with the exception of one *Eucalyptus* site that started at 200 m from the edge). The availability of suitable amphibian

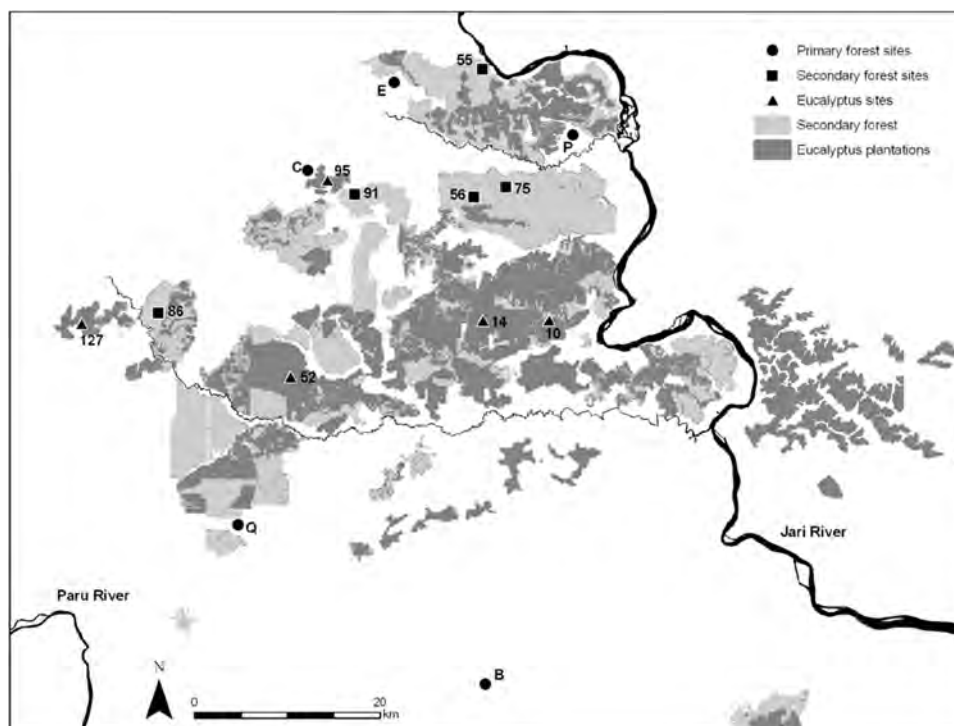


Figure 1. Locations of study sites in Jari, Brazilian Amazonia. Blank areas consist largely of undisturbed primary forest with the exception of small areas of settlement. Primary forest transects located near converted areas were placed perpendicular to the border. Site names match those identified in Table 1 (primary forest sites are labeled with letters: B, Bituba; Q, Quaruba; C, Castanhal; E, Estacao; P, Pacanari, with plantation and secondary forest sites labeled with company plot numbers).

reproductive habitat was similar between primary and secondary forests (all sites contained seasonal streams), but streams were absent from *Eucalyptus* sites.

Secondary forest plots were characterized by palms, *Inga* spp., and other pioneer species, whereas *Eucalyptus* sites were characterized by an understory of annuals (including many Asteraceae, Rubiaceae, Piperaceae, Poaceae, and Cyperaceae), lianas (e.g., *Davilla* spp. [Dileniaceae]), and small trees (e.g., *Vismia* spp. [Clusiaceae], *Mabea taquari*, and *Aparisthmium cordatum* [Euphorbiaceae]). Floristically, primary forest plots were dominated by Burseraceae, Sapotaceae, Lecythidaceae, and Leguminosae-Caesalpinioideae.

Amphibian and Lizard Sampling

We sampled lizards (including amphisbaenids) and leaf-litter amphibians at each site between May and September 2004 and again between January and June of 2005. In 2004 we deployed 10 arrays of pitfall traps (4 × 35 L buckets, with a 6-m-long by 80-cm-high plastic drift fence connecting them in a Y-shaped design composed of one central bucket and one bucket at the end of each arm). Consecutive arrays were arranged 100 m apart along each transect. In 2005 we used three additional and complementary sampling techniques at all sites: (1) funnel traps placed flush with the plastic fence along one side of each arm of every 35-L pitfall array, (2) three 62-L pitfall trap arrays (as for 35-L arrays but with larger buckets) arranged 100 m apart in sequence with the final 35-L array, and (3) 20 sticky trap boards (Victor rat traps, Lititz, Pennsylvania) placed 50 m apart along the transect and located on the base of tree trunks or fallen logs (Ribeiro-Júnior et al. 2006). Finally, we actively surveyed each site with visual encounter surveys (VES) along the first 500 m of each transect (strip width = 4 m, mean duration = 61 minutes, SE = 1 minute). Not all sampling techniques are equally effective at capturing all components of the amphibian and lizard faunas (e.g., sticky traps target semiarboreal and arboreal lizards, and VES are particularly effective for diurnal species), but when used in combination we were able to describe a wider assemblage than would be possible with a single method.

Each sampling technique was applied with an equal level of effort across all sites, and each site was sampled for a total of 7 consecutive days during 2004 and 14 days during 2005 (21 days in total for each site). We randomized sampling order of sites within each year with respect to habitat type to avoid any systematic bias from seasonal effects. Sampling was always conducted across two (2004) or three (2005) sites simultaneously, and in nearly every case we sampled sites from different forest types in each sampling session. Consequently, sampling in any given forest type (pooling across all sites and years) encompassed a wide range of environmental conditions and associated herpetofaunal activity patterns.

Analyzing the data for each year independently did not produce any qualitative difference in our results, suggesting that further sampling of the same sites in additional years would be unlikely to alter our conclusions. Sampling effort across all sites and years totaled 12,600 35-L pitfall trap nights (one trap night = 24 hours), 2520 62-L pitfall trap nights, 6300 funnel trap nights, 3600 glue trap nights, and 153 hours of encounter surveys (approximately 10/site).

Data Analyses

Other researchers consider leaf-litter amphibians and leaf-litter lizards a single assemblage (e.g., Crump 1971; Lieberman 1986; Heinen 1992; Vonesh 2001). Nevertheless, despite the fact that leaf-litter amphibians and lizards are likely to be ecologically more similar to each other than either is to mammals or birds (i.e., both are abundant poikilotherms), both taxa are characterized by markedly different life histories (Gibbons et al. 2000), and little research has been conducted in tropical forests to test whether this assumption is valid for studies concerned with the effects of habitat change. In particular few researchers have measured the response to disturbance for both taxa concurrently and across the same study sites. The sampling methods we used provided adequate data for the analysis of leaf-litter amphibians and lizards. Diurnal VES provided data for arboreal lizards, but not arboreal amphibians (requiring nocturnal searches) or snakes (which were rarely seen). To compare among assemblages, we separated the data, independently comparing patterns of diversity for each group (see Supplementary Material). We considered that arboreal lizards include all species that live primarily aboveground and not in the leaf litter (i.e., all arboreal and semiarboreal species).

We compared patterns of richness between forest types after standardizing for differences in abundance with individual-based rarefaction analysis (Gotelli & Colwell 2001; Colwell 2004). Each sampling method captured a similar proportion of the total number of individuals sampled in each habitat (e.g., the primary method, 351 pitfalls, captured 69%, 60%, and 47% of all captures in plantation, secondary forest, and primary forest sites, respectively), and combining captures from different sampling methods partially accounted for any potential detection biases among methods and thus provided a closer representation of the “true” community composition at each site. Comparisons among habitat types were made by visual assessment of overlapping 95% confidence intervals of the rarefaction curves. We assessed the completeness of each sample by calculating the number of observed species as a percentage of the total richness, which was estimated based on the average of two abundance-based nonparametric estimators—Chao 1 and jack 1 (Colwell 2004).

To describe patterns of beta diversity across the landscape we calculated the average number of species not

present in each site defined as $\beta = \gamma - \alpha$, where γ is the number of species sampled in the entire landscape (gamma diversity) and α is the average number of species present at a given site (alpha diversity). This approach is used as a measure of additive partitioning of diversity (Veech et al. 2002) and allows for a direct comparison between alpha and beta diversities in terms of the number of species (e.g., Pineda & Halffter 2004; Pineda et al. 2005).

To compare species-abundance patterns among forest types and between species assemblages, we used standardized Whittaker plots and compared the slopes of different communities with analysis of covariance (ANCOVA) (Magurran 2004). Identification of species on the rank-abundance plots allowed for the visual inspection of patterns of nestedness. We compared patterns of total assemblage abundance among each forest type with Kruskal-Wallis comparisons, followed by pairwise comparisons with Mann-Whitney *U* tests.

We used nonmetric multidimensional scaling (MDS) to define the overall differences in community structure and composition within and among habitat types. Ordinations were undertaken for both quantitative (abundance based, Bray-Curtis index) and qualitative (presence-absence based, Sørensen index) data. We used analysis of similarities (ANOSIM, Clarke & Warwick 2001) to test for

significant differences in multivariate community structure between forest types. We used SIMPER (similarity percentage, Clarke & Warwick 2001) to determine the contribution that individual species made toward distinguishing differences in quantitative community structure among habitats. Multivariate analyses were conducted in PcORD (version 4.25; McCune & Meffor 1999) and Primer (version 5; Clarke & Warwick 2001).

Results

Across all study sites and sampling methods we captured 1739 leaf-litter amphibians and 1937 lizards, for a total of 23 and 30 species, respectively. Leaf-litter lizards comprised the majority of the total lizard fauna (1307 individuals and 18 species, including *Amphisbaena fuliginosa* and *Bachia flavescens*, which are semifossorial). Twelve arboreal species comprised the remaining 630 individuals (see Supplementary Material).

Patterns of Alpha and Beta Diversity

Samples of lizards and leaf-litter amphibians captured at least 71% of the estimated total number of species present from these assemblages in each habitat, with lizards being slightly better represented (Table 1). Eighty-seven percent

Table 1. Capture success, species richness, and sample completeness for amphibians and reptiles sampled in primary, secondary, and plantation forests in the Jari region, Brazil.

Forest type and site	Amphibians					Lizards				
	n ^a	sobs ^b	coverage ^c	exclusive species (%) ^d	completeness (%) ^e	n	sobs	coverage	exclusive species (%)	completeness (%)
Primary										
Bituba	98	4	84	0	17	127	11	82	3	35
Castanhal	128	11	78	0	48	119	16	75	3	52
Estacao	85	14	71	13	61	91	14	78	3	45
Pacanari	120	9	60	4	39	218	15	77	3	48
Quaruba	84	8	73	0	35	126	12	100	0	39
All	515	22	86	35	96	681	25	86	33	81
Secondary										
Area 55	206	8	100	4	35	151	8	86	3	26
Area 56	80	9	100	0	39	103	11	75	0	35
Area 75	84	6	92	0	26	75	7	65	0	23
Area 86	61	8	71	0	35	85	7	84	0	23
Area 91	79	10	73	0	43	85	7	74	0	23
All	510	14	71	4	61	499	15	87	3	48
Eucalyptus										
Area 10	171	3	100	0	13	147	7	84	0	23
Area 127	87	2	74	0	9	143	6	100	0	19
Area 14	72	3	100	0	13	145	6	75	3	19
Area 52	104	2	100	0	9	180	5	72	3	16
Area 95	280	3	61	0	13	142	9	81	3	29
All	714	5	87	0	22	757	14	81	13	45
All data	1739	23				1937	30			

^aNumber of individuals captured.

^bNumber of observed species.

^cNumber of species observed as a percentage of the average estimated richness.

^dNumber of species not found elsewhere as a percentage of landscape total.

^eNumber of species observed as a percentage of the landscape total.

and 93% of sites contained more than 70% of the estimated true richness of amphibians and lizards, respectively. This result suggests that our comparisons of species richness among sites and habitats were valid for the purposes of describing patterns of community structure in the three forest types. Approximately one-third of both amphibians and lizards were only encountered in primary forest. With the exception of four lizard species that were only found in *Eucalyptus* plantations and one species of amphibian found only in secondary forest, all the remaining species occurred in primary forest (96% of all amphibians and 81% of all lizards) (Table 1).

We recorded significantly more amphibian and lizard species in primary forest than in either secondary forest or *Eucalyptus* plantations (Fig. 2). Secondary forest harbored significantly more amphibian species than plantation forests, which contained only five species. In contrast the number of lizards (either for the entire assemblage or for leaf-litter and arboreal species separately) in secondary

forest and *Eucalyptus* stands did not differ significantly, although the former tended to have slightly more species in general, and plantation sites had few arboreal lizards (Table 1, Fig. 2).

The gamma diversity of the entire landscape can be expressed in an additive form for leaf-litter amphibians ($23 [\gamma] = 6.6 [\alpha] + 16.3 [\beta]$) and all lizards ($30 [\gamma] = 9.4 [\alpha] + 20.6 [\beta]$) with the proportion of total diversity explained by beta diversity being almost identical for both groups (amphibians 71%; lizards 69%). Within each forest type beta diversity contributed about half of the total diversity for both amphibians (*Eucalyptus*, secondary, and primary forest: 48%, 41%, and 58%, respectively) and lizards (53%, 47%, and 46%).

Patterns of Abundance and Community Structure

Total abundance of either amphibians ($\chi^2 = 2.41$, $p = 0.3$) or lizards ($\chi^2 = 5.12$, $p = 0.077$) did not differ

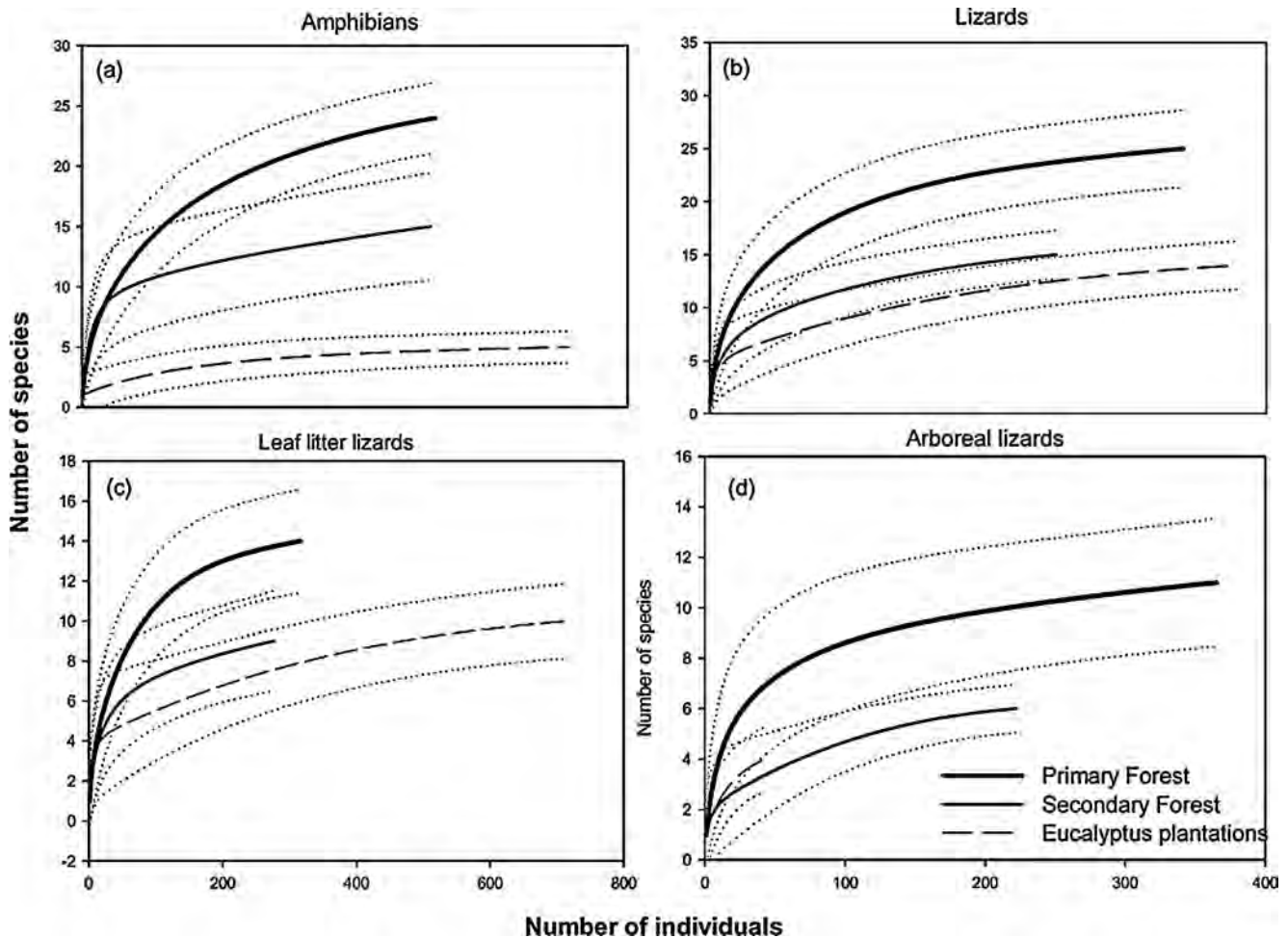


Figure 2. Individual-based rarefaction curves for (a) leaf-litter amphibians, (b) lizards, and separate (c) leaf-litter and (d) arboreal lizard assemblages within primary, secondary, and plantation forests of the northeastern Brazilian Amazon. Data are pooled from multiple sampling methods and both years. The 95% confidence intervals are fine dotted lines.

significantly among forest types. When considered separately, however, the abundance of both leaf-litter and arboreal lizards differed significantly among habitats ($\chi^2 = 9.43, p = 0.009$, and $\chi^2 = 10.0, p = 0.007$, respectively), with more leaf-litter lizards in *Eucalyptus* plantations than either primary ($U < 0.001, p = 0.008$) or secondary forest ($U < 0.001, p = 0.008$). Arboreal lizards were captured more frequently in primary forest than in plantations ($U < 0.001, p = 0.008$) but not more than in secondary forest ($U = 4, p = 0.095$), although secondary forest had more arboreal lizards than plantation sites ($U = 1.5, p = 0.016$).

The slopes of the species-rank abundance plots among the three forest types were significantly different for amphibians (ANCOVA; $F = 33.1, p < 0.001, df = 2$) and lizards ($F = 5.8, p = 0.006$), with an increase in evenness and the proportion of apparently rarer species from plantations to primary forest (Fig. 3). Furthermore, the species-abundance relationship was similar for amphibians and reptiles in primary ($F = 0.4, p = 0.54, df = 1$) and secondary forest ($F = 0.3, p = 0.58$), although not *Eucalyptus* plantations ($F = 9.1, p = 0.009$). The same general pattern was also reflected in the relationships for leaf-litter and arboreal lizards separately, with distinct differences in abundance patterns among habitats (leaf lit-

ter; $F = 13.9, p < 0.001, df = 2$, arboreal; $F = 8.3, p < 0.001$) but similar patterns among species assemblages for both plantation sites ($F = 1.4, p = 0.26, df = 1$) and secondary forest ($F = 4.9, p = 0.05$), although the primary forest communities were distinct ($F = 10.2, p = 0.004$), with the leaf-litter lizard community having a more even distribution.

Despite having similar species-abundance relationships in each forest type, however, amphibian and reptile communities differed with respect to the pattern of hierarchy in species abundance ranks among habitats (Fig. 3). *Adenomera* sp. was the most abundant amphibian in all forest types comprising 97% of all captures in *Eucalyptus* plantations, 38% in secondary forest, and 51% in primary forest. In contrast the three heliothermic leaf-litter species that dominated the lizard community in plantation sites (*Ameiva ameiva*, *Cnemidophorus cryptus*, and *Cercosaura ocellata*) were all uncommon, rare, or absent in both secondary and primary forest (Fig. 3). On the other hand, the pattern of dominance hierarchy between secondary and primary forest was similar for lizards, with *Coleodactylus amazonicus* and *Gonatodes humeralis* occurring in much higher numbers than all other species.

All forest types hosted distinct communities of amphibians and lizards (Fig. 4). The axes of the 2D scaling plots

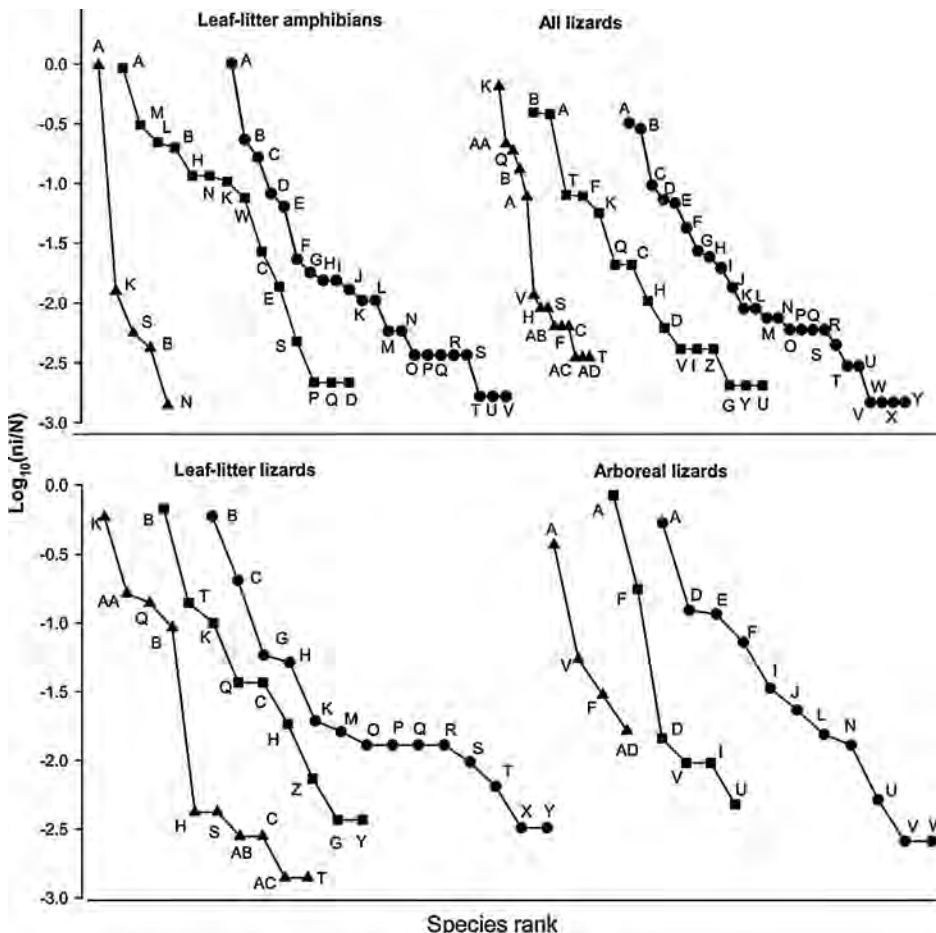


Figure 3. Dominance-diversity (Whittaker) plots for lizards and amphibians in primary (circles), secondary (squares), and plantation (triangles) forests of the northeastern Brazilian Amazon. Letters represent particular species, and each letter represents a different species within each group (i.e., an A in leaf-litter amphibians is not the same as the A species in arboreal lizards; exact definitions of all codes are available, see Supplementary Material). Species are ranked according to the number of individuals of each species (n_i) and the total number of individuals of all species (N) for each forest type.

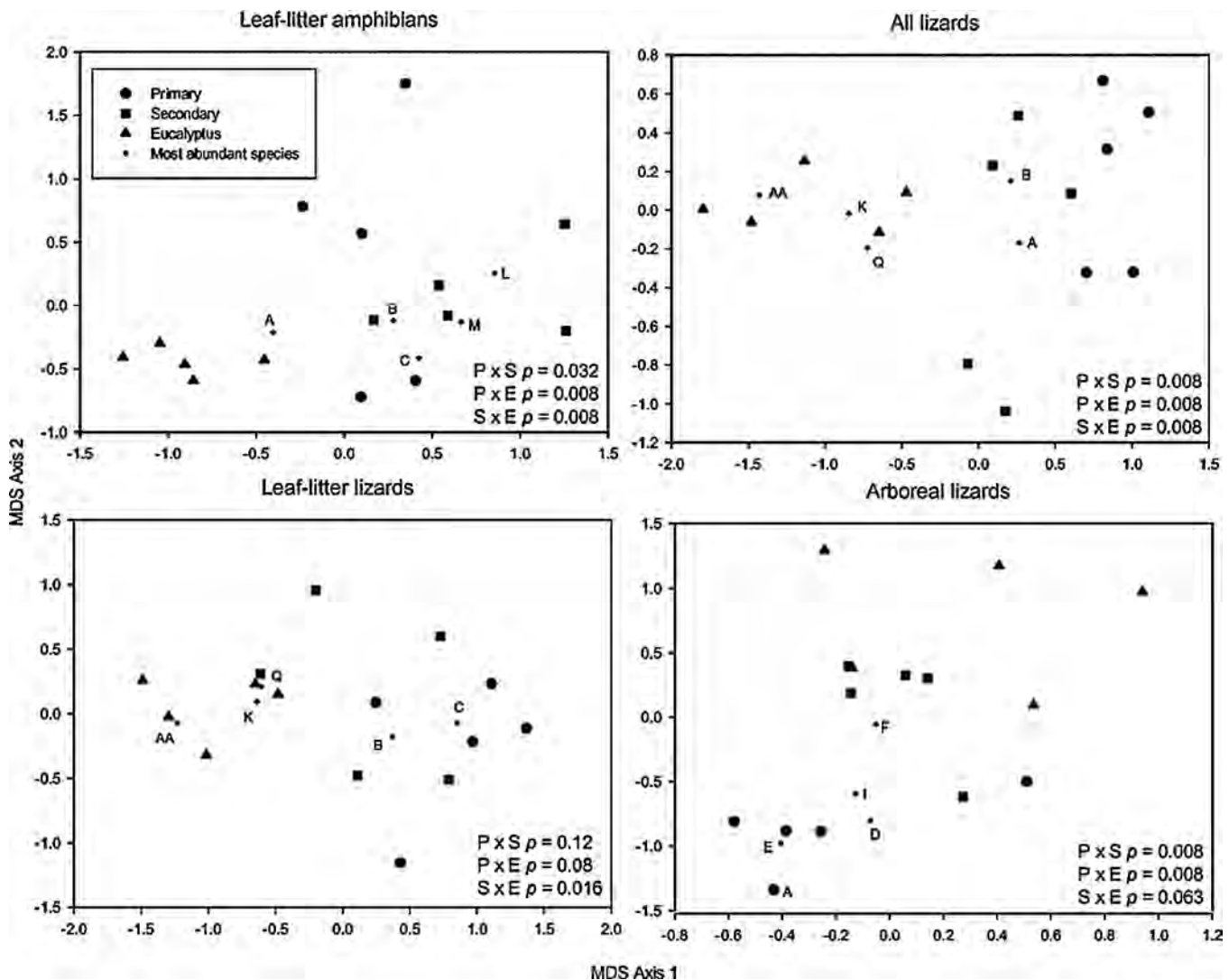


Figure 4. Nonmetric multidimensional scaling (MDS) ordinations for amphibian and lizard assemblages in primary, secondary, and plantation forests of the northeastern Brazilian Amazon. Ordination analyses are based on quantitative dissimilarity matrices. The position of the five most abundant species in each panel is plotted based on weighted averaging, which plots the average position of each species along each axis (McCune & Grace 2002). Letters represent particular species, and each letter represents a different species within each group (i.e., an A in leaf-litter amphibians is not the same as the A species in arboreal lizards; exact definitions of all codes are available, see Supplementary Material). The results of pairwise ANOSIM tests between each forest type are given in the bottom right corner of each panel (P, primary; S, secondary; E, Eucalyptus).

captured most of the variation in the original species dissimilarity matrices ($r^2 > 0.81$ in all cases). Differences in community structure among habitats were significant for all species assemblages whether they were based on quantitative (ANOSIM, $R > 0.57$, $p < 0.001$, Fig. 4) or qualitative data (ANOSIM, $R > 0.26$, $p < 0.004$). Furthermore, pairwise comparisons revealed that all habitats hosted distinct communities of amphibians and lizards (all species) (Fig. 4), although when analyzed separately the community structure of leaf-litter and arboreal lizards was less well defined (Fig. 4).

The SIMPER analysis illustrated that the community structure of both amphibians and lizards in primary forest sites was distinct from that of secondary and *Eucalyptus* sites due to an abundance of primary forest specialists rarely found in disturbed habitat (e.g., species of *Epipedobates* and *Leposoma*) and lower relative abundances (e.g., *Adenomera* sp., *Lithodytes lineatus*) or near absence (e.g., *Ameiva ameiva*, *Cnemidophorus cryptus*) of species found frequently in hyperabundance in either secondary forest or plantations (Table 2).

Table 2. Pairwise dissimilarities (diss.) between different forest types as defined by both amphibian and lizard assemblages.

Comparison	Overall diss. (%)	Species ^a	Average abundance	Average diss.	Average diss. SD	Contribution (%)	Cumulative contribution (%) ^b			
Amphibians										
primary v. <i>Eucalyptus</i>	53.8	Primary <i>Eucalyptus</i>								
		<i>Bufo</i> sp.	14.8	0.6	9.28	1.39	17.24	17.24		
		<i>Adenomera</i> sp.	53	139.4	7.94	3.16	14.74	31.97		
		<i>Epipedobates babneli</i>	11	0	5.01	0.69	9.29	41.27		
		<i>Epipedobates femoralis</i>	4.8	0	4.48	0.8	8.31	49.58		
		<i>Colostethus</i> sp.	6	0	3.65	0.72	6.78	56.36		
		<i>Leptodactylus stenodema</i>	2	0	2.77	1.16	5.15	61.5		
		<i>Bufo marinus</i>	1	1.8	2.6	1.33	4.83	66.34		
		<i>Leptodactylus mystaceus</i>	1.4	0	2.28	1.05	4.23	70.56		
secondary v. <i>Eucalyptus</i>	57.5	Secondary <i>Eucalyptus</i>								
		<i>Adenomera</i> sp.	38.8	139.4	9.94	3.29	17.27	17.27		
		<i>Bufo</i> sp.	10.2	0.6	8.42	2.28	14.63	31.9		
		<i>Litbodytes lineatus</i>	15	0	7.92	1.51	13.75	45.65		
		<i>Leptodactylus knudseni</i>	6.4	0.2	6.35	1.84	11.03	56.68		
		<i>Leptodactylus mystaceus</i>	6.4	0	5.98	1.43	10.39	67.07		
		<i>Bufo margaritifera</i>	11.2	0	4.98	0.95	8.65	75.71		
primary v. secondary	51	Primary Secondary								
		<i>Litbodytes lineatus</i>	0.6	15	5.56	1.45	10.88	10.88		
		<i>Leptodactylus knudseni</i>	0.6	6.4	4.64	1.6	9.09	19.97		
		<i>Epipedobates babneli</i>	11	1.8	4.2	0.93	8.22	28.19		
		<i>Bufo</i> sp.	14.8	10.2	3.91	1.39	7.67	35.86		
		<i>Bufo margaritifera</i>	1	11.2	3.65	1.07	7.16	43.02		
		<i>Leptodactylus mystaceus</i>	1.4	6.4	3.46	1.03	6.78	49.79		
		<i>Epipedobates femoralis</i>	4.8	1	3.43	1.04	6.72	56.51		
		<i>Bufo marinus</i>	1	5.8	3.37	1.28	6.59	63.11		
				<i>Adenomera</i> sp.	53	38.8	3.06	1.39	6	69.11
		<i>Colostethus</i> sp.	6	0.2	2.9	0.79	5.67	74.78		
Lizards										
primary v. <i>Eucalyptus</i>	76.2	Primary <i>Eucalyptus</i>								
		<i>Ameiva ameiva</i>	1.2	83.8	13.3	5.78	17.46	17.46		
		<i>Gonatodes humeralis</i>	41.4	7.2	7.21	2.18	9.46	26.93		
		<i>Cnemidophorus cryptus</i>	0	23.4	6.03	1.15	7.91	34.84		
		<i>Cercosaura ocellata</i>	0.8	20	5.73	2.09	7.52	42.36		
		<i>Anolis fuscoauratus</i>	9.6	0	5.33	3.62	7	49.35		
		<i>Coleodactylus amazonicus</i>	37	13.2	5.3	1.45	6.96	56.31		
		<i>Leposoma guianense</i>	12.6	0.4	4.37	1.34	5.73	62.04		
		<i>Tretioscincus agilis</i>	9	0	4.28	1.35	5.62	67.67		
				<i>Kentropyx calcarata</i>	5.6	0.4	3.28	1.47	4.31	71.98
secondary v. <i>Eucalyptus</i>	65.2	Secondary <i>Eucalyptus</i>								
		<i>Ameiva ameiva</i>	5.4	83.8	12.88	3.92	19.77	19.77		
		<i>Gonatodes humeralis</i>	35.4	7.2	10.02	1.55	15.38	35.15		
		<i>Coleodactylus amazonicus</i>	36.6	13.2	8.34	1.32	12.79	47.94		
		<i>Cnemidophorus cryptus</i>	0	23.4	7.27	1.14	11.16	59.1		
		<i>Kentropyx calcarata</i>	7.4	0.4	5.78	1.95	8.87	67.96		
		<i>Cercosaura ocellata</i>	2	20	5.72	1.77	8.78	76.75		
primary v. secondary	50.2	Primary Secondary								
		<i>Coleodactylus amazonicus</i>	37	36.6	5.68	2.04	11.15	11.15		
		<i>Anolis fuscoauratus</i>	9.6	0.6	4.6	2.26	9.04	20.19		
		<i>Tretioscincus agilis</i>	9	0	4.17	1.35	8.18	28.38		
		<i>Leposoma guianense</i>	12.6	2	4	1.61	7.86	36.24		
		<i>Gonatodes humeralis</i>	41.4	35.4	3.57	1.46	7	43.24		
		<i>Lepidoblepharis beyerorum</i>	0.4	7.6	3.16	0.85	6.21	49.46		
		<i>Kentropyx calcarata</i>	5.6	7.4	2.69	1.36	5.27	54.73		
		<i>Ameiva ameiva</i>	1.2	5.4	2.65	1.38	5.21	59.94		
		<i>Iphisa elegans</i>	3.6	0.2	2.36	1.16	4.64	64.58		
				<i>Cercosaura ocellata</i>	0.8	2	2.1	1.2	4.12	68.7
				<i>Plica umbra</i>	2.6	0.4	2.02	1.65	3.96	72.65

^aSpecies contributing the most toward distinguishing each habitat.

^bContributions for all species until a threshold of 70% of the total dissimilarity is explained between groups. Average dissimilarity values are measured across all replicate samples for each pairwise combination of forest types.

Discussion

Herpetofauna of Primary, Secondary, and Plantation Forests

The composition of tropical herpetofaunal assemblages is related to multiple environmental gradients, and community structure can be influenced by the presence of human activities (Crump 1971; Lieberman 1986; Pearman 1997). Forest conversion creates changes in the canopy structure and leaf-litter environment of tropical forests. Land-use changes can result in the loss of microhabitats necessary for many amphibians and lizards (e.g., Lieberman 1986; Vitt & Caldwell 2001; Vallan 2002). Fewer species occurred in secondary and plantation sites than in primary forest, and one-third of species confined to primary forest included those with specific breeding and microhabitat requirements that are known as primary forest specialists (e.g., Dendrobatids and species of *Eleutherodactylus* [Pearman 1997; Duellman 2005]; arboreal or semiarboreal lizards such as *Gonatodes* sp., *Tretioscincus agilis*, and *Thecadactylus rapicauda*; and some leaf-litter lizards such as *Ptychoglossus brevifrontalis*, and *Arthrosaura kockii* and *A. reticulata* [Ávila-Pires 1995; Duellman 2005]).

The value of timber plantations in tropical forest landscapes for biodiversity has received little attention (Kanowski et al. 2005). Moreover, comparisons with existing studies in other plantation systems are potentially confounded by differences in plantation type. For example, although *Eucalyptus* plantations were depauperate for amphibians but comparable to secondary forest in terms of the number of resident lizard species, Inger (1980) found the opposite result for rubber (*Hevea* sp.) plantations in Malaysia. Furthermore, levels of diversity and abundance similar to neighboring primary forest have been found for amphibians in shaded coffee plantations in Mexico (Pineda & Halffter 2004; Pineda et al. 2005), and for lizards and frogs in pine plantations in Uganda (Vonesh 2001). The absence of many amphibian species from plantation sites may be in part due to the limited availability of suitable reproductive habitat—a function of the fact that plantations in Jari are often on flat and more elevated sites (typically plantation forests located in areas most suitable for agriculture, Lindenmayer & Franklin 2002). In general we suggest that the particular characteristics of *Eucalyptus* plantations and differences in site history and stand management confound ecologically meaningful comparisons with other plantation forestry options. Nevertheless, the fact that *Eucalyptus* currently dominates tropical plantations means that more work is needed to determine the biodiversity value of this forestry option.

Secondary forest in our study area hosted approximately two-thirds of the total number of amphibian species and one-half of the total number of lizard species that occur in the landscape, a pattern comparable to that found for both amphibians in the central Brazilian Amazon (Tocher et al. 2002: >62%) and Madagascar (Vallan

2002: 52%) and for lizards in the eastern Amazon (Crump 1971: 46%). Moreover, two studies examining the entire leaf-litter herpetofauna in abandoned cacao plantations and neighboring primary forest in Costa Rica also found that roughly two-thirds of the species from all samples occurred in secondary forest (Lieberman 1986: 65%; Heinen 1992: 62%). The similarity in the results of these studies is striking, especially because they included an array of different landscape scenarios and because the secondary forests encompass a very broad range of environmental conditions (dependent on local differences in vegetation structure and composition and disturbance history; Dunn 2004). These results suggest that secondary forests are relatively permeable (or even favorable in the case of some species, see Supplementary Material) to a significant subset of native amphibians and lizards and can therefore make a valuable contribution to the overall diversity of degraded areas, allowing several species to persist within a landscape that may otherwise be dominated by a comparatively hostile matrix (e.g., Gascon et al. 1999; Pineda & Halffter 2004).

The only other similar study in primary and secondary forests and *Eucalyptus* plantations found that 35% of all amphibian species were confined to primary forests (eastern Madagascar, Vallan 2002), a proportion identical to that in our study. Nevertheless, in contrast to Vallan (2002), we did not find any amphibian species restricted to *Eucalyptus* plantations. Moreover, patterns of amphibian species occurrences and hierarchical dominance in abundance exhibited a strongly nested distribution, a conclusion supported by work elsewhere in the Amazon (Tocher et al. 2002). Consistency in the identity of dominant amphibian species across forest types in other tropical forest regions subjected to major habitat change is supported by the results of some studies (Crump 1971; Heinen 1992), but not by others (Pearman 1997; Vallan 2002; Pineda et al. 2005), indicating that community responses to forest conversion depend on the type of disturbance and the identity of the constituent species. In the case of lizards, plantation sites were dominated by large numbers of generalist heliothermic lizards common to open areas (Ávila-Pires 1995), which were rare (*Ameiva ameiva*, *Cercosaura ocellata*) or absent (*Cnemidophorus cryptus*) from both primary and secondary forest, indicating a marked turnover in community structure. Nevertheless, and contrary to expectations (Vitt et al. 1998), the presence of high densities of large teiid lizards (*Ameiva*) did not exclude a number of smaller non-heliothermic forest species (e.g., *Gonatodes humeralis*, *Coleodactylus amazonicus*) from occurring in relatively high abundances in plantations (see also Kanowski et al. 2006 for additional information).

The colonization of both plantation and second-growth forests can be influenced by the proportion of native habitat remaining in the neighboring landscape (Fischer et al. 2006). Nevertheless, we attempted to minimize the

influence of landscape factors by locating our samples within large forest blocks (average size 2200 ha), avoiding edge effects and maintaining a comparable distance to areas of primary forest among sites.

It has been predicted that disturbance mosaics containing both areas of primary forest and alternative agricultural or forestry options may reduce alpha diversity within disturbed sites but promote higher gamma diversity at the landscape scale (e.g., Pearman 1997; Vitt & Caldwell 2001). Our data support the prediction of an additive effect in the case of lizards (Veech et al. 2002) but not amphibians, which exhibited a dilution effect, with lower richness per unit area following the addition of more habitats. This suggests that it is difficult to make generalizations about the consequences of habitat change even at the assemblage level. The lack of an increase in landscape diversity for amphibians is most likely explained by the fact that our sampling targeted leaf-litter amphibians, which are known to be more sensitive to environmental degradation than many arboreal species (Pearman 1997; Tocher et al. 2002; Duellman 2005).

Confounding Factors in the Study of Biodiversity and Habitat Change

Our results show that primary forest holds significantly more species of amphibians and lizards than either secondary or plantation forests and that primary habitat is irreplaceable for many species (approximately one-third for each taxon, Table 1). Nevertheless, reviews of existing empirical studies on land-use change and biodiversity in tropical forests have revealed contradictory results (e.g., Hamer & Hill 2000; Hill & Hamer 2004; Barlow et al. 2007; this paper). We suggest that a number of factors have to be considered in both the planning and interpretation of studies concerned with habitat conversion and biodiversity (see also Gardner et al. 2007 for additional information).

First, logistical and/or financial constraints usually restrict the spatial scale and level of replication of herpetofaunal samples, with the consequence that few studies are conducted at subregional (i.e., >20 km) scales (Doan & Arriaga 2002). Alpha and beta diversity contributed roughly equal amounts to the overall diversity of each forest type in our study. Whether this is due to differences in edaphic or geomorphic conditions, site history, or temporal variability in species activity patterns, species that occur in high abundances in some sites can be rare or absent elsewhere within the same habitat type. An allied problem to obtaining independent treatment and control sites in studies of habitat value is to ensure that all sites are located within habitat blocks of sufficient size to minimize confounding edge and spillover effects (Vallan 2002) and to ensure that control sites are sufficiently large and undisturbed to adequately represent a “true” baseline.

Second, the fact that *Eucalyptus* plantations and secondary forests in our study region host similar numbers of lizard species does not mean they perform similar conservation services. Even in the absence of data on levels of threat, it is important to examine patterns of community composition as well as richness, especially when assemblage subgroups exhibit opposing responses to disturbance, and not all species are dependent on primary forest habitat (Pearman 1997). Our results revealed that mature forest specialists were likely to be particularly threatened when faced with large-scale deforestation. Moreover, such species may be considered to be in double jeopardy because disturbance-sensitive habitat specialists often have restricted range sizes (e.g., Dunn & Romdal 2005).

Finally, many herpetological studies that have examined habitat change have combined leaf-litter amphibians and lizards together, analyzing them as a single “ecologically coherent” assemblage (Lierberman 1986; Heinen 1992; Vonesh 2001; Fredericksen & Fredericksen 2002; Gillespie et al. 2005). Results of some of these studies showed either no effect (e.g. Fredericksen & Fredericksen 2002) or a positive effect (e.g., Vonesh 2001) of disturbance on assemblage diversity. In light of the often contrasting disturbance responses of these two taxa, we question whether researchers are justified in grouping leaf-litter amphibians and lizards together and suggest that this traditional practice may lead to dangerously misleading implications regarding the consequences of habitat change for biodiversity conservation (Gibbons et al. 2000).

Conclusions

The lack of consensus among studies regarding the consequences of land-use change for tropical forest herpetofauna can be partly attributed to limitations in study design, sampling effort, and data analysis. These factors often bias researchers against revealing the true diversity of tropical primary forest, and instead presenting a best-case scenario regarding the conservation value of alternative land uses (Dunn 2004; Gardner et al. 2007).

The unique opportunity presented by the Jari project allowed us to sample amphibians and lizard communities in replicate plantation and secondary forest blocks, while minimizing neighborhood effects from the surrounding landscape. Our data show that primary forest was significantly more diverse than plantations or secondary forest and indispensable for many species. *Eucalyptus* plantations have been described as resembling biological deserts, contributing little or no intrinsic value for native species in rainforest landscapes (Kanowski et al. 2005). Our data support this notion because the plantations we examined were species poor and dominated largely by

generalist species with widespread distributions. In contrast to plantations, secondary forests harbored a significant subset of native amphibians and lizards, indicating that these forests can make a valuable contribution to the conservation of forest species in degraded or abandoned land (Dunn 2004). Nevertheless, in the absence of data on patterns of faunal recovery in older regrowth forests (>20 years) and from regrowth forests in areas that are not adjacent to continuous primary forest, we caution against the optimistic claim that natural forest regeneration in abandoned lands will provide refuge for many species that are threatened by deforestation (Wright & Muller-Landau 2006, but see Brook et al. 2006; Laurance 2007; Gardner et al. 2007).

Acknowledgments

We thank the Brazilian Ministerio de Ciencias e Tecnologia (CNPq) and Ministerio do Meio Ambiente (MMA-IBAMA) for permissions to do this research and Grupo Orsa for support and permission to work on their land. The project was funded by the United Kingdom government's Darwin Initiative, Natural Environment Research Council (NERC), National Geographic Society, Conservation Food and Health Foundation, Conservation International, and the Brazilian Council for the Development of Science/CNPq (process 473287/04-8). We thank M. Donnelly and three anonymous reviewers for constructive comments that greatly improved an earlier version of this manuscript. This is publication 5 of the Land-Use Change and Amazonian Biodiversity project.

Supplementary Material

A list of species of herpetofauna caught by standardized trapping methods in the Jari landscape of northeastern Brazilian Amazonia is available in conjunction with the online version of this article from <http://www.blackwell-synergy.com/doi/abs/10.1111/j.1523-1739.2007.00659.x> (Appendix S1).

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