

Species richness and composition of amphibians and reptiles in a fragmented forest landscape in northeastern Bolivia

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Received 30 October 2006; accepted 28 September 2007

Abstract

We quantified patterns of species richness and species composition of frogs and reptiles (lizards and snakes) among three habitats (continuous forest, forest islands, and a seasonally flooded savannah) and between forest island size and isolation classes in a floristic transition zone in northeastern Santa Cruz Department, Bolivia. Species richness was similar across macrohabitats, as was faunal composition of forested habitats, although savannah harbored a distinct herpetofauna. On forest islands, richness and composition of forest frogs was largely related to isolation, whereas reptiles were affected by both isolation and habitat. The observation that isolation rather than area was the primary driver of distribution patterns on forest islands stands in contrast to many studies, and may be a function of (1) the greater range in forest island isolation values compared to area or (2) the long history of isolation in this landscape. © 2007 Gesellschaft für Ökologie. Published by Elsevier GmbH. All rights reserved.

Zusammenfassung

Wir bestimmten die Muster des Artenreichtums und der Artenzusammensetzung von Fröschen und Reptilien (Eidechsen und Schlangen) in drei Habitaten (geschlossener Wald, Waldinsel, saisonal überflutete Savanne) und für Klassen von Waldinselgröße und Isolation in einer floristischen Übergangszone im nordöstlichen Santa Cruz Bezirk, Bolivien.

Der Artenreichtum war für alle Habitate ähnlich, ebenso die Zusammensetzung der Fauna in den Waldhabitaten, die Savanne beherbergte aber eine eigenständige Herpetofauna. In den Waldinseln waren Artenreichtum und -zusammensetzung der Frösche weitgehend mit der Isolation verknüpft, während die Reptilien von beidem, Isolation und Habitat, beeinflusst wurden.

Der Befund, dass eher die Isolation als die Arealgröße der treibende Faktor für die Verteilungsmuster in den Waldinseln war, steht im Gegensatz zu zahlreichen Studien und könnte durch (1) die größere Streubreite der Isolationswerte gegenüber den Flächenwerten oder (2) eine lange bestehende Isolation in dieser Landschaft bedingt sein.

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Keywords: Biodiversity; Community ecology; Conservation; Fragmentation; Herpetology; Landscape ecology

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Introduction

Scientists have implicated habitat loss and fragmentation as among the most important threats to biodiversity, and it has been suggested that they may threaten up to one-half of the world's species with extinction (Brooks et al., 2002; Stockwell, Hendry, & Kinnison, 2003; Wilson, 2002). Although there is debate over the relative importance of habitat loss versus fragmentation (Andr n, 1994; Fahrig, 1997; Trzcinski, Fahrig, & Merriam, 1999), the conversion of a continuous expanse of habitat into smaller, discontinuous patches reduces the habitat area available to species and increases the importance of edge effects in patches, and these physical changes often result in a cascade of biotic changes (Harrison & Bruna, 1999; Laurance & Bierregaard, 1997). With the exception of studies from oceanic islands, there are relatively few data describing faunal assembly in landscapes other than forest remnants created by anthropogenic habitat destruction (Watson, 2002). We believe that an understanding of the effects of anthropogenic habitat fragmentation may be informed by a wider appreciation of faunal responses to habitat patchiness arising from both anthropogenic and natural processes (Watling & Donnelly, 2006). To that end, we present a case study describing patterns of amphibian and reptile community assembly across macrohabitats (forest, forest islands, and a seasonally flooded savannah) and forest island area and isolation gradients in a naturally fragmented landscape in the southern Amazon basin.

Macrohabitat is often the most important resource partitioned by adult amphibians and reptiles (Toft, 1985), and these animals tend to be associated with either forest or open habitats, but not both (Heyer, 1988). Such strict habitat associations imply that the fauna of forest islands should represent a characteristic forest fauna. Alternatively, species evolved for survival in open (grassland) habitats may invade forest islands, altering the composition of forest island assemblages either via mass effects (Shmida & Wilson, 1985) or because of habitat differences on forest islands compared to continuous forest. With respect to faunal assembly on forest islands, the Equilibrium Theory of Island Biogeography (ETIB, MacArthur & Wilson, 1967) suggests that species richness in patches is determined by extinction and colonization processes that are related to both patch area and isolation. Across a wide variety of patchy landscapes, there is consistent support for the notion that species richness increases with area, but less support for the relationship between richness and isolation (Watling & Donnelly, 2006).

Northeastern Bolivia lies in a climatic and biogeographic transition zone where the landscape consists of a mosaic of moist and dry forests and seasonally flooded and dry grasslands (Killeen, 1998). The distribution of

forest and grassland in northeastern Bolivia reflects a response to regional climate, and grasslands have been a characteristic part of the landscape for millennia (Burbridge, Mayle, & Killeen, 2004). As a result, the regional flora and fauna include widely distributed Amazonian species as well as species characteristic of extra-Amazonian open habitat formations (Killeen & Schulenberg, 1998). The interface between forest and grassland is often very abrupt, and from the El Refugio basecamp, we had access to a large patch of moist forest, a seasonally flooded grassland ('savannah' or 'pampa'), and forest islands occurring within the grassland matrix. Using species richness and species composition as response metrics, we utilize different taxonomic and ecological partitions of the local herpetofauna to investigate distributions across macrohabitats as well as forest island area and isolation gradients. On forest islands, we attempt to distinguish between responses to area and isolation per se, and habitat-mediated distribution patterns.

Materials and methods

Data were collected at the El Refugio-Huanchaca Biological Station (14°45'S, 61°01'W) in northeastern Bolivia from May 2003 to February 2004. Both the regional and local landscapes are mosaics of forest and grassland (seasonally flooded grasslands and non-flooded, Cerrado-like formations) with forest islands embedded in a grassland matrix (see Appendix A: Fig. 1). Details of floristic composition across habitat types in the region may be found in Killeen and Schulenberg (1998). The forest islands we studied are presumed to be remnants of a formerly continuous forest that were fragmented by wildfires and drying of the soil horizon (Killeen & Schulenberg, 1998). Rainfall at El Refugio averages 1420 ± 293 mm a year (mean \pm 1SD, 1996–2003 inclusive), and is distributed seasonally, with a rainy season from November to April and a dry season from May to October.

Habitat sampling

We measured seven habitat variables during the dry season (August–September 2003) and four during the rainy season (February 2004). We took measurements from two 12 m \times 12 m plots on each forest island or continuous forest sampling point in the dry season, and three plots during the rainy season. Plots were installed both around pitfall traplines (see Faunal sampling, below) and haphazardly in forest in the vicinity of traplines. In each of the four corners of all plots we counted the number of saplings (trees with diameter <2 cm) at breast height (DBH) and the number of

leaves pierced by a pair of forceps stuck in the ground. Canopy density was measured with a spherical densiometer four times (each reading at a 90° angle from the previous one) in each corner for a total of 16 measurements per plot. We estimated the percent cover of bare ground, grass, and herbaceous vegetation, and counted the number of fallen trees and branches greater than 10 cm in diameter in each plot. In the wet season, we measured leaf litter and canopy density as described above, but distinguished between understory palms and other saplings. In addition, we noted whether the soils on the forest islands were sandy or clay, and recorded the number of months forest islands were surrounded by standing water during the 2002–2003 rainy season. We did not record the last two variables from continuous forest because soils were not easily categorized as sandy or clay, and except for pitfall traps along the riverbank, the continuous forest did not flood.

Faunal sampling

We sampled amphibians and reptiles in three habitat types: continuous forest, seasonally flooded grassland, and forest islands. The 24 forest islands ranged in size from 0.6 to 8.5 ha, and were located 5–4820 m from the continuous forest (see Appendix A: Table 1). Forest islands were assigned to one of two size and isolation classes *a priori*. Large islands were between 2.5 and 8.5 ha, whereas small islands were 0.64–2.5 ha. Near islands were 5–600 m from continuous forest whereas far islands ranged from 670 to 4820 m from continuous forest. We used pitfall traps to sample animals along 12 m straight-line drift fences, with four 19 L buckets per drift-fence array in forest and on forest islands (Corn, 1994). Two drift fence arrays were installed at each of four sampling points in continuous forest, and on all large forest islands. Small forest islands were sampled with one 12 m array. Seasonal flooding in the savannah precluded the use of pitfall traps in that habitat, so we sampled the savannah using funnel traps located at the ends of a 12 m drift fence (Corn, 1994). One trap line was located at each of three sites in the savannah. Faunal samples were collected over 7564 trap nights between May 2003 and February 2004.

Statistical analysis

Habitat variables

We used multivariate statistics to model differences in habitat between continuous forest and forest islands, and between forest islands size and isolation classes. Analysis of Similarity (ANOSIM) calculates a test statistic (Global R) describing compositional similarity across levels of a factor (in this case habitat or forest island size or isolation class), and tests the significance of

the observed Global R value using a resampling approach (Clarke & Warwick, 2001). Non-metric Multi-dimensional Scaling (nMDS) allows for the visualization of the results of an ANOSIM; in an nMDS graph the distance between points on the graph is proportional to the compositional similarity of those points. Upon creating nMDS plots describing differences in habitat composition using all variables, we correlated individual habitat variables from each forest island with nMDS loading scores from each island along nMDS axes 1 and 2 to describe habitat gradients in nMDS space.

Faunal variables

We categorized species captured on forest islands as either forest specialists or habitat generalists, depending on whether we found more individuals per trap night in the forest or pampa at El Refugio. Species encountered only on forest islands were not categorized as either specialists or generalists. All amphibians captured were members of order Anura (frogs and toads), but because all toads are frogs, we use the more general term ‘frogs.’ Reptiles were represented by snakes, lizards, and one amphisbaenian, so we use the term ‘reptiles.’ We ran most analyses for (1) forest frogs, (2) generalist frogs, (3) forest reptiles, and (4) generalist reptiles.

Species richness

Observed species richness S_{obs} almost always underestimates true species richness S_{true} , and consequently, inferences made using S_{obs} may not be robust to subsequent sampling at a site (Herzog & Kessler, 2006). We estimated our sampling efficiency by comparing observed species counts from each site (forest island, forest trap array, or pampa trap) to a species richness estimate S_{est} from each site using extrapolated species richness estimates in program EstimateS (Colwell, 1997). We used two metrics of S_{est} , the Chao 1 and Chao 2 estimators, which have been recommended as robust species richness estimators (Walther & Moore, 2005). Sampling efficiency can be estimated as $S_{\text{obs}}/S_{\text{est}}$, with values near 1 indicating that most of the species estimated to occur at a site have actually been observed.

Because sampling intensity varied among habitats, we compared species richness among habitats by visual inspection of overlapping 95% confidence intervals from individual-based species accumulation curves. Because most species were associated with forested or open habitats, but not both, our analyses of species richness across habitats did not distinguish specialist species from generalists. On forest islands, we used the nMDS loading scores of each island along the axes of the habitat composition nMDS to describe the relative similarity of forest islands based on habitat characteristics. We modeled species richness on forest islands

using this metric of habitat quality in addition to forest island area and isolation. Our preliminary analyses indicated that relationships between species richness and area were best modeled by log–log transformation, whereas for isolation and habitat, untransformed variables provided the best fit.

To make our data comparable with existing literature, we began by using simple linear regression to investigate relationships between species richness and each of the three independent variables. Following the univariate tests, we used multiple regression to model $\ln(\text{species richness})$ of each taxonomic/ecological partition of the El Refugio herpetofauna as a simultaneous function of area, isolation, and habitat. Because of significant intercorrelation between two of the independent variables (see Results), we used the residuals of the regression equation describing the linear fit between those two variables in multivariate tests of species richness.

Species composition

We compared species composition among habitats and between forest island area and isolation classes using the same combination of multivariate statistical approaches described for the habitat data. We used a one-way ANOSIM to describe compositional differences across habitats, and a two-way test to investigate differences between forest island area and isolation classes. Because we only encountered forest reptiles at one pampa site, our analyses of forest reptiles tested for compositional differences between forest and forest islands only. We used Mantel tests to generate an R value describing relationships between species composition and habitat composition, using the poptools function in program Excel. Statistical significance for Mantel tests was estimated by counting the number of times correlations resulting from 999 randomizations of the two composition matrices resulted in a correlation coefficient greater than the observed value.

Finally, to test whether the dominance of amphibians or reptiles varied with forest island area or isolation, we related the dominance of frogs (as a percentage of the total fauna from each forest island) to area (in ha) or isolation (in m) using simple linear regression. All statistical tests not conducted in Primer or Excel were performed in JMP (SAS Institute, 2000).

Results

Habitat

The difference in habitat composition between forest and forest islands was statistically suggestive (Global

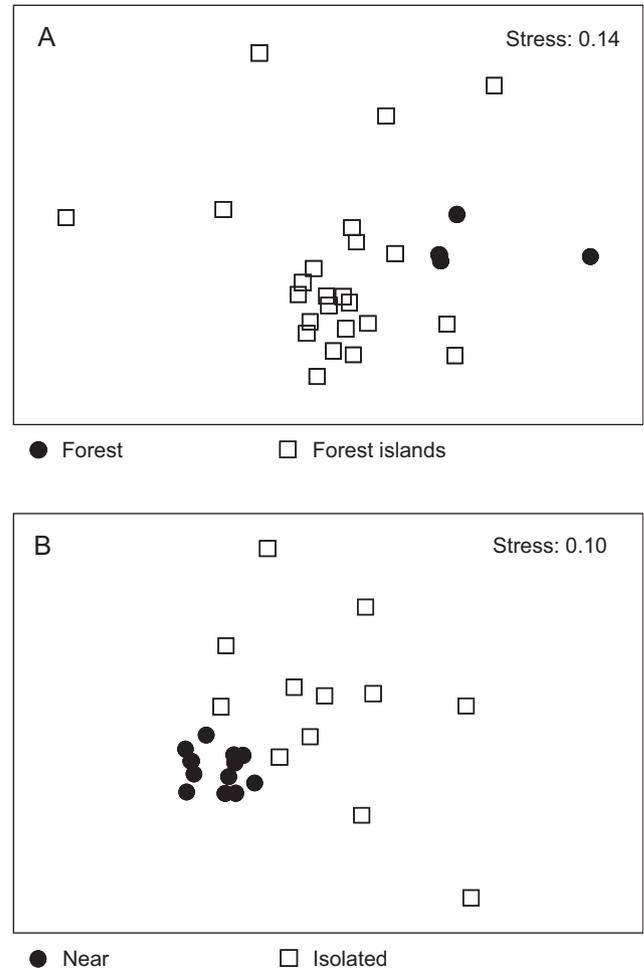


Fig. 1. nMDS plots of habitat composition between continuous forest and forest islands (A) and forest island isolation classes (B).

$R = 0.333$, $P = 0.054$; Fig. 1(A)). On forest islands, there was no difference in forest composition between size classes (Global $R = 0.079$, $P = 0.153$), but habitat on isolated forest islands was distinct from forest islands near the continuous forest (Global $R = 0.519$, $P < 0.001$). Both nMDS axes one and two described a gradient in forest cover, but subsequent analyses indicated that faunal richness was related only to nMDS axis 1, so we include only that variable as a metric of forest habitat. Low values on nMDS axis 1 described islands with dense canopy cover in the wet season, abundant leaf litter and logs, a few saplings or herbs and little bare ground. In other words, more forest-like conditions are represented by low values on nMDS axis 1 where the forest islands near continuous forest are clustered (Fig. 1(B)).

Species richness

Sampling efficiency was slightly higher for frogs than reptiles in forested habitats, whereas the opposite was

true in the pampa (see Appendix A: Table A1). The overall sampling efficiency averaged $82\% \pm 8.2$ (mean \pm 1SD), so we are confident that S_{obs} is a reasonable approximation of true species richness.

Overall, our trap data resulted in the observation of 44 species (16 frogs and 28 reptiles) across the three habitats. Most frog species occurred in forest habitat, followed by forest islands and savannah (Fig. 2(A)). For reptiles, we observed the most species in savannah, followed by forest and forest islands (Fig. 2(B)). However, there was a great deal of overlap in the error estimates for species richness for both faunal groups, and we conclude that species richness is broadly similar across the three macrohabitats.

The results of simple linear regressions describing the relationships between species richness and area, isolation, or nMDS axis 1 indicated that species richness of generalist frogs increased with island area ($\ln(\text{no. generalist frogs} + 1) = 0.2400(\ln(\text{area})) + 0.7736$, $P = 0.028$; Fig. 3(A)), and richness of forest frogs decreased with distance from continuous forest ($\text{no. forest frogs} = -0.0007(\text{isolation}) + 4.3839$, $P < 0.001$; Fig. 3(B)). Only forest frogs showed a relationship with habitat, with richness decreasing along the forest cover gradient represented by nMDS axis one (no. forest

$\text{frogs} = -1.0572(\text{nMDS axis 1}) + 3.6254$, $P = 0.002$; Fig. 3(C)). There were no relationships between reptile species richness and area or isolation.

Among the independent variables, area was not correlated either with isolation ($R = 0.158$, $P = 0.46$) or habitat ($R = -0.123$, $P = 0.57$), but the forest habitat metric was correlated with isolation ($R = 0.629$, $P = 0.001$). Therefore, we utilized the residuals of the regression equation describing the relationship between isolation and habitat as a metric of forest island isolation independent of the association between isolation and habitat. The residuals of the isolation-habitat regression were not correlated with area ($R = 0.303$, $P = 0.150$).

Multiple regression models largely corroborated the patterns revealed by simple linear regression. Although the overall models were not significant in most cases, there was a significant effect of isolation (after controlling for habitat) on richness of forest frogs ($P = 0.029$), and a significant effect of area on richness of generalist frogs ($P = 0.024$). Although reptile species richness showed no relationships with area, isolation, or habitat when analyzed using simple linear regression, the multiple regression was significant ($P = 0.041$), indicating that richness of forest reptiles, decreased with the isolation term ($P = 0.020$). Multiple regression revealed no significant effects of either area or isolation on generalist reptiles.

Species composition

Species composition of generalist frogs did not vary by habitat (Global $R = 0.191$, $P = 0.098$), but composition of forest frogs did vary among habitats (Global $R = 0.333$, $P = 0.009$; Fig. 4(A)). Pairwise comparisons indicated that forest and forest islands were compositionally indistinct, whereas pampa and forest and pampa and forest islands were distinct. The overall models of species composition for reptiles were statistically suggestive for generalist species (Global $R = 0.233$, $P = 0.05$; Fig. 4(B)), but not for forest species (forest versus forest islands only; Global $R = 0.191$, $P = 0.098$).

For both forest and generalist frogs, species composition differed significantly between forest island isolation classes (Global $R = 0.213$, $P = 0.019$ and Global $R = 0.509$, $P < 0.001$; Figs. 5(A) and (B)), but not by area (Global $R = 0.093$, $P = 0.153$, Global $R = 0.115$, $P = 0.113$). Community composition of forest reptiles differed between both area and isolation classes (Global $R = 0.206$, $P = 0.039$ and Global $R = 0.243$, $P = 0.015$; Figs. 5(C) and (D)), but species composition of generalist reptiles did not vary with either area or isolation (Global $R = -0.013$, $P = 0.516$ and Global $R = -0.032$, $P = 0.587$). The relationship between species

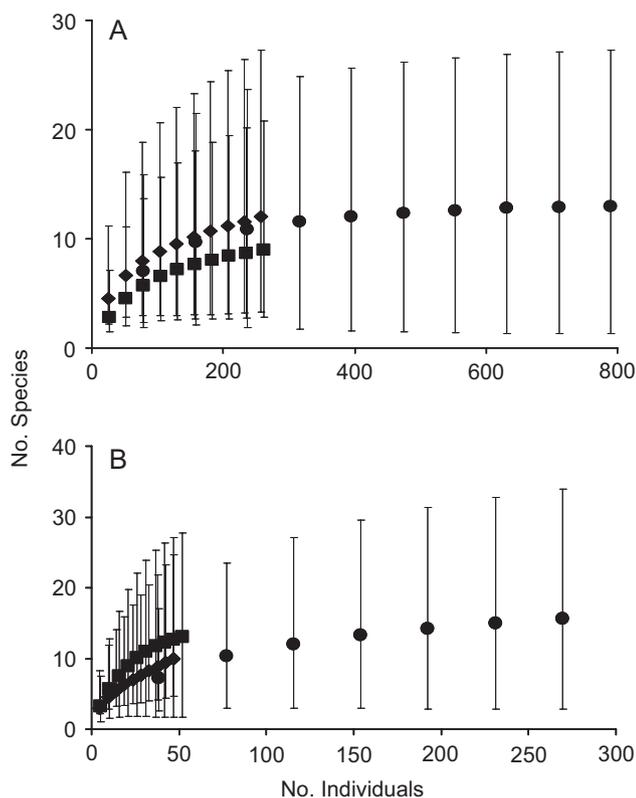


Fig. 2. Individual-based species accumulation curves in three macrohabitats (forest indicated by diamonds, pampa by squares, and forest islands by circles) with 95% confidence intervals for amphibians (above) and reptiles (below).

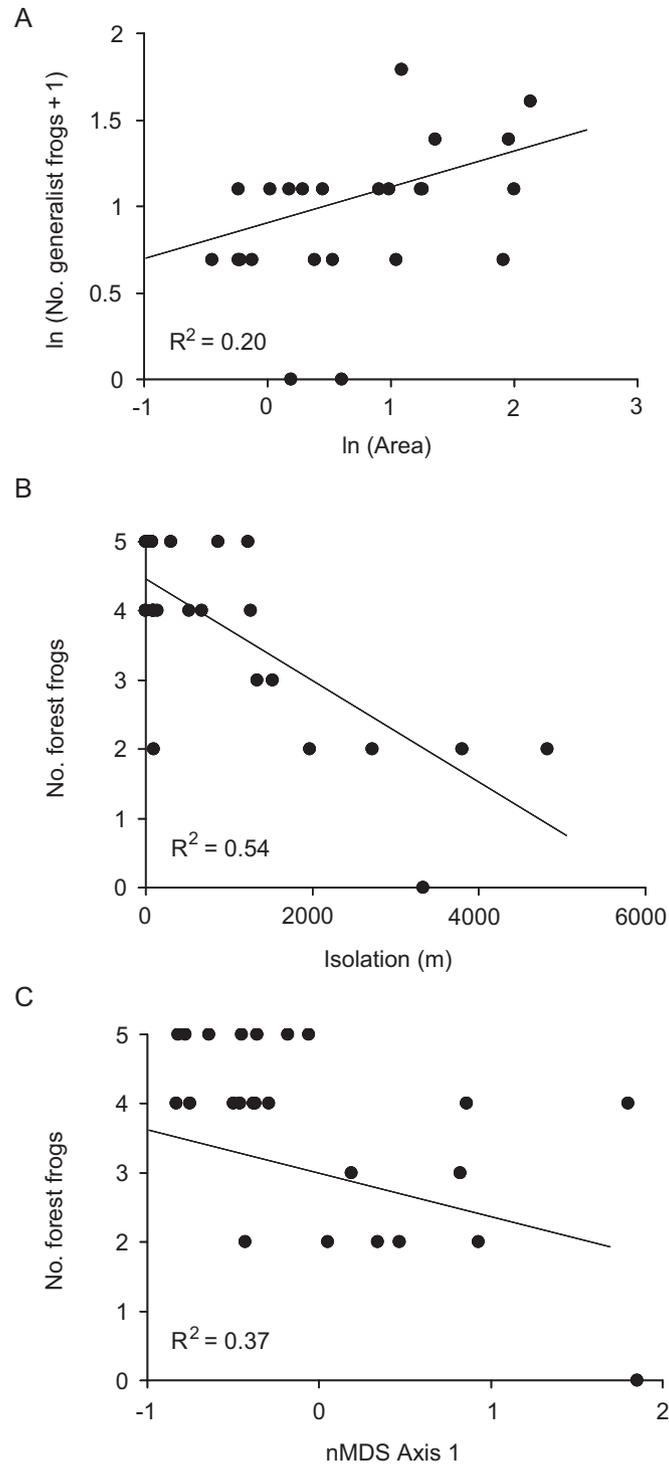


Fig. 3. Scatterplots illustrating relationships between (A) species richness of generalist frogs and area; (B) species richness of forest frogs and isolation; and (C) species richness of forest amphibians and forest cover gradient along nMDS axis 1.

composition and habitat composition was not significant for forest frogs ($R = 0.064$, $P = 0.262$, but was for generalist frogs ($R = 0.425$, $P < 0.001$). In contrast, species composition of forest reptiles was correlated with habitat composition ($R = 0.335$, $P = 0.002$), but there was no relationship between species composition

and habitat composition for generalist reptiles ($R = 0.006$, $P = 0.450$).

There was no relationship between frog dominance and area ($F_{1,22} = 0.979$, $P = 0.33$), but frog dominance decreased with forest island isolation ($F_{1,22} = 12.96$, $P = 0.002$; Fig. 6).

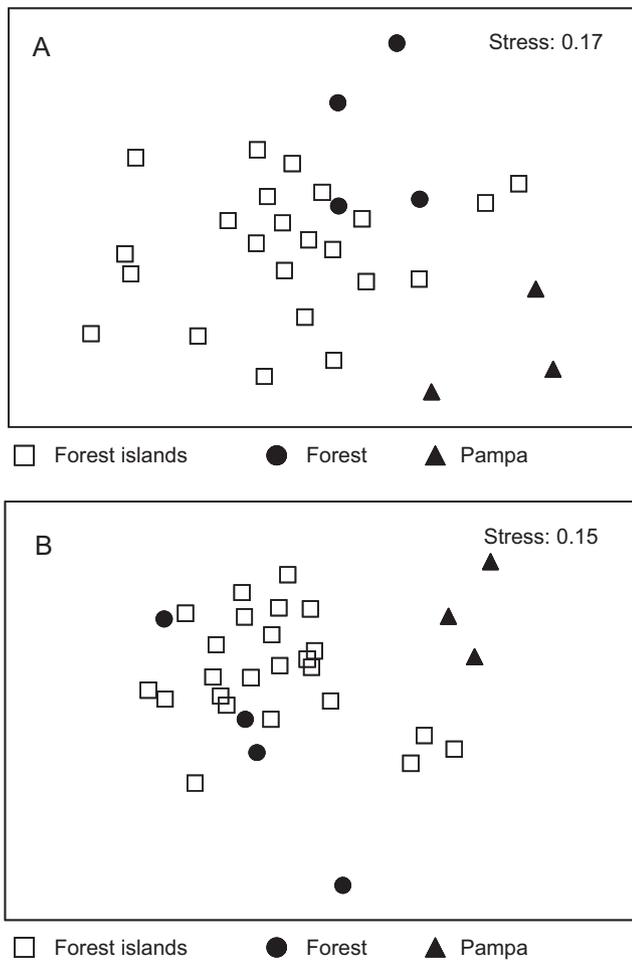


Fig. 4. nMDS plots of species composition between continuous forest and forest islands for amphibians (above) and reptiles (below).

Discussion

We found that species richness was broadly similar across habitats and that the fauna of the two forest habitats was, for the most part, compositionally indistinguishable, but different from species composition in the pampa. Although we suspect that the major conclusions resulting from our analyses across habitat are likely to be robust to further sampling, we acknowledge that differences in sample sizes across macrohabitats mean that these results should be interpreted with caution.

Species richness of generalist frogs increased with area and species composition of forest reptiles differed between forest island size classes. In contrast, isolation had a significant effect on forest island habitat composition, was associated with a decrease in species richness of forest frogs, a decrease in forest reptiles (in the multiple regression model), and led to an altered composition of forest reptiles, forest frogs, and

generalist frogs. Despite finding some effects of area on the forest island herpetofauna, we are reluctant to ascribe much importance to these observations because (1) it is not clear to us why species richness of generalist frogs would increase with area of forested habitat, given that we did not find any variation in habitat as a function of forest island area, and (2) although there was a significant difference in species composition of forest reptiles between area classes, the relationship was stronger between isolation classes. Therefore we focus the discussion on isolation effects on habitat, species richness, and species composition on forest islands.

The observation that forest frogs are influenced directly by isolation implies that these species are dispersal limited on forest islands, and this result is most succinctly summarized in Fig. 6: frog dominance decreases linearly with isolation. We suspect that the combination of water balance physiology and body size likely explains the relative importance of dispersal limitation for frogs compared to reptiles at this site. Amphibians in general are more reliant on ambient moisture than reptiles, and although some species are adapted for life in open habitats, amphibians with an evolutionary history in forested environments in South America likely lack the physiological capabilities to disperse through an open savannah (Heyer, 1988). We are not aware of studies directly comparing the water use efficiency of forest and generalist frogs, but it is well known that species from open habitats tend to show adaptations to water stress that are not shared by species with an evolutionary history in forest habitats (Duellman & Trueb, 1986; Jørgensen, 1997). Exacerbating the effects of moisture stress, frogs that occur on forest islands at El Refugio are smaller than forest island reptiles (mean $\ln(\text{mass}) = -0.539 \pm 0.049$ and mean $\ln(\text{mass}) = 1.251 \pm 0.075$ for frogs and reptiles, respectively), and all other things being equal, large species are generally thought to be better dispersers than small species (Etienne & Olf, 2004; Hager, 1998).

Species composition of both forest reptiles and generalist frogs was influenced by habitat, and habitat composition covaried with isolation. We suspect that the habitat differences between forest island isolation classes are a result of a differential influence of periodic fires. Wildfires are a natural feature of the savannah around El Refugio (Killeen, 1998), although fires of human origin also occur in the area (JIW, pers. obs.). We worked in the northern portion of a savannah complex that extends more than 20 km south of the most isolated forest island included in this study. Periodic cold fronts during the austral winter (the July–December dry season) bring strong winds from the south and it is during the later 3–4 months of the dry season when the savannah around forest islands burns. Thus the most isolated forest islands reported on here experience a higher intensity, and possibly frequency, of wildfires

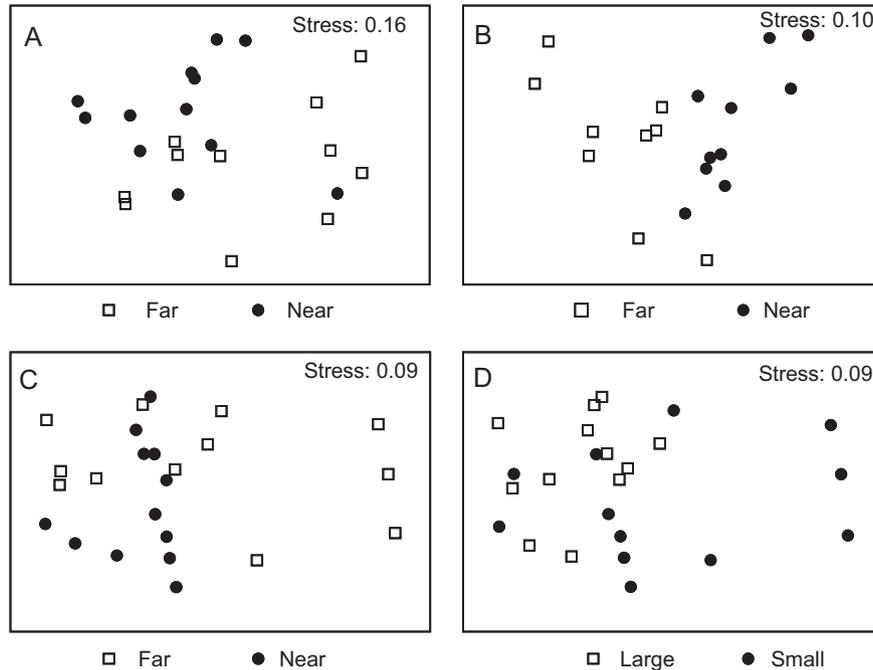


Fig. 5. nMDS plots of species composition between forest islands isolation classes for (A) generalist amphibians and (B) forest amphibians, and for forest reptiles between forest island area classes (C) and isolation classes (D).

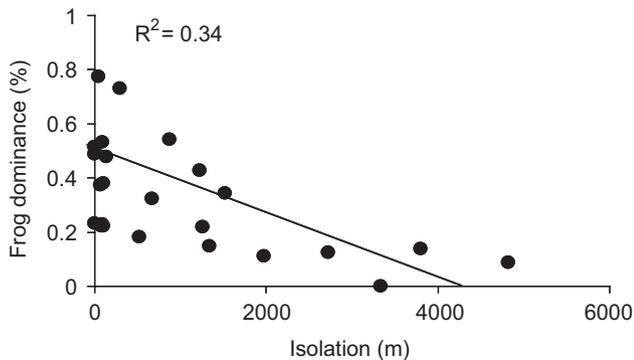


Fig. 6. Scatter plot showing the linear decrease in frog dominance (the proportion of all individuals on an island represented by frogs) with increasing forest island isolation.

than islands near continuous forest, and these fire effects may alter the habitat structure of isolated forest islands.

The vast majority of studies investigating the effects of patch area and isolation on species richness find an area effect, but relatively few report an isolation effect (Watling & Donnelly, 2006). Here we present a case study where isolation exerts a strong influence on species richness and species composition of a forest island fauna. The forest islands we studied ranged in size from 0.6 to 8.5 ha, but isolation from continuous forest ranged from 5 to 4820 m. The range in isolation values was much greater than the range in area values we studied, and this may help to explain why we found a strong effect of isolation on the forest island herpeto-

fauna. It is also possible that a time since isolation effect may also underlie some of our results (Gonzalez, 2000). Because the forest islands we studied are presumed to be old (at least relative to most studies of anthropogenic habitat patches) it may be that extinction-based faunal relaxation has already occurred, and that forest islands now manifest a footprint of dispersal limitation that only becomes apparent in relatively old habitat patches (e.g., sky islands, Watling & Donnelly, 2006). Finally, near islands are by definition closer to patches of ‘continuous’ forest, so the overall proportion of forest habitat surrounding forest islands is greater on near islands than far islands. The proportion of appropriate habitat in the landscape around patches is an important driver of fragmentation effects (Andrén, 1994; Fahrig, 1997), and the isolation effects we describe reflects the reduced proportion of forest habitat around isolated forest islands at El Refugio.

It has previously been suggested that habitat may be more important than island biogeography in determining distributions of Amazonian frogs (Zimmerman & Bierregaard, 1986). Although our data are not consistent with this notion, that argument was based on the distribution of breeding habitat; there were no appreciable differences in the distribution of breeding habitat on the forest islands studied here (JIW, pers. obs.), so we would not necessarily expect to find strong habitat effects on frog distributions in this landscape. Our description of differing responses to habitat patchiness between ecologically and taxonomically defined partitions of the total data set underscore the importance of

explicitly incorporating ecological knowledge into the investigation of faunal responses to habitat patchiness (i.e., Steffan-Dewenter & Tschardtke, 2000).

Acknowledgments

Funding for this research was provided by a STAR fellowship from the United States Environmental Protection Agency and a Dissertation Year Fellowship from Florida International University. The work reported on here was conducted under IACUC approval # 02-014 from FIU. We thank M. Harvey, B. Phillips, I. Phillips, R. Brooks, R. Choré, H. Choré, M. Choré, V. Roca, and M. Suarez for all their assistance both in and out of Bolivia. P. Coca, Y. Higuera, and particularly I. Zambrana provided assistance in the field. We thank J. Aparicio for arranging permits, J. Rossiman for providing access to forest islands on his property, and The Weeden Foundation for their support of JIW at El Refugio. A. Catenazzi, K. Bell, L. Collins, S. Koptur, H. Liu, M. McClain, T. Philippi, K. Ruiz, R. Saporito, H. Vasconcelos, R. Von May, and S. Whitfield made constructive comments on the manuscript. This is contribution number 131 from the Program in Tropical Biology at FIU.

Appendix A. Supplementary materials

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.baae.2007.09.009](https://doi.org/10.1016/j.baae.2007.09.009).

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