Microhabitat Variation Explains Local-scale Distribution of Terrestrial Amazonian Lizards in Rondônia, Western Brazil

Adrian A. Garda[1,8], **Helga C. Wiederhecker**[2], **Alison M. Gainsbury**[3], **Gabriel C. Costa**[1], **R. Alexander Pyron**[4],
Gustavo H. Calazans Vieira[5], **Fernanda P. Werneck**[6], and **Guarino R. Colli**[7]

[1] Laboratório de Anfíbios e Répteis, DBEZ–Centro de Biociências, Universidade Federal do Rio Grande do Norte, Campus Universitário, Lagoa Nova, Natal, RN, 59078-900, Brazil

[2] Centre for Tropical Biodiversity and Climate Change, School of Marine & Tropical Biology, James Cook University, Townsville, QLD, 4811, Australia

[3] Section of Integrative Biology, The University of Texas at Austin, University Station, C0900, Austin, TX, 78712, U.S.A.

[4] Department of Biological Sciences, The George Washington University, Washington, DC, 20052, U.S.A.

[5] Departamento de Sistemática e Ecologia, CCEN, Universidade Federal da Paraíba, João Pessoa, PB, 58051-900, Brazil

[6] Department of Biology, Brigham Young University, Provo, UT, 84602, U.S.A.

[7] Departamento de Zoologia, Universidade de Brasília, Brasília, DF, 70910-900, Brazil

ABSTRACT

We investigate the role of ecology and phylogeny in the association between lizard abundance and microhabitat variables in an Amazon rain forest site. Using pitfall trap arrays, we collected data from 349 individuals belonging to 23 lizard species. After accounting for spatial autocorrelation and using a canonical correspondence analysis (CCA), we found that lizard captures were significantly associated with microhabitat variables, which accounted for 48 percent of the observed variation. Furthermore, a canonical phylogenetic ordination (CPO) indicated that microhabitat variables are more important in determining the distribution of lizard species than phylogenetic relationships among species. Termite nests, canopy openness, and tree circumference were strongly associated with the number of captures of certain lizard species. Our results confirm autecology studies of individual lizard species for which data are available. We suggest that maintaining heterogeneous forested microhabitats should be a central goal for sustaining a high lizard biodiversity in Amazon rain forests.

Abstract in Portuguese is available in the online version of this article.

Key words: Amazon; canonical correspondence analysis; canonical phylogenetic ordination; community structure; phylogenetic ANOVA; squamata.

COMMUNITY COMPOSITION VARIES GEOGRAPHICALLY IN RESPONSE TO PHYLOGENETIC HISTORY, ecological interactions, and biogeography (Brown & Lomolino 1998). Thus, the relative importance of factors affecting composition and structure depends on spatial, temporal, and phylogenetic scales under consideration (Webb *et al.* 2002, Graham & Fine 2008). Biogeographic processes work at broader spatial scales, whereas density-dependent interactions and environmental filtering are prominent forces at local and habitat scales (Cavender-Bares *et al.* 2009). Phylogenetic community structure has been assessed through comparisons of species relatedness in specific communities against the relationships of regional pools or by evaluating the concordance of phylogenetic and ecological dissimilarities among species within individual assemblages (Cavender-Bares *et al.* 2009, Vamosi *et al.* 2009).

The first attempts to compare such changes in community composition relied on species-per-genus ratios and assumed that values smaller than expected by chance resulted from competitive

interactions limiting species coexistence, whereas higher values indicated that only similar species are able to coexist in the community (Elton 1946, Moreau 1948). Subsequently, the role of competitive interactions succumbed to criticisms concerning taxonomic uncertainty (limited use of ratios as proxy of phylogenetic relationships), null models assumptions (Gotelli & Graves 1996), and the increasing appreciation of the role of phylogeny in shaping community structure (Ricklefs & Schluter 1993). Recently, the possibility of evaluating processes that act on different time and spatial scales has fueled a renewed interest in the subject because of the availability of several well-resolved phylogenies (Webb *et al.* 2002).

In spite of the recent blossom of literature on phylogenetic community structure, whether community structure and assembly is affected primarily by present-day ecological factors, historical contingencies, or other neutral processes remains a fundamental question (Tilman 1982, Ricklefs & Schluter 1993, Hubbell 2001). To fully accomplish the merger of community ecology and phylogenetics, data on phylogenetic community structure must be evaluated along with species niche dimensions from communities

being analyzed (Webb *et al.* 2002). Otherwise, the relative contributions of habitat filtering, competition, neutral processes, and biogeography cannot be separated (Cooper *et al.* 2008, Rabosky *et al.* 2011). At regional scales, distributions are mediated by forces along a continuum, from strictly historical to ecological parameters mediated by environmental filtering (Cavender-Bares *et al.* 2009). As such factors are inexorably entangled, the study of community structure must use phylogenetic information, ecological niche characteristics, and null models to fully understand local species composition and community assembly (Rabosky *et al.* 2011). Detailed analysis of individual assemblages is therefore of paramount importance to clarify the effects of phylogenetic community structure and niche segregation (Webb *et al.* 2002).

Numerous studies of phylogenetic impacts on community structure are available for different taxonomic groups, but local microhabitat characteristics have been featured less prominently (but see Rocha & Bergallo 1997, Vitt *et al.* 2007a, Rabosky *et al.* 2011). Relatively few studies have evaluated the impact of microhabitat use on community structure by explicitly analyzing species relationships (but see Vitt *et al.* 1999, Cavender-Bares *et al.* 2004, Pennington *et al.* 2006). Lizards are a good model system to investigate structure in microhabitat use: they are locally abundant and easy to collect, and the relationship between lizard distribution and microhabitat variation is expected to differ from other terrestrial vertebrates, given their relative small size, limited mobility, and low energy and water requirements (Heatwole & Taylor 1987, Nagy *et al.* 1999). Recent studies on local lizard assemblages in the tropics evaluated the effects of phylogeny on microhabitat use in lizards from the Cerrado (Mesquita *et al.* 2006b) and Seasonally Dry Tropical Forests (SDTF) (Werneck *et al.* 2009). Both found that communities were not structured with respect to microhabitat, and that microhabitat use was not associated with phylogeny. In contrast, one Amazon forest lizard assemblage was structured with respect to microhabitat use, although independent of phylogenetic effects (Vitt *et al.* 1999).

Herein, we evaluate local relationships among lizard species and microhabitat parameters in an Amazon rain forest site in Rondônia state, Brazil. By sampling lizard species and quantifying key microhabitat parameters, we evaluate: (1) lizard species richness and number of captures; (2) whether microhabitat parameters determine patterns of species distributions; and (3) whether phylogenetic relationships at the community level determine the association between lizard distribution patterns and microhabitat parameters. We discuss the implications of our results for phylogenetic community ecology and relate them to current knowledge of lizard species autecology. Finally, we discuss how our methods can contribute to studies of lizard community structure and management decisions in the Amazon region.

METHODS

STUDY SITE.—The study site is located in southwestern Amazonia, near the city of Guajará-Mirim (10° 48′S, 65° 22′ W), Rondônia state, Brazil (Fig, S1). Mean annual air temperatures vary from 24°C to 26°C, and rainfall from 2000 to 2500 mm per year (Nimer, 1989). The dominant vegetation in Guajará-Mirim is *terra firme* forest with undulating terrain at low altitudes, mostly below 100 m asl.

We installed 74 pitfall trap arrays with drift fences, each consisting of four 30 L buckets placed in a Y-shape (one at the center and three at the tips, forming 120° angles), 5 m apart from each other, and connected with plastic drift fences. We placed pitfall trap arrays along a 1460 m long linear transect, approximately 20 m apart from each other. We inspected traps daily during 31 days (from 29 December 2000 to 28 January 2001). Lizards were collected and killed by lethal injection of Tiopental® and deposited in the Coleção Herpetológica da Universidade de Brasília (CHUNB).

MICROHABITAT VARIABLES.—We measured the following eight microhabitat parameters at each pitfall trap array: (1) nearest tree distance, from the central bucket to the nearest tree with diameter greater than 10 cm at 120 cm above ground; (2) nearest tree circumference, at 120 cm aboveground; (3) number of aboveground termite nests; (4) number of logs; (5) number of burrows; (6) leaf litter weight, with a spring scale, within three randomly selected 50 cm by 50 cm quadrats; (7) canopy openness, at the same locations as leaf litter weight, within a 30 × 30 cm square (36 squares) placed 2.3 m aboveground and by counting the number of squares containing 50 percent or more of light penetration; (8) stems, all plant individuals less than 10 cm in circumference at 120 cm above ground, counted at 40 cm in height in a 90 cm radius area. Parameters 3, 4, and 5 above were quantitated within a 6 m radius from the center of each pitfall trap array. The three measurements of parameters 6, 7, and 8 at each array were later summed, to yield a single measurement for each parameter at each array.

STATISTICAL ANALYSES.—We used a Kolmogorov–Smirnov test in SPSS® v. 10.0 to test whether total lizard captures were homogeneously distributed throughout pitfall trap arrays. We used a Canonical Correspondence Analysis (CCA) to investigate the association between species captures and microhabitat parameters using CANOCO® v. 4.5 (Ter Braak & Smilauer 2002) with the following settings: symmetric scaling, biplot scaling, species data not transformed, and rare species downweighted. To identify the most powerful predictors of species captures, we used manual selection of microhabitat parameters and 9999 Monte Carlo replications for a permutation test. To account for the effects of spatial autocorrelation, we used the position of each pitfall trap array along the linear transect as a covariable. Permutation type was restricted for spatial structure, with permutations restricted for line transects. We visually inspected dispersion graphics to identify potential outliers. Extreme values of vegetation parameters (three times larger than the largest values observed in all other pitfall trap arrays) were replaced with the next highest value, thus reducing the impact of extreme values but at the same time maintaining its characteristic as a high value (Tabachnick & Fidell 2001).

To assess the importance of phylogenetic relationships in structuring the assemblage, we used a modification of CCA, the

Canonical Phylogenetic Ordination (CPO, Giannini 2003). Here, the Y matrix contained weighted averages of microhabitat parameters in columns and lizard species in the assemblage in rows, whereas the X matrix consisted of species in rows and monophyletic groups in each column, with each species coded as one if they were members of the clade or zero if they did not belong to that group. The analysis thus consisted of finding the subset of groups (columns of X) that best explained the variation in Y, using CCA coupled with Monte Carlo replications. We performed CPO in *vegan* package (Oksanen *et al.* 2009) of R (R Core Development Team 2010), using 9999 permutations. We created a cladogram of the lizard species in the assemblage based on a variety of sources (Harvey & Gutberlet 2000, Glor *et al.* 2001, Castoe *et al.* 2004, Townsend *et al.* 2004, Giugliano *et al.* 2007, Gamble *et al.* 2011, Fig. 1). The placement of Gymnophthalmidae sp. was based on unpublished results (GRC).

As an additional test for the potential influence of phylogenetic relatedness on community structure, we implemented a phylogenetic ANOVA/MANOVA (Garland *et al.* 1993) for the number of captures and CCA scores, using family as the grouping variable. The phylogenetic ANOVA calculates the critical value of the *F*-statistic from the observed data, and generates a null distribution (1000 replicates) of test statistics (*F*-values), by simulating random data on the phylogeny. The empirical *F*-statistic is then compared with the null distribution, using a one-tailed test. Significance of this test indicates that the data are more structured than expected by chance, while accounting for the phylogenetic relationships among species. Thus, we tested whether lizard families varied in number of captures (ANOVA on log-transformed count data) or their association with microhabitat data (MANOVA using Wilk's lambda on the scores of the first two CCA axes), while accounting for group relationships. We performed the test using both equal and ultrametric branch lengths on our phylogeny (Fig. 1). These tests were implemented in the *geiger* package (Harmon *et al.* 2008) of R (R Core Development Team 2010).

RESULTS

We captured 349 individuals from 23 species, representing seven lizard families (Figs. 1 and 2). The distribution of species captures per pitfall trap array yielded a typical log curve, and the number of species captured per trap varied from zero to eight. The distribution of total lizard captures across pitfall trap arrays was not uniform (Kolmogorov–Smirnov $Z = 2.38$, $N = 23$, $P < 0.01$). This suggests that local factors exert a strong influence on spatial variation in lizard abundance.

The CCA demonstrated that species captures are significantly associated with microhabitat parameters (all canonical axes: $F = 1.36$, $P = 0.02$). Microhabitat parameters explained 48 per-
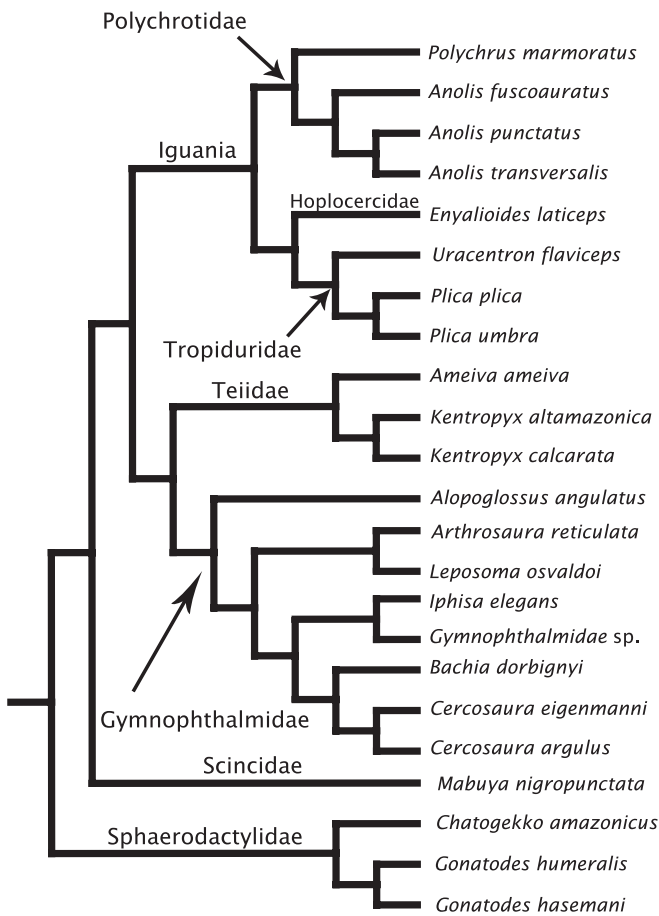

FIGURE 1. Phylogenetic relationships of species in the lizard assemblage found at Guajará-Mirim, Rondônia State, Brazil. The topology was compiled from several studies (see text for details).
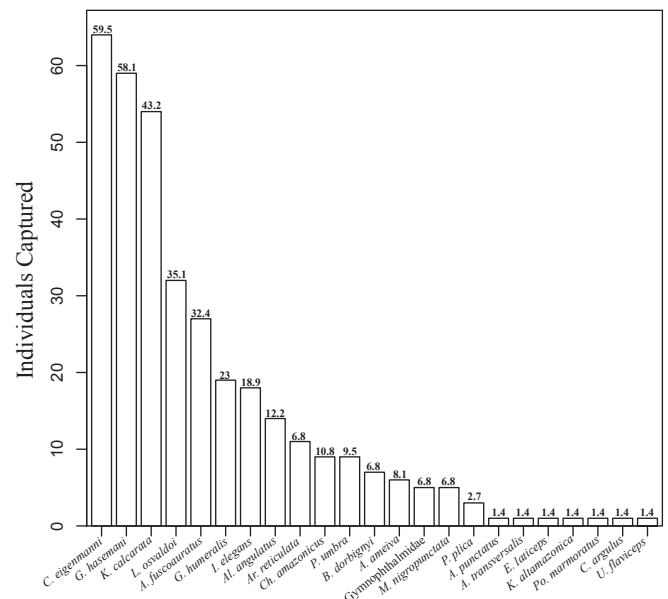

FIGURE 2. Bar plot showing species captures in pitfall trap arrays in Guajará-Mirim, Rondônia State, Brazil. Numbers above bars indicate percentage of pitfall arrays where the species was registered.

cent of the total variation in species captures, with the spatial autocorrelation (covariable) accounting for 4.53 percent of the total variation. Manual selection of microhabitat parameters indicated that number of termite nests, nearest tree circumference, and canopy openness are the most important microhabitat parameters to explain species captures (Table 1).

A Monte Carlo permutation test (Manly 1990) indicated that the first CCA axis was significantly correlated with species captures ($P = 0.04$), accounting for 32.3 percent of the association between lizard captures and microhabitat. The first CCA axis represented primarily a change from pitfall trap arrays close to large circumference, sparsely distributed trees, with many fallen logs and burrows, to arrays close to numerous termite nests (Table 2). *Alopoglossus angulatus* (CC1 = 2.20), *Arthrosaura reticulata* (CC1 = 0.97), Gymnophthalmidae sp. (CC1 = 0.97), *Kentropyx calcarata* (CC1 = 0.53), and *Anolis transversalis* (CC1 = 0.52) were more captured in sites with numerous termite nests, distant from large trees, and with few fallen logs and burrows; conversely, *Cercosaura argulus* (CC1 = −3.37), *Uracentron flaviceps* (CC1 = −3.34), *Enyalioides laticeps* (CC1 = −1.88), *Polychrus marmoratus* (CC1 = −1.71), *Cercosaura eigenmanni* (CC1 = −0.65), and *Mabuya nigropunctata* (CC1 = −0.61) were more captured in sites with fewer termite nests, close to large trees, and with more fallen logs and burrows (Fig. 3).

The second canonical axis explained an additional 18.9 percent of the association between species captures and microhabitat parameters. This axis represented a gradient of canopy cover, understory stems density, and leaf litter thickness (inter set correlation with second axis, respectively, of 0.4201, 0.2897, −0.2672, Fig. 3). *Ameiva ameiva* (CC2 = 1.95), *Enyalioides laticeps* (CC2 = 1.48), *Plica umbra* (CC2 = 1.33), *Bachia dorbignyi* (CC2 = 1.13), Gymnophthalmidae sp. (CC2 = 0.73), *Gonatodes humeralis* (CC2 = 0.70), and *Cercosaura argulus* (CC2 = 0.58) were more captured in sites with less canopy cover, thicker understory, and thinner leaf litter; whereas *Polychrus marmoratus* (CC2 = −4.43), *Anolis punctatus* (CC2 = −3.21), *An. transversalis* (CC2 = −0.79), *Arthrosaura reticulata* (CC2 = −0.52), and *Leposoma osvaldoi* (CC2 = −0.51), were associated with sites with opposite characteristics (Fig. 3). The remaining species were either associated with intermediate microhabitat parameter values or

TABLE 1. *Canonical correspondence analysis results performed with manual selection of microhabitat parameters explaining the variation in lizard captures.*

Microhabitat parameters	Variation	Percent variation	F	P
Termite nests	0.095	18.8	2.102	0.0295
Nearest tree circumference	0.082	16.2	1.834	0.0220
Canopy openness	0.074	14.7	1.686	0.0359
Stems	0.068	13.5	1.563	0.1567
Burrows	0.057	11.3	1.164	0.2861
Logs	0.052	10.3	1.082	0.4136
Nearest tree distance	0.047	9.3	0.765	0.7234
Leaf litter	0.030	5.9	0.665	0.8350

TABLE 2. *Inter-set correlations of environmental variables with canonical axes.*

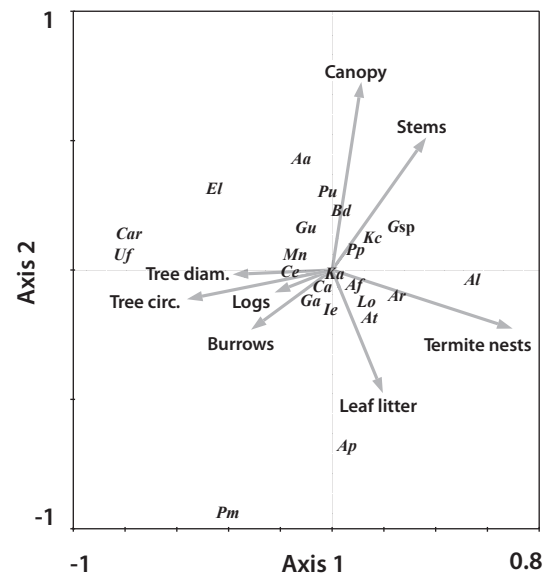| Variable	Ax1	Ax2	Ax3	Ax4
Fr. Extracted	0.08	0.05	0.07	0.02
Termite nests	0.4933	−0.1339	0.1090	−0.1892
Burrows	−0.2209	−0.1361	−0.1780	−0.0685
Logs	−0.1425	−0.0467	−0.3876	0.0350
Stems	0.2461	0.2897	0.2207	0.2412
Leaf litter	0.1317	−0.2672	0.1551	−0.1191
Canopy openness	0.0781	0.4201	−0.2713	−0.2394
Nearest tree distance	−0.2541	−0.0094	0.4534	−0.0977
Nearest tree circumference	−0.3916	−0.0659	0.0107	−0.1122

FIGURE 3. Canonical correspondence analysis ordination diagram showing relationships among lizard species and microhabitat parameters. Species scores represented abbreviations and microhabitat variables represented by arrows jointly reflect species distributions along each microhabitat parameter. Long arrows represent microhabitat parameters more strongly correlated with ordination axes. Tree diam. = nearest tree distance; Tree circ. = nearest tree circumference; Termite nests = termite nests; Canopy = canopy openness; Leaf litter = leaf litter; Burrows = burrows; Logs = fallen logs; stems = number of stems. *Alopoglossus angulatus* = Al; *Ameiva ameiva* = Aa; *Anolis fuscoauratus* = Af; *An. punctatus* = Ap; *An. transversalis* = At; *Arthrosaura reticulata* = Ar; *Bachia dorbignyi* = Bd; *Cercosaura argulus* = Car; *Cercosaura eigenmanni* = Ce; *Chatogekko amazonicus* = Ca; *Enyalioides laticeps* = El; *Gonatodes hasemani* = Ga; *Gonatodes humeralis* = Gu; *Gymnophthalmidae sp.* = Gsp.; *Iphisa elegans* = Ie; *Kentropyx altamazonica* = Ka; *K. calcarata* = Kc; *Leposoma osvaldoi* = Lo; *Mabuya nigropunctata* = Mn; *Polychrus marmoratus* = Pm; *Uracentron flaviceps* = Uf; *Plica plica* = Pp; *Plica umbra* = Pu.

were not strongly associated with any of them. Species dispersion across the two axes formed a single cloud, denser in the center and with some peripheral species. Species were not grouped

according to taxonomic proximity. Species from different families were scattered all around the graph (Fig. 3). None of the pairs formed by related species (congeneric) were close to each other considering the two first axes.

Some lizards were associated with environmental variables related to particular aspects of their natural history. The CPO, however, indicated that microhabitat use by the lizard assemblage was not associated with phylogenetic structure (all canonical axes, $F_{15,7} = 1.81$, $P = 0.16$). Therefore, phylogenetic relationships do not affect associations between captures and microhabitat parameters. The phylogenetic ANOVA showed a lack of significance for the capture data ($F_{8,16} = 1.49$, $P = 0.24$), which was also not significant when compared with the phylogenetic null distribution using equal ($P = 0.81$) or ultrametric ($P = 0.92$) branch lengths, indicating that frequencies of occurrence did not vary significantly by family. The phylogenetic MANOVA for the scores on the first two CCA axes showed significant differences between families for the direct comparison (Wilk's Lambda = 0.28, $P = 0.04$), but lack of significance when compared to the phylogenetic null distribution using equal ($P = 0.74$) or ultrametric ($P = 0.94$) branch lengths. Thus, neither lizard captures nor microhabitat association varied significantly between families at this site when accounting for phylogeny.

DISCUSSION

Lizard species richness recorded in our study site (23 species of five families) is similar to reports in other Amazon rain forest localities (Martins 1991, Vitt et al. 1999, 2008). Although lacking semiaquatic species, such as *Crocodilurus amazonicus*, *Dracaena guianensis*, and *Neusticurus* spp. (Vitt & Avila-Pires 1998, Martins 2006, Mesquita et al. 2006a), our results represent most of the expected lizard richness for an Amazon rain forest site. Furthermore, the uneven distribution of lizards among pitfall trap arrays indicates distinct opportunities for lizard species across the study site.

We found that local microhabitat parameters are important in determining the spatial distribution of lizard species. The lack of phylogenetic structure in microhabitat use found in the CPO reinforces the results of the CCA. The phylogenetic ANOVA/ MANOVA also confirmed that phylogenetic structure does not affect capture patterns, or association with microhabitats. This means that current patterns of habitat use, although ultimately a result of evolutionary history, reflect ecological interactions and are associated with environmental variables. Previous studies on lizard assemblages in open formations revealed the lack of both ecological and phylogenetic structure in habitat use (Mesquita et al. 2006b in Cerrado, Werneck et al. 2009 in a SDTF). Based on a small number of studies, it would appear as lizard communities in the Amazon forest are structured by microhabitat (present study and Vitt et al. 1999), whereas lizard communities in open formations (Cerrado and SDTFs) are not.

Two factors may potentially confound our interpretation that lizard communities in Amazon forest are structured by microhabitat but those from open formations are not. First, both studies in the Amazon region include larger and phylogenetically more diverse assemblages, and ecological data sets on species-poor lizard assemblages can make real historical effects undetectable because major taxa are underrepresented (Mesquita et al. 2006b). Second, microhabitat complexity in the Amazon rain forest can be higher than in open biomes, at the scale in which these studies were conducted. In the Amazon rain forest, variation in habitat heterogeneity is more pronounced vertically, i.e., from the forest floor to the tree canopies (Pires & Prance 1985), whereas in open biomes, such as the Cerrado, this variation is more pronounced horizontally, as one moves across different physiognomies (Colli et al. 2002). In other words, there is greater within-habitat variation in the Amazon forest, whereas between-habitat variation is more pronounced in Cerrado. Even though both kinds of variation result in similar lizard diversity at the local scale (Colli et al. 2002), point diversity should be higher in the Amazon rain forest due to greater microhabitat variation. Therefore, structure in microhabitat use by lizards should be easier to detect on a smaller geographic scale in the Amazon rain forest than in open biomes, such as the Cerrado and SDTFs. Variation in habitat availability, as well as differential microhabitat selectivity, have been described as important forces driving geographic variation in a species' habitat use, with potential impacts for community assembly and, ultimately, speciation (Schoener 1974, Endler 1977, Johnson et al. 2006). More studies, at comparable scales, are necessary to explore the generality of these results and determine the outcomes that structure in microhabitat use has on the diversification of associated lizard lineages in open versus forested biomes.

Despite using a passive capture method for sampling lizards, our results are remarkably consistent with data on the autecology and natural history for several species. For example, *U. flaviceps* and *E. laticeps*, both canopy dwellers (Vitt & Torre 1996), were associated with thicker tree trunks, whereas *A. ameiva*, a typical species from open habitats (Colli 1991, Sartorius et al. 1999, Vitt et al. 2000), was more captured in areas with open canopy. *Gonatodes humeralis* was more associated with open canopy and *G. hasemani* with fallen logs, which corroborates the microhabitat partitioning in these species described previously (Vitt et al. 1997). *Gonatodes hasemani* uses lower perches with larger diameters primarily because individuals are typically found on fallen logs, whereas *G. humeralis* uses higher and thinner perches because individuals are typically found on tree trunks and vines (but see Miranda et al. 2010).

Natural history studies can explain associations between species and environmental features (Vitt et al. 1998b, 2001, Mesquita et al. 2006a), but these relationships might be difficult to characterize at the assemblage level because of interactions with other species. Furthermore, to individually study all species-microhabitat interactions across assemblages is prohibitive. Our CCA, however, detected three environmental parameters explaining about half of the variation in lizard distributions, which are not associated with phylogenetic structure. Occurrence tends to be associated with microhabitats that fulfill species requirements, given that most of them have a relatively small size, often limited mobility, and low energy and water demands

(Heatwole & Taylor 1987, Nagy *et al.* 1999). The variables selected, canopy openness, nearest tree circumference, and termites nests may be interpreted as indirect indicators of habitat quality. Canopy openness, for example, has been directly implicated in the occurrence and abundance of lizards in the Amazon and in costal Restinga habitats in Brazil (Rocha & Bergallo 1997, Sartorius *et al.* 1999).

From a lizard's perspective, termite nests play variable roles in a microhabitat. Some studies have found a positive association between lizard richness and termites in savanna-like environments (Morton & James 1988, Colli *et al.* 2006, Costa *et al.* 2008). Termites have a lower importance in lizard diets in the Amazon compared with the Cerrado (Costa *et al.* 2008), however, and termite nests represent more than just prey for lizards. Nests offer favorable microhabitats for oviposition (Vitt *et al.* 2007a, Knapp & Owens 2008), thermal requirements (Vitt *et al.* 2007b), and shelter (Vitt & Caldwell 1993), and can influence distributions at the microhabitat scale (Vitt *et al.* 2007a). The other two variables, canopy openness and nearest tree circumference, are structural aspects of the environment that reflect the natural succession of a forest dynamic: old, large, and sparse trees are replaced at the end of their lives by younger, thinner, and more numerous individuals. Looking up from the understory of a *terra firme* forest, it is easy to understand how these gap dynamics determine the distribution of sunny patches on the forest floor, creating heterogeneous thermoregulation opportunities (Sartorius *et al.* 1999). The association between lizards and these variables demands more detailed studies. For example, termite nests may indirectly describe other microhabitat characteristics, such as distance to water, altitude, or soil type. These other correlated variables might underlie the true biological meaning behind distributional patterns.

The finding that phylogeny does not explain variation in microhabitat use has important implications for the study of phylogenetic community structure (Webb *et al.* 2002). Large-scale studies analyzing the phylogenetic structure of the regional pool with respect to the local community often do not analyze phylogenetic variation in ecological traits (microhabitat, diet, activity, etc., *e.g.,* Cooper *et al.* 2008). Many studies have demonstrated the influence of phylogeny on ecological traits in communities (*e.g.,* Vitt & Pianka 2005, Colston *et al.* 2010). As phylogenetic niche conservatism has become an influential principle in studies of trait evolution (Wiens *et al.* 2010), many implicitly assume that phylogenetic overdispersion is evidence for competitive interactions (Cooper *et al.* 2008). Our results stress the fact that information on ecological traits and their association with phylogeny is crucial for determining what processes influence community structure at local scales. Also, it is fundamental to compare several assemblages on a regional scale to evaluate patterns of phylogenetic community structure while controlling for habitat filtering (Rabosky *et al.* 2011). This way, community patterns resulting from competition, habitat filtering, or neutral processes can be disentangled (Cooper *et al.* 2008, Rabosky *et al.* 2011).

Furthermore, one known impact of land use is microhabitat structural modification, which tends to reduce environmental complexity, yielding open canopies, thin trees, increased numbers of termite nests, and reduced leaf litter volume (Vitt *et al.* 1998a). Based on our results, this would potentially lead to a decrease in lizard diversity through the elimination of some species, such as gymnophthalmids, due to lack of shelter and protection from heat and predators. At the same time, we would predict an increase in lizards, such as *A. ameiva*, that use these opened habitats (Sartorius *et al.* 1999). Lizard diversity in southwestern Amazonia is directly proportional to microhabitat heterogeneity (Vitt *et al.* 1998a); thus, it is vital to preserve habitat diversity to maintain high species diversity. Understanding how habitat variables impact distributional patterns is crucial for making proper management decisions to reduce the impacts of anthropogenic habitat modification. For example, data on the effects of reduced impact logging (RIL; the methodology adopted by the Brazilian government for logging concessions) are scarce, and usually pertain to the sustainability of commercial timber species and impacts of different logging methods (reduced impact versus conventional, Valle *et al.* 2007, Zarin *et al.* 2007). In contrast, little is known about the potential impacts of RIL on animals. Protected areas in Brazil rely on management plans that involve a biodiversity assessment phase that frequently uses pitfall trap surveys. Such inventories could easily adopt our methodology to evaluate correlations between species' occurrences and microhabitat variables and use these to predict outcomes of various activities on the local community.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

FIGURE S1. Map of South America, with the inset showing Rondônia State in Brazil and the study site near Guajará-Mirim.

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