



Juxtaposition and Disturbance: Disentangling the Determinants of Lizard Community Structure

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ABSTRACT

Disturbance alters the structure and dynamics of communities. Here, we examined the effects of seasonal flooding on the lizard community structure by comparing two adjacent habitats, a seasonally flooded and a non-flooded forest, in a Cerrado–Amazon ecotone area, the Cantão State Park, Tocantins state, Brazil. Despite the strong potential impact of seasonal flooding, the only significant environmental difference detected was more termite mounds in non-flooded forests. Species richness was significantly higher in the non-flooded forest. *Colobosaura modesta*, followed by *Mabuya frenata* and *Anolis brasiliensis*, were the only species that differed in number of captures between sites. *Colobosaura modesta* was exclusively found in the non-flooded forest, while *Anolis brasiliensis* was the most captured in the flooded forest. *Mabuya frenata* is indicated as an indicator species in the flooded forest, and *Colobosaura modesta* in the non-flooded forest. We found a significant association between lizard abundances and habitat characteristics, with flooding, canopy cover, and logs being the best predictors. A phylogenetic community structure analysis indicated a lack of structure in both lizard assemblages. Overall, we show that seasonal flooding can strongly impact species richness and species occurrence patterns, but not phylogenetic community structure. The Amazon–Cerrado transition is undergoing pronounced transformations due to deforestation and climate change. Despite being species-poor compared with central areas in Amazon or Cerrado, this ecotone harbors species with important adaptations that could hold the key to persistence in human-disturbed landscapes or during periods of climate change.

Abstract in Portuguese is available with online material.

Key words: Amazonia; Cerrado; ecotone; flooding; lizards.

DISTURBANCE IS A POWERFUL AGENT THAT ALTERS THE STRUCTURE AND DYNAMICS OF BIOLOGICAL COMMUNITIES (Levin 1974, Levin & Paine 1974). Dramatic, infrequent events such as asteroid impacts (Alvarez *et al.* 1980, Alvarez & Muller 1984, Schulte *et al.* 2010), severe weather related to climate change (Hallam & Wignall 1999, Parmesan *et al.* 2000, Doney *et al.* 2012), and volcanic activity (Del Moral & Bliss 1993, Wignall 2001, Hesselbo *et al.* 2002) may eradicate whole biotas and set the stage for the development of new communities. Other, less dramatic events, such as severe winters or droughts, wildfires, and floods, may occur periodically and with higher frequency. These disturbances will often work as an environmental filter, selectively affecting populations in a community by favoring tolerant species and eliminating those less capable of coping with change (*e.g.*, Lake 2000, Humphries & Baldwin 2003, Matthews & Marsh-Matthews 2003, Costa *et al.* 2013). Ecological theory postulates that the effects of disturbances vary according to their intensity/frequency, such that species richness should be highest at intermediate disturbance levels

(Connell 1978, Mackey & Currie 2000, 2001, dos Santos *et al.* 2011). If disturbances are too intense/frequent, only a few tolerant species will persist and species in the community will tend to be phenotypically attracted, *i.e.*, share similar traits (Ding *et al.* 2012, Letcher *et al.* 2012). If traits that confer tolerance are phylogenetically conserved, species in the community will also be phylogenetically clustered; conversely, if these traits are convergent, the community will show phylogenetic repulsion or overdispersion (Webb *et al.* 2002, Kraft *et al.* 2007, Vamosi *et al.* 2009). Too little disturbance may lead to competitive exclusion by dominant species (phenotypic repulsion), such that niche overlap is minimized, and phylogenetic overdispersion when ecological traits are phylogenetically conserved, or to phylogenetically random communities, when traits are convergent.

Riparian communities that are subject to massive seasonal flooding may be prevented from reaching a stable structure and, therefore, comprise a small number of specialized, disturbance-adapted species (Naiman & Decamps 1997, Pollock *et al.* 1998). Flood pulses promote stress periods with impeded gas exchange, interrupting or at least reducing photosynthesis levels and thereby promoting lower plant diversity in flooded areas (Kubitzki 1989,

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Junk & Piedade 2010, Wittmann *et al.* 2010). As a result, flooded forests have relatively simple structures, usually resulting in reduced animal diversity and abundance, especially of terrestrial species. The impacts of seasonal flooding have been reported for many organisms, including arthropods (Dobel *et al.* 1990, Ellis *et al.* 2001, Lamberts *et al.* 2008, Sterzynska *et al.* 2014), fishes (Freeman *et al.* 1988, Agostinho *et al.* 2004, Arthington *et al.* 2005), frogs (Gascon 1996, Wassens *et al.* 2008), birds (Shimada *et al.* 2000, Royan *et al.* 2013), and mammals (Peres 1997, Haugaasen & Peres 2005, Pereira *et al.* 2013). Lizards can provide insight into the impact of seasonal flooding on community structure, particularly in the Cerrado of Brazil, because the regional species pool is large and includes terrestrial, arboreal, and scansorial species (Colli *et al.* 2002, Costa *et al.* 2007, Brites *et al.* 2009), in addition to species highly adapted to particular microhabitats (*e.g.*, inside of termite nests, see Vitt *et al.* 2007).

The Bananal Island floodplain of South America is one of the largest in the continent, with a maximum area subject to inundation of 58,550 km² (Hamilton *et al.* 2002). This hyperseasonal (Sarmiento 1983, 1984) floodplain is located along the Araguaia River, a major tributary of the Tocantins River, in central Brazil, at the transition between the Cerrado (Oliveira & Marquis 2002) and the Amazon Forest (Prance & Lovejoy 1985). It is inundated by a single annual flood pulse that can reach 8.2 m (Hamilton *et al.* 2002) and lasts for 4–5 months, after which it is subject to strong desiccation during the dry season, when burns are common (Eiten 1985, Maracahipes *et al.* 2014). Here, we examine the effects of seasonal flooding on lizard community structure by comparing communities in two adjacent habitats, a seasonally flooded and a non-flooded forest, within a riparian zone. We predict that the lizard community in the flooded forest should have lower species abundance and richness compared to the non-flooded forest. Further, considering that niche preferences are often phylogenetically conserved among squamates (Vitt *et al.* 2003b, Vitt & Pianka 2005), we predict that lizard species in flooded forests are phenotypically and phylogenetically clustered.

METHODS

STUDY AREA.—We conducted the study during the dry season, from 6 September to 10 October 2005, in the ‘Parque Estadual do Cantão’, Casera municipality, Tocantins state, Brazil (9°18′45.38″ S, 49°57′29.72″ W) (Fig. S1). Our long-term experience sampling the Cerrado and Amazonia showed that 1 month of sampling is adequate to detect patterns in lizard communities. Collecting all species in a given area remains a challenging task and requires several years (see Duellman 1978, Gotelli & Colwell 2001). However, our goal was not to make a complete list of the lizard species from Cantão, but rather to compare areas (flooded and non-flooded), using standardized collecting methods. In addition, collecting samples in both dry and rainy seasons would be desirable. However, this was not possible, as the flooded area was under water during the rainy season.

The area (90,000 ha) consists predominantly of open grasslands with stunted trees and large numbers of termite nests with

a dry and largely deciduous gallery forest along waterways. This protected area is surrounded by the Araguaia, Coco, and Javaés rivers, which promote the formation of many islands, lakes, and flooded forests. Just before the wet season and prior to flooding, we selected two areas, a seasonally flooded forest (regionally called ‘impuca’) (Barbosa *et al.* 2011, Maracahipes *et al.* 2014) and a non-flooded forest, near the visitor center along the margin of the Coco River, *ca.* 4.5 km apart. In these areas, the soil varied from alluvial to lateritic, and was covered by a thick layer of leaf litter.

SAMPLING LIZARDS AND ENVIRONMENTAL DATA.—In each area, we sampled the lizard communities using 25 pitfall trap arrays, evenly spaced along an *ca.* 2 km linear transect. Each pitfall trap array consisted of a central 20 L plastic bucket sunk into the ground with the top flush with the surface, three 5 m drift fences at angles of 120° from each other, with a 20-L bucket also sunk flush with the ground surface at the end of each drift fence. We monitored the traps for captured lizards twice a day (early morning and late afternoon). For each lizard captured, we identified the species and recorded the time of day and array number. To maximize our ability to assess species composition at each site, we used additional survey methods to supplement pitfall trap arrays. We constructed 20 funnel trap arrays at each site. Each funnel trap array consisted of a 10 m linear drift fence with two funnel traps on each end, one on each side. We also collected lizards opportunistically while monitoring pitfall and funnel traps and this effort was similar between sites, as both efforts involved the same number of people and transects of approximately the same length. We euthanized all captured lizards with a lethal injection of sodium thiopental, preserved them, and deposited them in the Coleção Herpetológica da Universidade de Brasília (CHUNB). As this study forms a part of a bigger project, involving other studies, we could not use alternative, non-lethal techniques. In the expedition, we did not kill any globally or locally endangered species (*e.g.*, IUCN listed as threatened). All processes take in account the ethical guidelines provided by the American Society of Ichthyologists and Herpetologists (ASIH), Herpetologists’ League (HL), and Society for the Study of Amphibians and Reptiles (SSAR). Finally, IBAMA (Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis) and NATURA-TINS (Instituto Natureza do Tocantins) provided all necessary permissions to sample animals at PE do Cantão.

At each array, we measured the following environmental variables: (1) leaf litter mass, (2) percent open ground, (3) percent of canopy open to the sky, (4) number of plant stem contacts, (5) number of burrows in ground, (6) number of termite nests within 6 m, (7) distance to nearest tree, (8) trunk circumference as a measure of tree size, and (9) total number of fallen logs. To do this, we used a 0.5 × 0.5 m frame from wooden dowels and placed strings across at 0.1 m intervals to form 25 equal-size squares. In each area of the three 120° sectors delineated by the drift fence wings of each array, the frame was thrown over a researcher’s shoulder; we used its landing point as our random sample site. We counted squares represented by more than 50

percent open ground, picked up all leaf litter under it, and weighed the leaf litter to the nearest gram. At the center of the spot where the frame landed, we placed a vertical stake with a 1 m horizontal dowel 20 cm above the ground and rotated the stick 360°, counting the number of plant stem contacts with the horizontal stick. We also measured canopy openness by placing the frame above the head and counting the number of squares where the canopy did not intercept direct sunlight. We then measured the distance to the nearest tree from the landing point of the frame. This procedure gave three independent measurements for each variable at each array. We used means for each array for analyses. From 1 m beyond the end of the drift fence wings to the center bucket (a 6 m radius for each array), we counted all burrows, all termite nests, and the total number of logs (diameter >5 cm) in the array.

STATISTICAL ANALYSES.—To assess differences in structural habitat parameters between the flooded and non-flooded sites, we used a generalized linear model (GLM) with a binomial error distribution and a logit link function, *i.e.*, a logistic regression analysis (Quinn & Keough 2002, Crawley 2013). In this analysis, the grouping variable was the site, whereas we used the environmental variables as predictors. Used in this fashion, logistic regression is equivalent to discriminant function analysis (DA), which uses a combination of predictors to assess group membership. However, the logistic regression is more flexible than the DA, because predictors are not assumed to be normally distributed, linearly related, or homoscedastic (Tabachnick & Fidell 2007). To test the adequacy of the full model, we compared it to an intercept-only (null) model with the Pearson χ^2 statistic; to determine predictor importance, we used a manual forward selection approach by sequentially adding and dropping variables, starting with a null model, and assessing model improvement with a significance (χ^2) test of the reduction in scaled deviance (Crawley 2013).

We compared total lizard captures and richness between the flooded and non-flooded sites. To compare the number of captures between the two sites, we used a binomial test (Crawley 2013). We built species rarefaction curves based on individuals and traps to evaluate our sampling success and to compare species richness and density between the two communities (Gotelli & Colwell 2001), using package *vegan* (Oksanen *et al.* 2013). We compared lizard richness between the two sites with rarefaction. To reduce the effects of undersampling and account for the presence of undetected species, we computed the Chao1 and ACE abundance-based estimators of species richness (Chao 1987, Colwell & Coddington 1994), using package *vegan* (Oksanen *et al.* 2013).

To assess differences in lizard abundance between the flooded and non-flooded forest, we used a generalized linear model (GLM) with a Poisson error distribution and a log link function (Quinn & Keough 2002, Crawley 2013). In this analysis, the dependent variable was the number of captures, whereas site (flooded vs. non-flooded) and species were the predictors. To test for independence between sites and species, we compared the full model with one devoid of the interaction term (sites vs. species)

using the Pearson χ^2 statistic (Crawley 2013). We used the χ^2 residuals to determine the lizard species that most contributed to differences between sites: once finding the species with the largest sum of squared residuals, we removed it from the analysis and repeated the GLM until the sites versus species interaction was not statistically significant.

We conducted indicator species analyses to identify species that could be used as indicators of environmental changes due to flooding (Dufrêne & Legendre 1997). Species sensitive to environmental change can be used as ecological indicators to monitor environmental changes and assess the impacts of disturbances on an ecosystem (Dufrêne & Legendre 1997, Carignan & Villard 2002). We calculated the indicator value index (IndVal), modified to deal with combinations of trap groups (De Cáceres & Legendre 2009, De Cáceres *et al.* 2010), separately for each site. We calculated the indicator value of a species as the product of two quantities, A and B (Dufrêne & Legendre 1997, De Cáceres & Legendre 2009). For species capture data (IndVal_{ind}), A is the mean capture of the species in the target group of traps (flooded or non-flooded site) divided by the sum of its mean capture over all groups. Using the sum of the mean captures over all groups, instead of the sum of the actual captures over all groups, controls for the effect of unequal sizes of the trap groups. B is the relative frequency of occurrence of the species inside the target trap group (*i.e.*, the number of traps where the species occurs in the target group divided by the total number of traps in that group). IndVal_{ind} is equal to the group-equalized indicator value index (IndVal_{ind}^g, herein reported in square-root form) (De Cáceres & Legendre 2009). Furthermore, we used a modification of the index that incorporates combinations of the trap groups (De Cáceres *et al.* 2010). This modification considers the association between the target species and each of the possible groups of traps formed by combining all possible combinations of the habitat groups. Given k different habitat groups (two in our study), there exist $2^k - 1$ possible combinations of habitat groups including all sites (three in our study). The trap-group combination showing the strongest association with the target species is retained. We assessed the significance of the index by comparing the observed values to a null distribution of values obtained by randomly reassigning species capture values to traps 10,000 times. As we reported the results of indicator species analysis for several species, we used Holm's method (Holm 1979) to control the family-wise error rate. We performed the indicator species analyses using package *indicspecies* (De Cáceres & Legendre 2009).

To test for an association between the abundance of lizard species and habitat characteristics at each site, we used a canonical correspondence analysis (CCA) (ter Braak 1986, 1987). Canonical correspondence analysis is a multivariate ordination procedure that directly associates variation in species abundances (dependent variables) to habitat characteristics (independent variables). A significant association between lizard species abundances and habitat characteristics would indicate a structured assemblage, whereas no association would suggest a lack of structure in the assemblage. We performed CCA with *vegan* (Oksanen *et al.* 2013), only considering lizards captured in the pitfall trap arrays. After determining the significance of the full model, *i.e.*, including all

predictors, we used an information theory approach, based on the Akaike information criterion (AIC), to identify the best predictors and build a reduced model (Burnham & Anderson 2002, 2004). We used a stepwise approach, starting with an intercept-only model and sequentially adding and trying to drop predictors based on model significance and AIC values (Oksanen *et al.* 2013). We assessed model significance with 1000 Monte Carlo simulations.

To determine the presence of non-random patterns of phylogenetic community structure, we assembled a phylogenetic tree uniting all sampled species by pruning the squamate phylogeny of Pyron *et al.* (2013). As *Anolis brasiliensis* and *Gymnodactylus amarali* were not sampled in that phylogeny, we replaced them by their close relatives, *A. nitens* and *Phyllopezus periosus*, respectively (Fig. 1). We assumed this should not substantially affect the results because most evolutionary changes in the squamate tree occurs at deeper nodes. To further explore this issue, we conducted a sensitivity analysis based on 10 simulations, in each reducing the age of divergence between *Hemidactylus mabouia* and *Phyllopezus periosus* by 1/10th of the observed value. For each simulation, we tested the communities for phylogenetic structure. Next, we estimated the phylogenetic diversity (PD, Faith 1992), mean phylogenetic distance (MPD), and mean nearest taxon distance (MNTD) (Webb 2000, Webb *et al.* 2002) for each lizard community (flooded vs. non-flooded forest) and determined their significance by comparison with a null distribution of the respective values (PD, MPD, MNTD) generated by shuffling the taxon labels on the phylogeny 10,000 times. These analyses were implemented with packages *ape* (Paradis *et al.* 2004) and *picante* (Kem-

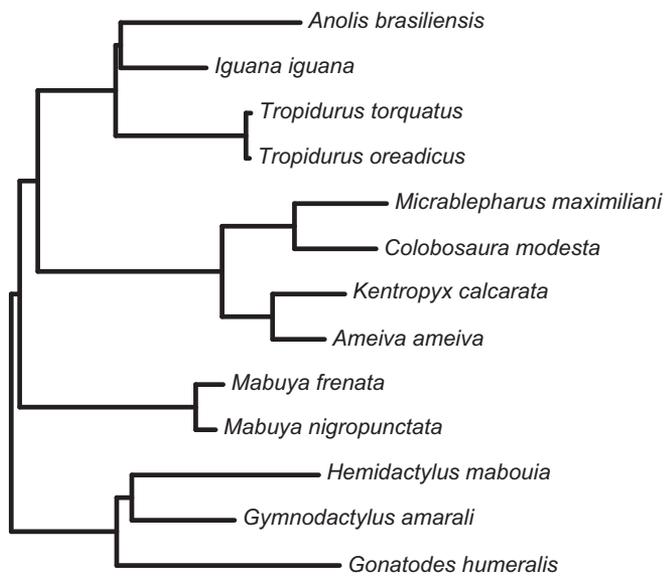


FIGURE 1. Dated phylogenetic tree pruned from Pyron *et al.* (2013) relating the lizard species captured with pitfall trap arrays in flooded and non-flooded forest sites in Parque Estadual do Cantão, Caseara, Tocantins, Brazil. *Anolis brasiliensis* and *Gymnodactylus amarali* were not sampled in that phylogeny, and were replaced by their close relatives, *A. nitens* and *Phyllopezus periosus*, respectively.

bel *et al.* 2010). We conducted all statistical analyses under R version 3.1.0 (R Core Team 2014) using the significance level of 5 percent.

RESULTS

THE CANTÃO LIZARD FAUNA.—We captured a total of 209 lizards during this study using our combined methods. Regardless of collecting method or site, the most common species were *Mabuya nigropunctata* ($N = 40$), a widely distributed species in Amazonia and Cerrado; *Ameiva ameiva* (33), a widely distributed species in South America; *Anolis brasiliensis* (31), a species that also occurs in the Cerrado and in mesic areas of Caatinga; *Gymnodactylus amarali* (27), a crepuscular/nocturnal gecko that is typically found inside termite nests; and *Colobosaura modesta* (26), a species associated with forested habitats, but also occurring in open areas on the ground (Table 1). The rarest species were *Micrablepharus maximiliani* ($N = 1$), usually found in sandy soils and inside termite nests; *Hemidactylus mabouia* (2), an introduced species that occupies human edifications; *Tropidurus torquatus* (4), a common species associated with disturbed areas but naturally occurring in gallery forests; *Tupinambis teguixin* (4), an Amazonian species that also occupies the gallery forests along river margins south of the Amazon; and *Gonatodes humeralis* (5), a common gecko in Amazonia that also occurs in gallery forests in western Cerrado as it transitions into the Amazon Forest (Table 1).

FLOODING EFFECTS.—The logistic regression analysis indicated that the number of termite mounds was the only measured environmental variable that differed between the flooded and non-flooded sites ($\chi^2 = 7.49$, $df = 49$, $P = 0.006$), with the mean number of termite mounds per pitfall array being significantly higher in the non-flooded forest (Table 2). Pitfall arrays captured 75 individuals of 11 species, which included 47 individuals of 9 species in non-flooded forest and 28 individuals of 5 species in flooded forest (Table 1). Pooled lizard captures were significantly higher in the non-flooded forest ($\chi^2 = 4.32$, $df = 1$, $P = 0.038$). The rarefaction curves indicated that both species richness, as indicated by the individual-based rarefaction curve, and species density, as indicated by the sample-based curve, were higher in the non-flooded forest (Fig. 2). The rarefaction analysis indicated that lizard species richness was significantly higher in the non-flooded forest ($\alpha = -2.21$, $P = 0.014$). Estimated species richness was also higher for the non-flooded forest (Flooded: Chao1 = 6.00, ACE = 6.92 \pm 1.18; Non-flooded: Chao1 = 12.00 \pm 11.66, ACE = 13.44 \pm 1.65).

Species composition differed significantly between the flooded and non-flooded forests ($\chi^2 = 52.63$, $df = 10$, $P < 0.001$). The analysis of χ^2 residuals indicated that *Colobosaura modesta*, followed by *Mabuya frenata* and *Anolis brasiliensis*, were the only species that differed in number of captures between the flooded and non-flooded forest sites (Fig. 3). *Colobosaura modesta* was exclusively found in the non-flooded forest, where it was by far the most-captured species. *Anolis brasiliensis* was the most-captured species in the flooded forest, whereas *Mabuya frenata* was only captured in the flooded forest (Fig. 3). The indicator species analyses

TABLE 1. Composition and abundance of lizards collected in flooded and non-flooded forest at Parque Estadual do Cantão, Caseara, Tocantins, Brazil. Records from the flooded and non-flooded forest refer only to specimens captured in pitfall trap arrays.

Species	Flooded forest	Non-flooded forest	Funnel traps	Hand collected	Total
Iguanidae					
<i>Iguana iguana</i>	—	—	—	7	7
Dactyloidae					
<i>Anolis brasiliensis</i>	14	6	1	10	31
Tropiduridae					
<i>Tropidurus oreadicus</i>	—	1	6	4	11
<i>Tropidurus torquatus</i>	1	—	—	3	4
Sphaerodactylidae					
<i>Gonatodes humeralis</i>	—	1	—	4	5
Phyllodactylidae					
<i>Gymnodactylus amarali</i>	—	1	—	26	27
Gekkonidae					
<i>Hemidactylus mabouia</i>	—	—	—	2	2
Teiidae					
<i>Ameiva ameiva</i>	6	6	18	3	33
<i>Kentropyx calcarata</i>	1	5	—	—	6
<i>Tupinambis teguixin</i>	—	—	1	3	4
Gymnophthalmidae					
<i>Colobosaura modesta</i>	—	24	2	—	26
<i>Micrablepharus maximiliani</i>	—	1	—	—	1
Scincidae					
<i>Mabuya frenata</i>	6	—	—	6	12
<i>Mabuya nigropunctata</i>	—	2	34	4	40
Total	28	47	62	72	209

revealed one indicator species in the flooded forest, *Mabuya frenata* ($\sqrt{\text{IndVal}}_{\text{ind}}^{\text{S}} = 0.447$, $P = 0.049$), and one in the non-flooded forest, *Colobosaura modesta* ($\sqrt{\text{IndVal}}_{\text{ind}}^{\text{S}} = 0.663$, $P < 0.001$).

ASSOCIATION BETWEEN LIZARD ABUNDANCES AND HABITAT CHARACTERISTICS.—The CCA based on the full model (including all predictors) revealed a significant association between lizard abundances and habitat characteristics ($F_{11,22} = 1.55$, $P = 0.04$). Our manual, stepwise selection of predictors indicated that site (flooded vs. non-flooded), canopy cover, and logs were the best predictors of species abundances ($F_{3,30} = 2.89$, $P = 0.001$). This reduced model accounted for 22 percent of the total variation in lizard abundances among trap arrays. Three canonical axes were retained, the first explaining 50 percent of the constrained variation, the second 26 percent, and the third 24 percent (Fig. 4). The first canonical axis largely depicted the contrast between the flooded and non-flooded forest (with logs being more numerous in the latter), with *Tropidurus torquatus*, *Mabuya frenata*, *Anolis brasiliensis*, and *Ameiva ameiva* being associated with the former,

TABLE 2. Vegetation and structural habitat characteristics of 50 pitfall trap arrays placed in Parque Estadual do Cantão, Caseara, Tocantins, Brazil. Values indicate mean \pm SD. Minimum and maximum are in parentheses.

Habitat characteristic	Flooded forest	Non-flooded forest
Leaf litter mass (g)	214.05 \pm 88.36 (96.67–450.00)	190.67 \pm 52.63 (133.33–328.33)
Proportion of squares open ground	0.03 \pm 0.13 (0.00–0.67)	0.05 \pm 0.16 (0.00–0.67)
Proportion of squares open to sky	0.91 \pm 0.10 (0.57–1.00)	0.89 \pm 0.14 (0.48–1.00)
Number of plant stem contacts	4.61 \pm 2.86 (0.00–11.67)	5.11 \pm 2.24 (0.67–10.33)
Number of burrows	0.04 \pm 0.20 (0.00–1.00)	0.20 \pm 0.41 (0.00–1.00)
Number of termite nests	0.00 \pm 0.00 (0.00–0.00)	0.32 \pm 0.75 (0.00–3.00)
Distance to nearest tree (m)	2.80 \pm 1.16 (1.00–5.40)	2.60 \pm 1.17 (0.80–4.50)
Trunk circumference (m)	0.89 \pm 0.53 (0.19–2.24)	0.70 \pm 0.28 (0.34–1.36)
Number of fallen logs	2.20 \pm 1.29 (0.00–5.00)	2.04 \pm 1.54 (0.00–6.00)

whereas *Gonatodes humeralis*, *Gymnodactylus amarali*, *Colobosaura modesta*, *Kentropyx calcarata*, and *T. oreadicus* were more associated with the latter (Fig. 4). On the other hand, the second canonical axis depicted primarily a canopy cover gradient, with *Micrablepharus maximiliani*, *T. oreadicus*, and *Ma. nigropunctata* being strongly associated with more open sites, whereas *An. brasiliensis*, *Gy. geckoides*, and *Go. humeralis* were associated with more closed sites (Fig. 4).

COMMUNITY STRUCTURE.—The analyses of phylogenetic community structure indicated a lack of phylogenetic structure based on PD, MPD, or MNTD for both the flooded forest and the non-flooded forest lizard assemblages (Table 3). The sensitivity analysis produced the same results (not shown).

DISCUSSION

THE CANTÃO LIZARD FAUNA.—We recorded 14 species in the two forest sites, representing elements of the Cerrado and Amazonian lizard fauna. This was expected because the sites are located at the transition between the Amazon and the Cerrado and ecotones often contain a mixture of species of the neighboring areas (Shmida & Wilson 1985, Risser 1995). Further, by harboring species that are characteristic or endemic (Odum 1953), ecotones generally have high species richness (Kark & van Rensburg 2006, Kark 2007, Fahr & Kalko 2011); nevertheless our results corrob-

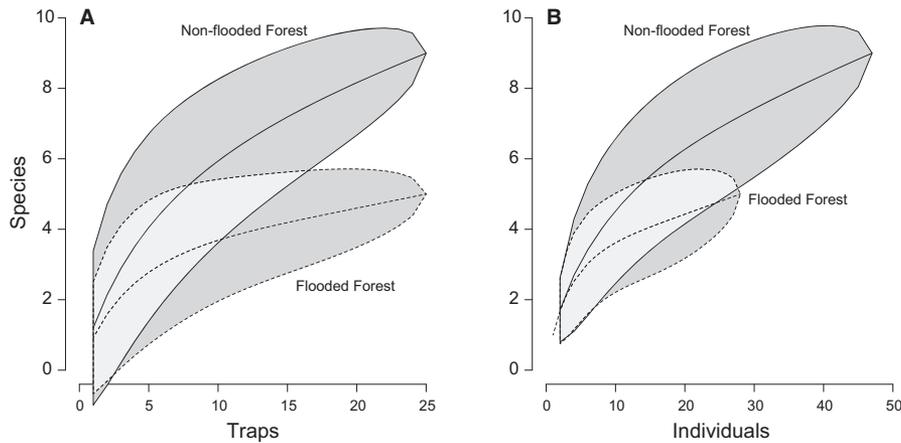


FIGURE 2. Sample-based (A) and individual-based (B) rarefaction curves of lizards collected with pitfall trap arrays in flooded and non-flooded forest sites in Parque Estadual do Cantão, Caseara, Tocantins, Brazil. Gray polygon indicates 95% confidence interval.

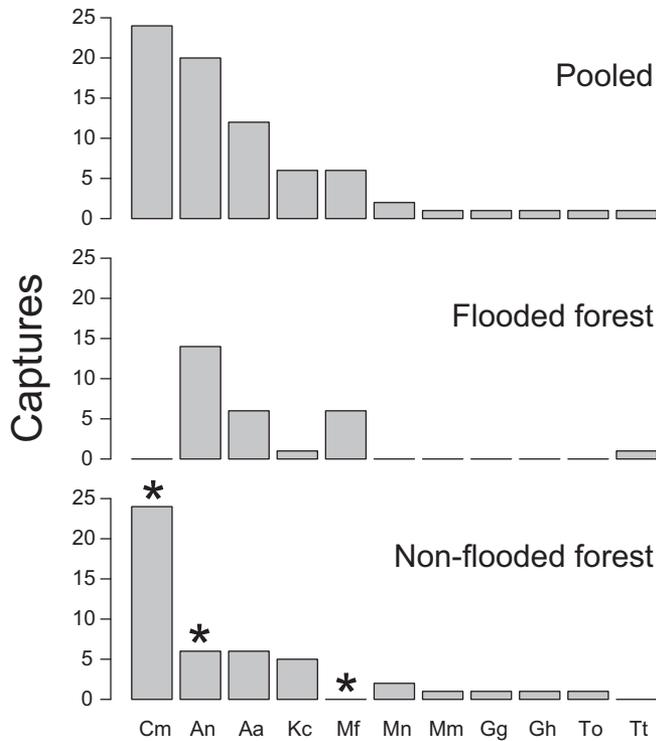


FIGURE 3. Number of captures of lizard species collected with pitfall trap arrays in flooded and non-flooded forest sites in Parque Estadual do Cantão, Caseara, Tocantins, Brazil. Asterisks indicate significant differences in captures between flooded and non-flooded forest sites based on generalized linear models. Cm, *Colobosaura modesta*; Ab, *Anolis brasiliensis*; Aa, *Ameiva ameiva*; Kc, *Kentropyx calcarata*; Mf, *Mabuya frenata*; Mn, *Mabuya nigropunctata*; Mm, *Micrab-lepharus maximiliani*; Ga, *Gymnodactylus amarali*; Gh, *Gonatodes humeralis*; To, *Tropidurus oreadicus*; and Tt, *Tropidurus torquatus*.

orate neither of these patterns. The lizard communities at PE do Cantão have lower richness than do those in the Amazon Forest (Vitt 1996, Vitt & Zani 1996) or Cerrado sites (Colli *et al.* 2002,

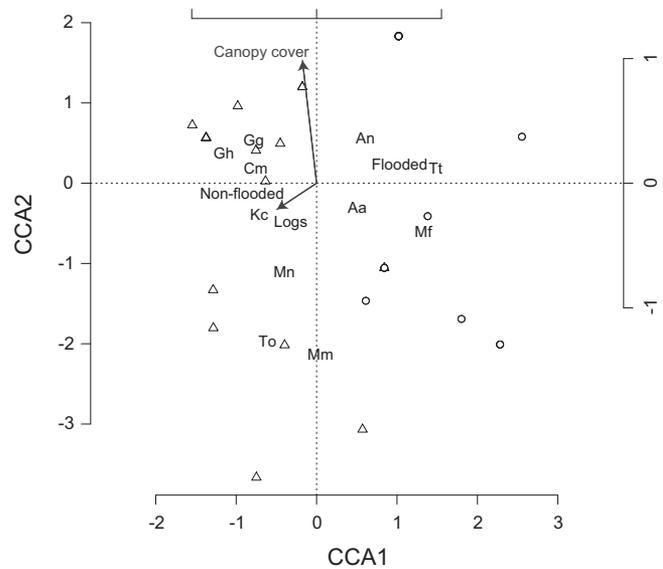


FIGURE 4. Biplot of canonical correspondence analysis relating environmental parameters to the abundance of lizard species collected with pitfall trap arrays in flooded and non-flooded forest sites in Parque Estadual do Cantão, Caseara, Tocantins, Brazil. The plot shows weighted averages of lizard captures among pitfall trap arrays on the first two canonical axes. Triangles represent arrays in the non-flooded forest, while circles represent arrays in the flooded forest. Lengths of microhabitat vectors indicate strength of the correlation and arrow tips represent centroids of the impact of environmental parameters on each species' distribution among arrays. For species abbreviations, see Fig. 3.

Vitt *et al.* 2005, Mesquita *et al.* 2006) we sampled using the same methods and we found no species endemic to the ecotone. This pattern seems to be characteristic of the Amazon–Cerrado ecotone (unpubl. data). This environmental transition is a very complex landscape, resulting from a mosaic of soil types with varying nutrient content and moisture-holding capacity (Askew *et al.*

TABLE 3. Phylogenetic distance (PD), mean phylogenetic distance (MPD), and mean nearest taxon distance (MNTD) for lizard communities in a flooded and non-flooded forest at Parque Estadual do Cantão, Caseara, Tocantins, Brazil. Values of Z and P are based on 10,000 randomizations of taxon labels in the phylogeny.

Forest type	Species	PD			MNTD			MPD		
		Observed	Z	P	Observed	Z	P	Observed	Z	P
Non-flooded forest	9	1040.81	0.68	0.77	165.05	0.79	0.79	294.12	-0.34	0.34
Flooded forest	5	656.20	-0.21	0.39	193.48	-0.37	0.31	294.77	-0.08	0.42

1970, Daultrey 1970). However, the prevailing hyperseasonal environmental conditions, *i.e.*, flooding during the wet season and desiccation during the dry season (Sarmiento & Monasterio 1975, Sarmiento 1983), seemingly act as a variable permeability filter (Wiens *et al.* 1985) that only a few species of the Amazon Forest and the Cerrado can tolerate, resulting in species-poor communities.

FLOODING EFFECTS.—Our results indicate high similarity in habitat structure between the two sites, the only difference being the number of termite nests, probably due to the flooding regime. The CCA revealed a strong association between species abundances and habitat characteristics, with site (flooded vs. non-flooded), canopy cover, and logs being the best predictors of lizard abundances. Flooding had a profound effect on the structure of the lizard communities in the study area, with significantly lower species richness and abundance in the seasonally flooded forest. Similar results were found for non-volant rodents across the flooded and unflooded gallery forests in the Cerrado-Amazon ecotone (Pereira *et al.* 2013): species composition differed between forest types, with the unflooded area showing higher species richness. However, there were no differences in mammal abundances. These differences were associated with the decreased resource availability for strictly terrestrial mammals in the flooded forests, the heterogeneity promoted by seasonal floods being pivotal for maintaining the regional mammal diversity in the area (Pereira *et al.* 2013).

Our results indicate that the flooding regime also affected the composition of the lizard communities. *Colobosaura modesta*, a strictly terrestrial species, dominated the community in the non-flooded forest and apparently could not withstand the seasonal inundation in the flooded forest. *Colobosaura modesta* is ecologically similar to its closest relatives *Acratosaura mentalis* (Garda *et al.* 2013), *Alexandresaurus camacan* (Rodrigues *et al.* 2007, 2009), *Iphisa elegans* (Vitt & Zani 1996), and *Stenolepis ridleyi* (Vanzolini 1974), and to most other gymnophthalmids from open habitats (Vitt *et al.* 1998, 2003a, Mesquita *et al.* 2006). In addition, *C. modesta* exhibits similar habits in another area (Jalapão, Tocantins state), suggesting a high degree of niche conservatism in this species (Mesquita *et al.* 2006). *Anolis brasiliensis*, which uses both terrestrial and arboreal microhabitats (Vitt *et al.* 2001, 2008), was the dominant species in the seasonally flooded forest. Similarly, *Mabuya frenata*, an indicator species of the flooded forest, also uses both terrestrial (usually saxicolous) and arboreal (mainly tree trunks) environments (Vrcibradic &

Rocha 1998). The success of these species in seasonally flooded areas is possible due a higher degree of plasticity in their ecology, including their ability to use both terrestrial and arboreal microhabitats.

In spite of historical constraints, many species, especially anoles, can be very plastic in responding to environmental changes. For example, native *Anolis* lizards of Grand Cayman Island show changes in habitat use and morphology due to the competitive pressure exerted by an introduced anole species (Losos *et al.* 1993). On the other hand, species in non-flooded forest exhibited similar habitat use to conspecifics in other environments, thus demonstrating the importance of historical factors in structuring lizard communities (Vitt 1991, Vitt *et al.* 1997b, Mesquita *et al.* 2006). A variety of adaptations enables the seasonal shift to arboreality in species that occur in flooded forests, including powerful claws in dactylids, iguanids, and polychrotids (Tulli 2012) and toe pads in some anoles (Elstrott & Irschick 2004) and geckos (Arnold 1993). Most anoles tend to have at least some degree of arboreality (Losos *et al.* 1993, Losos & de Queiroz 1997, Losos 2009) and even those mainly found on the ground, like *A. brasiliensis*, do not lose the ability to climb (Vitt *et al.* 2008). Similarly, *Mabuya frenata* and *M. nigropunctata* are usually found in the leaf litter or logs, but can climb trees (Vitt *et al.* 1997b, Vrcibradic & Rocha 1998). In addition, highly terrestrial species such as *Kentropyx* spp. can also shift to arboreality during seasonal flooding periods (Vitt & Carvalho 1992, Vitt *et al.* 1995).

We also found species typically encountered in the disturbed areas, like *Ameiva ameiva* and *Tropidurus torquatus*, in the flooded forest, whereas they were either absent (*T. torquatus*) or had lower abundance (*A. ameiva*) in the non-flooded forest. Seasonal flooding promotes frequent disturbance events, which is reflected in the associated fauna (Gascon 1996, Shimada *et al.* 2000, Haugaaen & Peres 2005). *Ameiva ameiva* is a moderate-sized lizard widely distributed in South America (Vitt & Colli 1994) that rapidly colonizes anthropogenically disturbed areas (Sartorius *et al.* 1999). *Tropidurus torquatus* is widely distributed in the Cerrado and Atlantic Forest, mainly in southeastern and east-central Brazil. It occurs primarily in open areas or forest clearings, is common in urban areas, and always occurs in high density (Rodrigues 1987, Wiederhecker *et al.* 2002, 2003). The abundance of both species in the flooded forest reflects their ability to colonize disturbed areas (Vitt & Colli 1994, Sartorius *et al.* 1999).

ASSEMBLAGE ANALYSIS.—The structure (organization) of biological communities can be determined by examining their habitat, their

ecological interactions, and evolutionary relationships among taxa (Pianka 2000, Webb *et al.* 2002, Ricklefs 2003). However, structure can also be influenced by disturbance. In stable environments, assemblages are more likely to be structured because species can reach an equilibrium resulting from ecological interactions, whereas assemblages from unstable environments are more likely to be unstructured because species cannot reach equilibrium via ecological interactions due to the stochastic nature of the environment (Uetz *et al.* 1979, Peres 1997, Lambeets *et al.* 2008). Traditionally, structure within an assemblage is characterized by non-random patterns of resource use among species (Winemiller & Pianka 1990). More recently, with the growing number of phylogenetic hypotheses becoming available, community ecology is increasingly becoming tied to evolutionary relationships among species (Webb 2000, Webb *et al.* 2002). We found that the lizard communities of the flooded and non-flooded forests are not phylogenetically structured. The PE do Cantão region lies at the Amazon–Cerrado ecotone, an area characterized by ecological and evolutionary instability (Haffer 1969, Werneck *et al.* 2012), which can be unfavorable to species establishment and survival, affecting community structure as a whole (van der Maarel 1990, Temple 1998). Our results suggest that the ability to withstand the harsh conditions at the Amazon–Cerrado ecotone is convergent and, as a result, the lizard communities show phylogenetic overdispersion (Webb *et al.* 2002, Kraft *et al.* 2007, Vamosi *et al.* 2009).

Localized, rare disturbance events tend to have a low impact on the regional communities and can help specialist species that are able to rapidly respond to environmental changes (Lambeets *et al.* 2008). Environmental changes can be especially pronounced in riverine landscapes. We have shown that seasonal flooding can strongly impact the structure of lizard communities. Ecotones are often more exposed to climate changes (King *et al.* 2013) compared with more stable areas at the core of biomes (Safriel *et al.* 1994). Despite being species-poor, compared with central areas in the Amazon or Cerrado, ecotone communities harbor species with important adaptations that could hold the key to persistence in human-disturbed landscapes or even during periods of climate change. Finally, the environmental pressures at the ecotone could promote habitat shifts that lead to speciation (Vanzolini & Williams 1981, Moritz *et al.* 2000, Schilthuizen 2000), rendering the Amazon–Cerrado ecotone an important source of evolutionary novelty.

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SUPPORTING INFORMATION

Additional Supporting Information may be found with online material:

APPENDIX S1. Specimens examined.

FIGURE S1. Study area in northeast Tocantins State, Brazil.

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