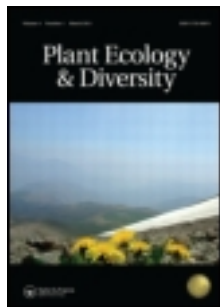


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### Diversity, abundance and distribution of lianas of the Cerrado-Amazonian forest transition, Brazil

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## Diversity, abundance and distribution of lianas of the Cerrado–Amazonian forest transition, Brazil

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**Background:** Lianas strongly influence tropical forest dynamics and diversity.

**Aims:** To determine the relationship among richness, diversity, abundance and distribution of liana species in different vegetation formation types along a gradient within a savanna–forest transition zone in central Brazil.

**Methods:** All liana species were identified and their girth measurements ( $\geq 5$  cm) taken in one 1 ha plot at each of 15 sites that encompassed a range of vegetation types: dystrophic cerradão (tall closed woodland cerrado), gallery forest, flooded forest, semi-deciduous seasonal forest (one monodominant) and evergreen forest. We evaluated and compared the communities in terms of richness, community diversity (Shannon's  $H'$ ), equitability (Hurlbert's,  $PIE$ ), and the distribution of liana abundance.

**Results:** In total, 1467 individual lianas belonging to 65 species, 41 genera and 17 families were recorded in the 15 ha sampled. The value of  $H'$  varied from 0–2.47, and that of  $PIE$  ranged from 0–0.90. While flooded forests had remarkably high liana densities, their liana community was dominated by just one species, *Combretum laxum* (64% of stems); the most abundant liana in non-flooded forests was *Heteropterys eglandulosa* (13%). The different liana species showed varying affiliations with vegetation type, with distinct species groupings associated with the different vegetation types.

**Conclusions:** Variations in species composition and distribution of lianas in this savanna–forest transition were found to be driven by environmental gradients that cause distinct species associations with discrete vegetation formation types.

**Keywords:** *Combretum laxum*; environmental gradient; flooded forests; tropical forests; woody climber

### Introduction

Lianas are an important ecological group in the transition zone that occurs between the two largest South American biomes: Cerrado (a form of savanna) and Amazon forest. Lianas contribute significantly to the overall plant species richness of this region (Marimon et al. 2001, 2002). Studies over the past two decades in closed-canopy tropical forests indicated that the geographical variations in the distribution, composition and richness of lianas might be directly related to both local and regional factors (Avalos et al. 1999; van der Heijden et al. 2008; Addo-Fordjour et al. 2009; van der Heijden and Phillips 2009a). Understanding is very limited, however of how liana communities vary along the zone of transition from forest to savanna in southern Amazonia.

Within closed-canopy tropical forests, the distribution, composition, and richness of lianas is related to a number of factors, including the structure of the supporting tree and/or shrub communities as well as average size of gaps, humidity, soil, light, rainfall, fire regime, altitude and climate conditions (Putz 1984; Putz and Chai 1987;

Nabe-Nielsen 2001; Schnitzer 2005; Jirka et al. 2007; Addo-Fordjour and Anning 2008).

Soil physical conditions may also affect liana abundance. For example, in north-central Mato Grosso in southern Amazonia lianas have been observed to be more abundant on soils with impeded drainage, e.g. campinarana (Jirka et al. 2007). In other cases, where soil physical conditions are combined with water limitations, such as in cerrado on rocky soil (cerrado rupestre), the abundance of lianas can be extremely low (see Maracahipes et al. 2011), especially after repeated fires. Likewise liana abundance is low in seasonally flooded communities because many liana species apparently lack ecophysiological characteristics, such as hypertrophied lenticels on stems through which potentially toxic compounds associated with anaerobiosis are released (Joly and Crawford 1982; Scarano et al. 1994; Ivanauskas et al. 1997) to aid survival during seasonal flooding events.

In this context, we anticipated that flooded forests in the Amazon forest–Cerrado transition zone should have lower

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richness, diversity and equitability of lianas compared with non-flooded forests. Such flooding effects on liana abundance and species richness would, however, be expected to be superimposed on those of climate and/or soil gradients, factors which are known to influence the species diversity of trees and lianas (Gentry 1991; Sfair and Martins 2001).

It is also known that lianas are key drivers for woody vegetation dynamics (Putz 1980, 1984; Gentry 1991), as lianas affect the growth and mortality of tree and shrub species, and can determine the dynamics of gaps created by tree-fall (Schnitzer and Bongers 2002). They also affect tree seedlings dynamics (Pérez-Salicrup et al. 2001), carbon turnover (Phillips and Gentry 1994) and strongly impact litter production in some tropical forests (Gentry 1983). Thus they contribute significantly to a range of biogeochemical processes. Moreover, high liana abundances have the potential to reduce total forest biomass through competition with carbon-dense tree species and, consequently, to decrease the carbon sequestration capacity of mature forests (Phillips et al. 2002; Schnitzer and Bongers 2002; van der Heijden and Phillips 2009a). There is strong evidence that lianas as an ecological guild have become more dominant recently across many neotropical forests (e.g. Phillips et al. 2002; Schnitzer and Bongers 2011), but this average tendency may mask a suite of possible causes, given the sheer diversity of forest vegetation in South and Central America, and the possibility that different liana taxa may be favoured by different environmental conditions. The ecological impacts of lianas may be especially marked in the southern Amazon forest transition zone, where current research has indicated that these forests were 'hyperdynamic' (Marimon

et al. 2014), with much faster turnover of tree populations than reported from most core Amazon forests (e.g. Phillips 1996). It is therefore important to improve basic understanding of how and why lianas vary in the transition zone, both as important organisms in their own right and in order to better comprehend how lianas affect the rich variety of forest communities here.

The aim of this study was to determine the relationship among richness, diversity and distribution of liana species in contrasting vegetation types within the savanna–forest transition zone in central Brazil. Our main objectives were thus: (i) to determine and compare liana abundance, richness, diversity, equitability and distribution among the most common woody formations of the Amazon forest–Cerrado transition zone of central Brazil; and (ii) to assess the extent to which the observed species are restricted to defined habitats and/or vegetation formation types.

## Materials and methods

### Study area

The study was carried out in 15 long-term permanent plots in southern Amazonia, eastern Mato Grosso State, Brazil: one gallery forest, one dystrophic cerradão (tall savanna woodland), one semi-deciduous seasonal forest, one monodominant forest of *Brosimum rubescens* Taub., three evergreen forest stands and eight seasonally flooded forest stands (Figure 1). These sites were selected as they represent the range of vegetation types found within the transition zone, have long-term measurements, and are relatively undisturbed by recent anthropogenic activities.

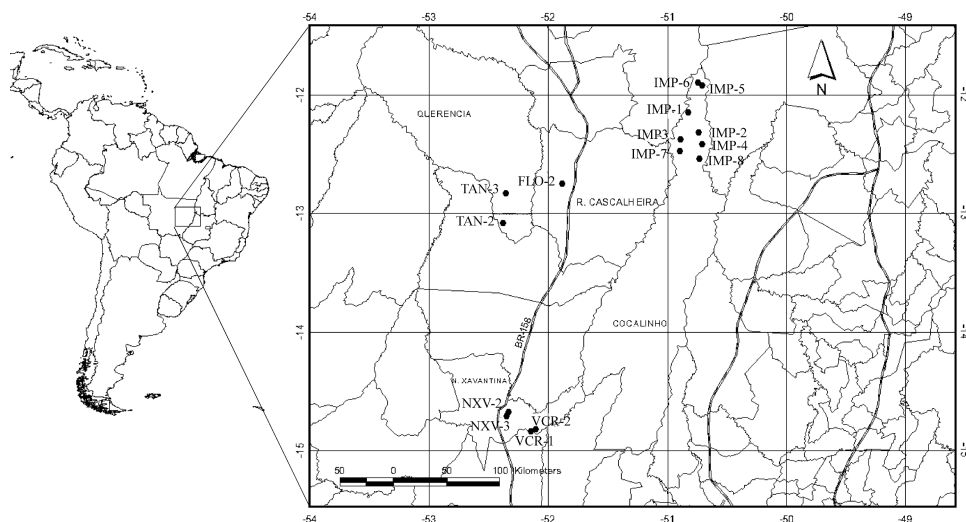


Figure 1. Geographical location of 15 1-ha plots established in the Cerrado–Amazonian forest transition, eastern Mato Grosso State, Brazil. IMP-1 to IMP-8, seasonally flooded forest; TAN-2, TAN-3 and FLO-2, evergreen forest; VCR-1, monodominant semi-deciduous forest; VCR-2, semi-deciduous seasonal forest; NXV-2, dystrophic cerradão, NXV-3, gallery forest. Details of the vegetation studied are as follows: a monodominant forest of *Brosimum rubescens* Taub. (VCR-1) and a semi-deciduous seasonal (non-monodominant) forest (VCR-2) located on Fazenda Vera Cruz, Nova Xavantina, MT (Marimon et al. 2001; Marimon and Féfili 2006); dystrophic cerradão (NXV-2) and gallery forest (NXV-3) located at the Bacaba Municipal Park, Nova Xavantina, MT (Marimon et al. 2002, 2010; Marimon-Junior and Haridasan 2005); evergreen forest (Ivanauskas et al. 2008) sampled within the reserve of Fazenda Floresta (FLO-2), in Ribeirão Cascalheira, MT, and at Fazenda Tanguro (TAN-2 and TAN-3), in Querência, MT. The plots located within flooded forests (impucas) (IMP-1 to IMP-8) were in the Araguaia State Park, Novo Santo Antônio, MT (Marimon et al. 2008).

All these vegetation types are dominated by tree species with heights ranging from 8–30 m, with palms, lianas and some shrubs present (Marimon et al. 2001, 2002, 2006; Ivanauskas et al. 2004b, 2008; Marimon-Junior and Haridasan 2005; Feldpausch et al. 2011; Torello-Raventos et al. 2013). Most of the vegetation is well-drained (terra firme) forest, but seasonally flooded forests (*impucas*) also occur. *Impucas* have unique floristic and structural characteristics (Marimon et al. 2008; Barbosa et al. 2011) and are found only on floodplains of eastern Mato Grosso State and in Tocantins State, usually being associated with natural depressions of the terrain (Marimon et al. 2008).

The climate of the region is tropical savanna type, Aw, according to Köppen (Silva et al. 2008), characterised by two well-distinguished seasons, one dry, from April to September, and one rainy, from October to March. Annual precipitation ranges from ca. 1500 mm in Nova Xavantina (Marimon et al. 2010) to 1700 mm in Santa Terezinha (Eiten 1985) and 1740 mm in Querência (Balch et al. 2011).

#### Collection of floristic data

In each 100 m × 100 m plot, we established 25 permanent sub-plots of 20 × 20 m and measured the diameter of all live lianas stems ≥ 5 cm diameter at 1.3 m along the stem from the highest rooting point. Plots were established at least 250 m from the forest edge (except for gallery and flooded forest, which were fully sampled) in areas without logging and no recent history of fires. All stems rooted in the plot were measured, and each rooted stem was considered a new individual following Schnitzer et al. (2008). The species were identified in the field and, when necessary, specimens were collected for comparisons with the NX Herbarium collection (State University of Mato Grosso, UNEMAT, Campus of Nova Xavantina), UB Herbarium (University of Brasília, Brasília) and UFMT Herbarium (Federal University of Mato Grosso, Cuiabá), or were sent to specialists. All material was archived at the NX Herbarium. The taxonomy and phytogeographical domains of the species follow Forzza et al. (2010).

#### Data analysis

Sampling effort quality in each 1 ha plot was evaluated through species accumulation curves based on 1000 randomisations of the original data with the software *EstimateS* 8.0 (Colwell 2008). Species diversity was determined by the Shannon index ( $H'$ ) using the napierian (natural) base (Magurran 1988). Community equitability was calculated by the Hurlbert's Probability of Interspecific Encounters (*PIE*) (Hurlbert 1971). Both tests were obtained by using 1000 randomisations with the software *EcoSim* 7.0 (Gotelli and Entsminger 2001).

Species richness and equitability comparisons among vegetation types were made through the rarefaction method, executing 1000 randomisations with the software *EcoSim* 7.0 (Gotelli and Entsminger 2001), followed by  $Z$  tests (Zar

2010) conducted in the 'vegan' package (Oksanen et al. 2010) of the R software environment (R Development Core Team 2009). To estimate the total richness of each area, the estimators ICE, Chao 2, Jackknife 1 and 2 were evaluated, with values obtained from the software *EstimateS* 8.0 (Colwell 2008). The estimators were chosen based on abundance data, according to Hortal et al. (2006). The best estimator was chosen based on the regression analysis of the observed and estimated values of richness for each area, whereas the measure of precision of the estimator was based on the  $R^2$  value of the regression (Brose et al. 2003).

Liana species associations with the various woody formation types were evaluated through a graphic model known as 'composed or generic graph'. The  $y$  axis was represented by the species and their abundances, and ordered according to the weighted average of the species in vegetation formation types (represented by the  $x$  axis). The routine for the graph preparation was provided by Victor L. Landeiro, and calculated in the software R 'vegan' package (Oksanen et al. 2010). We also used a method of hierarchical, divisible and polythetic classification, TWINSPAN (Hill 1979), which provides information about indicator and preferential species. According to Kent and Coker (1992), a species is an 'indicator' when it occurs exclusively on one or other side of a dichotomy and is 'preferential' to one side if it is more than twice as likely to occur on that side than on the other. Species with densities lower than three individuals per ha were excluded from the ordination and classification analyses, as recommended by Felfili and Rezende (2003). The analysis was carried out by using the software PC-Ord 5.0 (McCune and Mefford 2006).

In order to compare the liana abundance between flooded and non-flooded forests, we used the non-parametric Mann–Whitney  $U$  test (Zar 2010). Sites with ≤ 50 individuals were removed from the analysis (Felfili and Rezende 2003). The analysis was carried out by using the software Statistica 7.0 (Stat Soft 2004).

#### Results

Within the 15 plots, 1467 liana individuals ≥ 5 cm diameter were inventoried, distributed among 65 species, 41 genera and 17 families (online supplemental material, Table S1). Overall species richness ranged from 0–18 species per plot, with richness in the flooded forest plots ranging from 0–12 species and in non-flooded plots from 8–18 species (Table 1).

Shannon diversity ( $H'$ ) ranged from 0–2.47 and Hurlbert's equitability (*PIE*) between 0–0.90. In general, non-flooded forests had lower ecological dominance and higher diversity ( $1.3 < H' < 2.5$ ) and equitability ( $0.63 < PIE < 0.90$ ) than the flooded forests which had a more marked dominance by certain species, with lower diversity and equitability ( $0.0 < H' < 1.6$ , and  $0.00 < PIE < 0.69$ ) (Table 1).

There was a continuous increase in the species accumulation curves for the lianas for some of the forests, especially VCR-2, NXV-3, FLO-2 and IMP-4 (Figure 2).

Table 1. Liana richness, number of individuals, estimated richness (first-order Jack-knife estimator), Shannon species diversity ( $H'$ ) and Hurlbert's equitability (Probability of Interspecific Encounter =  $PIE$ ), of 15 forests located in the Cerrado-Amazonian forest transition, eastern Mato Grosso State, Brazil. Values are presented in descending order of richness. Values followed by the same letters indicate absence of difference in richness or equitability ( $P > 0.05$ ), based on rarefaction analysis followed by  $Z$  test.

Vegetation type	Individuals	Species	Jack-knife 1	$H'$	$PIE$
Semi-deciduous seasonal forest (VCR-2)	163	18 <sup>a</sup>	24	2.47	0.90 <sup>a</sup>
Gallery forest (NXV-3)	55	14 <sup>ab</sup>	17	2.22	0.87 <sup>ab</sup>
Evergreen forest (TAN-3)	70	12 <sup>c</sup>	15	2.01	0.83 <sup>c</sup>
Seasonally flooded forest (IMP-4)	129	12 <sup>def</sup>	17	1.44	0.66 <sup>d</sup>
Seasonally flooded forest (IMP-6)	186	12 <sup>e</sup>	15	1.62	0.69 <sup>de</sup>
Evergreen forest (TAN-2)	104	11 <sup>ef</sup>	13	1.99	0.83 <sup>f</sup>
Monodominant forest (VCR-1)	137	10 <sup>egi</sup>	12	1.78	0.79 <sup>g</sup>
Seasonally flooded forest (IMP-5)	142	10 <sup>egh</sup>	13	1.31	0.63 <sup>h</sup>
Dystrophic cerradão (NXV-2)	114	9 <sup>eghi</sup>	10	1.31	0.63 <sup>hi</sup>
Evergreen forest (FLO-2)	26	8 <sup>cefgij</sup>	13	1.56	0.75 <sup>bgi</sup>
Seasonally flooded forest (IMP-2)	184	6 <sup>k</sup>	6	1.03	0.46 <sup>k</sup>
Seasonally flooded forest (IMP-3)	125	5 <sup>l</sup>	6	0.58	0.26 <sup>l</sup>
Seasonally flooded forest (IMP-1)	28	3 <sup>lm</sup>	4	0.49	0.26 <sup>lm</sup>
Seasonally flooded forest (IMP-8)	4	3	4	ns	ns
Seasonally flooded forest (IMP-7)	0	0	0	0	0

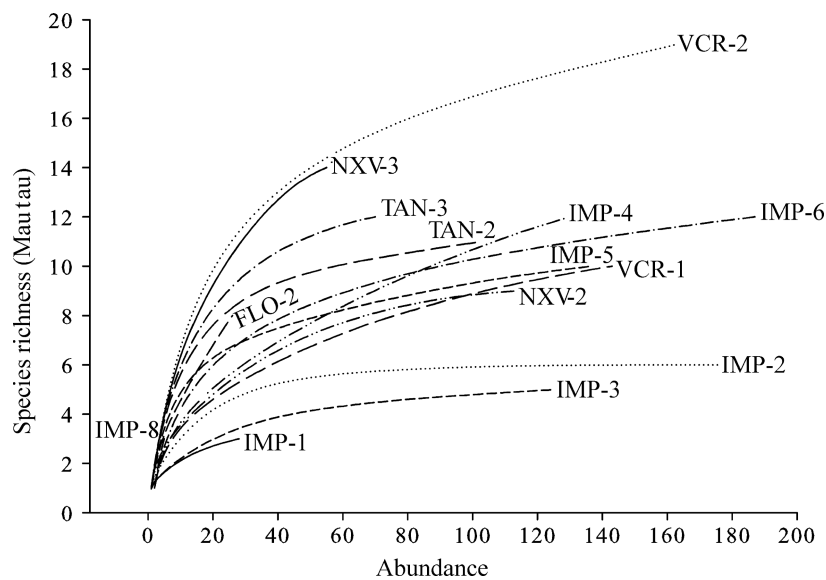


Figure 2. Species accumulation curves (Mao Tau,  $S_{obs}$ ) for the liana communities of the Cerrado-Amazonian forest transition, eastern Mato Grosso State, Brazil. IMP-1 to IMP-8, seasonally flooded forest; TAN-2, TAN-3 and FLO-2, evergreen forests; VCR-1, monodominant semi-deciduous forest; VCR-2, semi-deciduous seasonal forest; NXV-2, dystrophic cerradão, NXV-3, gallery forest. Values are derived from 25 20 m  $\times$  20 m sub-plots per 1-ha plot.

For estimated richness (Jackknife 1,  $r^2 = 0.97$ ,  $P < 0.001$ ), the total richness was not reached with the current sampling effort, with richness above 90% only for the dystrophic cerradão (NXV-2) and for one flooded forest (IMP-2) (see estimated richness (Jack 1), Table 1). After controlling for the number of individuals, three non-flooded forest plots (VCR-2, TAN-3 and NXV-3) had significantly greater, and four flooded forest plots (IMP-1, 2, 3 and 8) had significantly lower richness than the other communities (Table 1).

The number of individuals recorded differed significantly between flooded and non-flooded forests (flooded = 798 individuals, non-flooded = 669;  $U = 5688$ ,  $P = 0.01$ ). In flooded communities *Combretum laxum* was the

most abundant species (except for IMP-8), representing 64% ( $n = 509$ ) of all individuals, and being an order of magnitude more abundant than the second (*Salacia impressifolia*,  $n = 58$ ) and third (*Machaerium inundatum*,  $n = 49$ ) species. Together, these three taxa represented 77% of all individuals (Table S1). This was in contrast to the non-flooded forests and cerradão, where liana individuals were much more evenly distributed amongst species, with *Heteropterys eglandulosa* ( $n = 85$ ), accounting for 13%, *Diplopterys pubipetala* (62) and *Forsteronia rufa* (57) together representing less than a third of all individuals sampled (Table S1).

In terms of their phylogeographical domain, our sampled liana species were well distributed among the main

biomes, with 87% having been reported as occurring in the Amazonian forest, 72% occurring also in the Cerrado (*sensu lato*), 51% in the Atlantic forest, 36% in Caatinga (a thorn-scrub type formation occurring in north-eastern Brazil (Andrade-Lima 1981; Torello-Raventos et al. 2013), and 26% in the Pantanal wetlands (Forzza et al. 2010). According to the database of Forzza et al. (2010), six of all the liana species sampled in our study should occur exclusively in the Amazonian forest, two exclusively in the Cerrado and one in the Atlantic forest. Considering only the flooded forests, 92% of the sampled species have been reported to exist in the Amazonian forest, 69% in the Cerrado, 46% in the Atlantic forest, 38% in Caatinga, and 23% in Pantanal. Among the non-flooded forests, 83% of species are known to occur in the Amazonian forest, 79% in Cerrado, 55% in Atlantic forest, 41% in Caatinga, and 34% in Pantanal.

Characteristic groups of species were identified for each vegetation formation type according to the distribution and

the classification of species (Figures 3 and 4). Remarkably, only *Hippocratea volubilis* and *Moutabea excoriata* were present in both flooded and non-flooded forests (Figures 3 and 4). In the first division of TWINSPAN, the flooded forests were separated from the non-flooded (Figure 4). In the flooded forest group, *Combretum laxum*, *Salacia impressifolia*, *Machaerium inundatum*, and *Passiflora haematostigma* were identified as preferential species, while *Deguelia amazonica*, *Forsteronia rufa*, *Phanera coronata* and *Strychnos* sp.4 were preferentially associated with non-flooded forests. Within the non-flooded vegetation types, dystrophic cerradão (NXV-2) was separated from the evergreen and semi-deciduous forests, with *Diplopterys pubipetala*, and *Strychnos* sp.3 identified as preferential species. The evergreen forests of the Municipalities of Ribeirão Cascalheira (FLO-2) and Querência (TAN-2 and TAN-3), which are geographically close to each other and to the Amazonian forest, had *Deguelia amazonica*, *Dollicarpus amazonicus* and

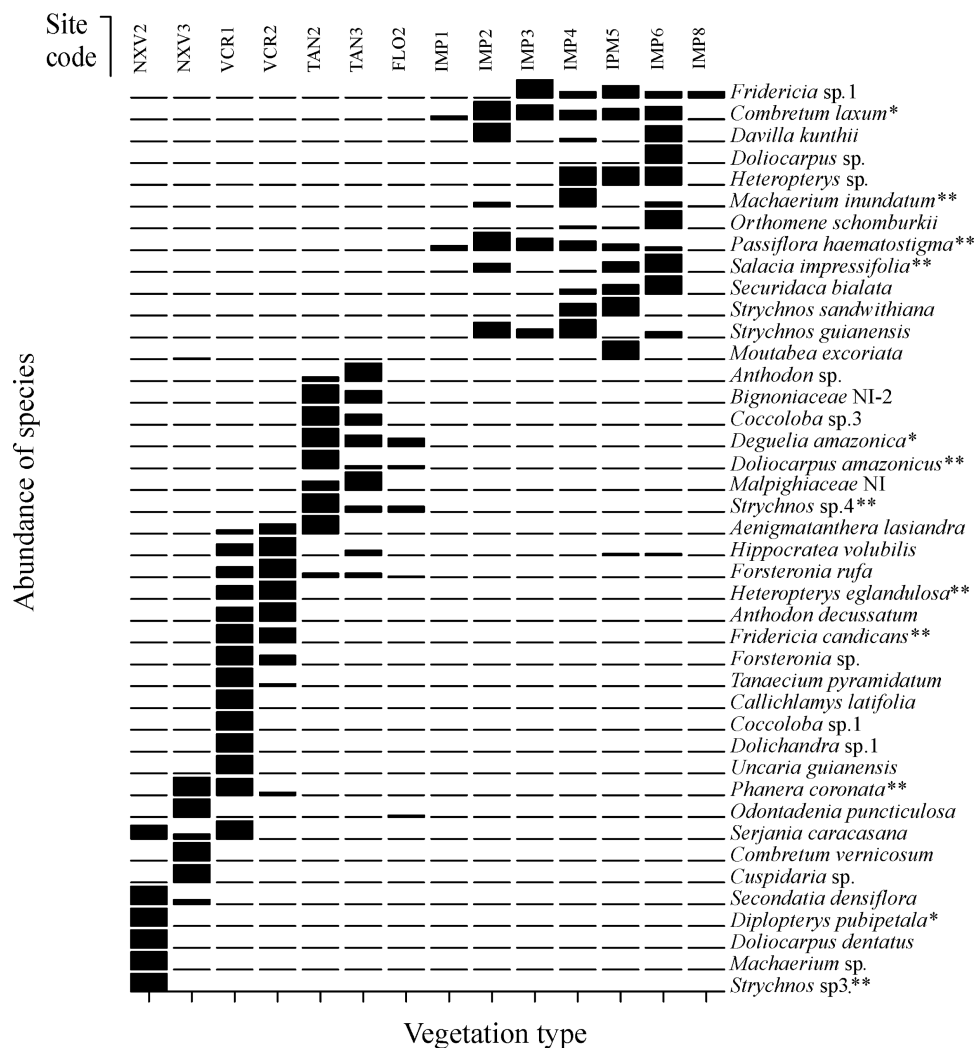


Figure 3. Ordination of liana species in woody vegetation types of the Cerrado–Amazonian forest transition, eastern Mato Grosso, Brazil. Indicator species are designated with one asterisk and preferential species with two asterisks, according to a TWINSPAN analysis. IMP-1 to IMP-8, seasonally flooded forest; TAN-2, TAN-3 and FLO-2, evergreen forests; VCR-1, monodominant semi-deciduous forest; VCR-2, semi-deciduous seasonal forest; NXV-2, dystrophic cerradão; NXV-3, gallery forest. Black rectangles represent the pondered average of the species abundance.

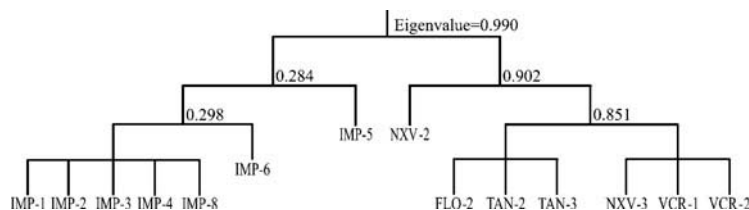


Figure 4. Classification (TWINSpan) of the liana communities of the Cerrado–Amazonian forest transition, eastern Mato Grosso, Brazil. IMP-1 to IMP-8, seasonally flooded forest; TAN-2, TAN-3 and FLO-2, evergreen forest; VCR-1, monodominant semi-deciduous forest; VCR-2, semi-deciduous seasonal forest; NXV-2, dystrophic cerradão; NXV-3, gallery forest.

*Strychnos* sp.4 as preferential species, and were separated from three other non-flooded plots (VCR-1, VCR-2 and NXV-3), two semi-deciduous and one gallery forest. The final group of plots was restricted to the Municipality of Nova Xavantina, being located in close proximity to each other – and to the very different dystrophic cerradão (NXV-2) (Figure 1).

## Discussion

Liana species richness in the non-flooded vegetation types was relatively low (8–18 species) compared with values reported for other non-flooded forests in South America. In Amazonia, for example, Gerwing and Farias (2000) reported 31–66 liana species  $\text{ha}^{-1}$  in the east, and Laurance et al. (2001) recorded 83 species in 2.88 ha in central Amazonia. Across a wider range of neotropical forests van der Heijden and Phillips (2009b) reported 3–51 liana species in 0.1 ha plots, while in a Panamanian tropical forest Dewalt et al. (2000) found 89 species  $\text{ha}^{-1}$  and in a south-eastern Brazilian forest Hora and Soares (2002) reported 45 species in 0.75 ha. Although our individual plots had relatively low species richness, the overall total accounted for considerable richness of lianas (65 species).

The diversity and equitability indices of the liana species ranged widely between the studied communities, with lower values observed for flooded forests. Equitability values were similar to those reported for other non-flooded forest communities (Hora and Soares 2002; Addo-Fordjour et al. 2009), but values for species diversity (both flooded and non-flooded communities) were lower than observed by Hora and Soares (2002) for a liana community in a semi-deciduous seasonal forest in south-eastern Brazil. As a general rule, extreme environmental conditions tend to depress species diversity and equitability of vascular plants (Joly and Crawford 1982; Leitão-Filho 1982); for our flooded forests, extended periods of anaerobiosis due to water-logging was probably a limiting factor. Under these conditions, the most tolerant species possess specific adaptive morphological (e.g. pneumatophores) and physiological characteristics (e.g. storage of carbohydrates in underground organs before the rainy season), which may provide a competitive advantage (Scarano et al. 1994; Ivanauskas et al. 1997) and thus produce a high density of individuals for these well-adapted species. This occurred in our plots for *Combretum laxum* that represented nearly

two-thirds of all liana individuals sampled in the seasonally flooded forests. This species possesses additional adaptations which may contribute to its dominance in flooded forests. It has a rich spectrum of secondary metabolites that may contribute to reducing rates of herbivory, and its fruits are dispersed by water (Croat 1974; Bisoli et al. 2008).

Some studies of woody species in tropical forests have suggested that 1 ha represents sufficient sampling effort to encounter enough species to be able to reliably deduce the total community species richness (e.g. Oliveira and Amaral 2005; Araujo et al. 2009), but others indicated that a greater sampling area was often necessary (Ivanauskas et al. 2004a; Turner 2004; Gonçalves and Santos 2008). In our study, species accumulation curves did not approach an asymptote for the non-flooded communities (Figure 2), suggesting that a larger sampling area would almost certainly have yielded more species. Non-flooded forests had a greater number of species (observed and estimated), probably due to the structural heterogeneity of these communities (Ricklefs 1977) as well as the lack of water-logging. A positive association between the richness of liana species and environmental and spatial heterogeneity has been noted in another study (Sfair and Martins 2011).

The much lower richness observed in the flooded forests is likely due to seasonal flooding, since only those taxa with ecophysiological adaptations to survive the conditions of a periodically saturated rooting zone can thrive (Scarano et al. 1994; Ivanauskas et al. 1997). Indeed, all flooded forest plots had rather similar floristic composition to one another, with *Combretum laxum* being almost universally dominant among lianas in these forests. If the local processes of random extinction and immigration proposed in Hubbell's neutral theory (2001) were at play here, then we would expect a less skewed abundance/diversity distribution, and when communities are replicated, we would expect most replicate to have different dominant species. The fact that the flooded communities of the Amazon forest–Cerrado transition zone do not conform to this supports instead a niche-related interpretation that these vegetation types have environmental conditions that favour dominance by a particular, well-adapted species. In non-flooded forests a clear neutral vs. niche-based interpretation is harder to sustain. Here many environmental factors may contribute to the pattern of distribution of liana abundance, especially the type and amount of tree support available (Feldpausch et al. 2011), light, temperature, and soil (Putz

1984; Putz and Chai 1987; Schnitzer 2005). Thus the finding that no single species was dominant overall, but instead with relative abundance varying from place to place and across vegetation types, is potentially consistent with both a stochastic (neutral) and a deterministic (niche) community ecological perspective. Nevertheless, the separation of the dystrophic locality in the species ordination and vegetation classification results indicates that environmental factors are structuring liana communities here too.

Although very few liana taxa are able to cope with the conditions of the flooded forest, those that do have thrived, with the example of *Combretum laxum* most obvious. Thus, and quite remarkably, the low species richness of the liana community in comparison with better-drained neighbouring vegetation types is apparently irrelevant for the relative magnitude of ecosystem effects of lianas. The results indicated that total liana abundance was rather similar between the two hydrologic regimes, but with the flooded forests having more liana individuals than non-flooded communities. This result has similarities to those reported from north-central Mato Grosso for a different vegetation type (Jirka et al. 2007), where there was a five-fold greater abundance of lianas > 1 cm diameter in campinarana vegetation on sandy soils with a restrictive layer (concretions or indurations) inhibiting root penetration, that resulted in a seasonally perched water table and greater water stress during the dry season compared with that of a terra firme forest (Jirka et al. 2007). At a broader scale, while one cross-continental study of lianas along a rainfall gradient indicated that their abundance and dominance were negatively related to moisture supply (Schnitzer 2005; Swaine and Grace 2007), neotropical analyses across multiple liana communities have found little evidence for an effect of rainfall on liana dominance, at least within the moist and wet forest biomes (Phillips et al. 2002; van der Heijden et al. 2008). In sum, our study indicates that while liana diversity is depressed by seasonal inundation, abundance is certainly not, and that some species, such as *Combretum laxum* in this case, can be strongly favoured by seasonal soil saturation. Whether lianas play as an important role in the dynamics of flooded forests as they do in defining forest structure remains to be seen, and this question is being addressed as part of the long-term surveillance of permanent plots in the region.

That the liana species of the present study are associated mainly with the Cerrado and Amazon forest biomes is hardly surprising, since the sampled plots are located in the transition between these biomes. For both the flooded and non-flooded forests, the Amazonian forest emerged as the main centre of distribution of liana species. However, one species observed in our study, *Niendenzuela glabra*, has until now been considered as an endemic to the Atlantic forest (Forzza et al. 2010). This indicates that even within the comparatively well-sampled and more populous areas of Brazil, there may remain substantial work to characterise species distributions fully. Some of the liana species recorded (*Dioclea glabra*, *Forsteronia rufa*, *Moutabea excoriata*, *Niendenzuela glabra*, *Passiflora haematostigma*

and *Piptocarpha matogrossensis*) are endemic to Brazil (Forzza et al. 2010). This emphasises the importance of conserving the remaining transitional forests and savannas in which they occur, to help protect biodiversity. Over the last decade much of the extensive transitional belt throughout Mato Grosso and beyond has been converted into livestock rearing and agricultural production areas (Alencar et al. 2004). Conservation of the remaining transition forests would help maintain the diversity of Cerrado and Amazon forest biomes, as well as contributing to the conservation of biodiversity normally associated with more geographically distant biomes, such as the Atlantic forest.

In the present study, lianas were shown to be an important group to clearly characterise the different forests of the transition zone, since species distribution varied distinctly according to forest type. We suggest that two main factors drive the segregation of lianas among the studied communities: seasonal flooding and geographical proximity to the Cerrado or to the Amazonian domain (See TWINSPAN, Figure 4). Therefore, not only local factors (flood, soils, and forest structural aspects), but also regional factors contribute to determining liana species composition of the transition zone between the two largest South American tropical biomes.

Liana species most tolerant of specific limiting factors, such as flooding, may dominate certain environments. It might therefore be anticipated that one should systematically encounter specific species assemblages in non-flooded versus flooded forests. In this respect, we note that Scudeller and Souza (2009) reported *Combretum laxum*, *Salacia impressifolia*, and *Securidaca bialata* among the liana species in an igapó (dystrophic flooded forest) in central Amazonia, showing that these species have consistent habitat affiliations across a wide geographic area, thriving in environments with a similarly strong level of hydric saturation. Other lianas in our study that have been suggested as species characteristic of environments without moisture saturation, such as *Deguelia amazonica* and *Securidaca amazonica* were also reported in non-flooded evergreen forest in the southern border of the Amazon Basin (Ivanauskas et al. 2004a), while *Forsteronia rufa* was also sampled in semi-deciduous seasonal forests in south-eastern Brazil (Santos et al. 2009).

## Conclusions

Taking all our studied communities together, we observed moderate regional floristic liana richness relative to other studies and low local species richness in individual plots. This indicates that the high spatial segregation of liana taxa in the transition forest zone helps ensure their potential to have a greater number of species than consideration of measures of local diversity (e.g. alpha-diversity) alone would suggest. In general, our flooded forests had lower richness, diversity and equitability, and greater abundance of lianas than non-flooded forests, suggesting that only a few species possess the relevant ecophysiological adaptations to survive in these seasonally flooded environments.



Nevertheless, these special abilities allow them to thrive and dominate the liana community composition.

The floristic variation of liana communities is likely to result from factors acting at different spatial scales. At the local scale, flooding may be the principal determinant factor, while at the regional scale, geographical proximity to the Cerrado or to the Amazonian forest is likely to be the main factor. There are clear distinctions between liana composition in a seasonally flooded community under a strong influence of the Amazonian flora and a non-flooded community under the influence of the Cerrado biome. Our study shows that the conservation of forest communities in these transitional areas may be important to maintain liana species diversity, since they are host to a combination of widely distributed species, more geographically restricted species, and species endemic to Brazil.

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