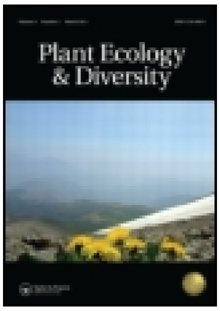

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Beatriz S. Marimon[a], Ben Hur Marimon-Junior[a], Ted R. Feldpausch[bc], Claudinei Oliveira-Santos[d], Henrique A. Mews[e], Gabriela Lopez-Gonzalez[b], Jon Lloyd[bh], Daniel D. Franczak[f], Edmar A. de Oliveira[d], Leandro Maracahipes[d], Aline Miguel[g], Eddie Lenza[a] & Oliver L. Phillips[b]

[a] Universidade do Estado de Mato Grosso, Departamento de Ciências Biológicas, Nova Xavantina, Brasil

[b] School of Geography, University of Leeds, Leeds, UK

[c] College of Life and Environmental Sciences, University of Exeter, Exeter, UK

[d] Universidade do Estado de Mato Grosso, Programa de Pós-graduação em Ecologia e Conservação, Nova Xavantina, Brasil

[e] Universidade de Brasília, Programa de Pós-Graduação em Ciências Florestais, Brasília, Brasil

[f] Universidade de Brasília, Programa de Pós-graduação em Botânica, Brasília, Brasil

[g] Universidade do Estado de Mato Grosso, Programa de Pós-graduação em Ciências Ambientais, Cáceres, Brasil

[h] School of Earth and Environmental Science, James Cook University, Cairns, Australia
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[a]*Universidade do Estado de Mato Grosso, Departamento de Ciências Biológicas, Nova Xavantina, Brasil;* [b]*School of Geography, University of Leeds, Leeds, UK;* [c]*College of Life and Environmental Sciences, University of Exeter, Exeter, UK;* [d]*Universidade do Estado de Mato Grosso, Programa de Pós-graduação em Ecologia e Conservação, Nova Xavantina, Brasil;* [e]*Universidade de Brasília, Programa de Pós-Graduação em Ciências Florestais, Brasília, Brasil;* [f]*Universidade de Brasília, Programa de Pós-graduação em Botânica, Brasília, Brasil;* [g]*Universidade do Estado de Mato Grosso, Programa de Pós-graduação em Ciências Ambientais, Cáceres, Brasil;* [h]*School of Earth and Environmental Science, James Cook University, Cairns, Australia*

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Background: The zone of transition (ZOT) between the Cerrado and the Amazon forest in southern Amazonia represents a unique and rapidly shrinking area due to land-use change.
Aims: To compare the dynamics and above-ground biomass of vegetation located in the ZOT with core Amazon forest and to determine how ZOT dynamics differ within vegetation types for different tree diameter classes.
Methods: Censuses of trees were conducted in seven plots in monodominant forest, semi-deciduous seasonal forest, gallery forest, cerrado sensu stricto and cerradão, in north-eastern Mato Grosso, Brazil from 1996 to 2010, including data for the 2005 drought year. Separate analyses of stem dynamics and biomass were carried out for two different diameter (d) classes: $5 \leq d < 10$ cm and $d \geq 10$ cm.
Results: For trees with $d \geq 10$ cm the average mortality rate was 2.8% year^{-1}, with an estimated above-ground dry biomass of 210 Mg ha^{-1}. Trees with $5 \leq d < 10$ cm constituted only a small fraction of the total biomass store (ca. 10 Mg ha^{-1}) and had a mortality rate of 7.4% year^{-1} and recruitment of 6.5% year^{-1}. Overall, mortality and recruitment in the ZOT were greater than in core Amazonian forests (1–2% year^{-1}).
Conclusions: The distinct vegetation formations of the southern Amazon ZOT are markedly more dynamic than core Amazonian forest. Continued long-term monitoring throughout the region is required to assess whether they also respond differently to climate change.

Keywords: biomass; ecotone; forest dynamics; mortality; permanent sample plot; recruitment; tropical

Introduction

Amazonia has been described as a vast and distinctive phytogeographic province possessing one of the world's most diverse floras (Ackerly et al. 1989) and a mosaic of different vegetation patterns (RADAMBRASIL 1981; Pitman et al. 2008), including transitional formations at savanna–forest boundaries (Pires 1974). This transitional vegetation, especially in southern Amazonia, has experienced several phases of expansion and contraction, where cerrado (savanna) advanced into the forest and vice versa, as the climate changed, with alternating dry and wet events, especially during the late Quaternary (Ab'Saber 1982; Prance 1982; Mayle et al. 2000). As a result a large, unstable, and permanent zone of (ecological) tension (ZOT) has formed along the southern margin of the Amazonian forest, resulting in a state of dynamic transition attributable to fluctuations in precipitation (Ratter 1992; Ratter et al. 1997). This, in turn, can result in a potentially perpetual succession from forest to cerrado (during dry events) and vice versa (wet events), as a result of which a hyperdynamic ecological environment might be expected to prevail in the ZOT. In this paper we probed this idea by examining properties of vegetation dynamics measured in this transitional zone and comparing them with existing measurements in the core Amazonian forests.

Several vegetation formation types (sensu Torello-Raventos et al. 2013) are found in the transition zone between cerrado and core Amazonian forest. These include gallery forests along small streams, monodominant forests of *Brosimum rubescens* (Marimon et al. 2001), dry forest (Soares 1953; Ratter et al. 1973; Pires 1974), cerrado sensu stricto (typical savanna) and cerradão (a dense and tall woodland formation) (Ratter et al. 1973). Dry forest is the true Amazonian forest in the transition zone, an evergreen forest (Ivanauskas et al. 2008) considered as part of a continuum from the cerrado to the Amazonian evergreen forests (see Ackerly et al. 1989; Marimon et al. 2006). Often consisting of a mixture of forest and savanna species, cerradão can be considered as either forest or tall closed woodland, this depending on its species composition

*Corresponding author. Email: biamarimon@hotmail.com

(Torello-Raventos et al. 2013), and is usually found forming a band of contact between dry forest and cerrado sensu stricto, only a few kilometres wide (Ratter et al. 1973). It is likely that cerradão of this region represents a successional stage that reflects a recent advance of the Amazon forest into cerrado vegetation (Ratter 1992; Marimon et al. 2006; Franczak et al. 2011), thus providing insights into the ecology and dynamics of the forest–savanna boundaries in southern Amazonia.

Studies of vegetation dynamics, based on a comprehensive assessment of mortality, recruitment and growth, can improve our understanding of the ecological processes that govern plant communities (Phillips et al. 2011) and may help reveal the population consequences of disturbances or successional changes (Durigan and Ratter 2006). Climatic variations, such as periods of drought, can be one determinant of plant community dynamics, especially for communities not usually subject to large fluctuations (ter Steege 2009). Furthermore, in tropical forests, small-stature plants (species and individuals) may show more mortality and higher dynamism than taller or mature trees (Bierregaard et al. 1992; Newbery et al. 1999). These smaller plants may be especially sensitive to change, and are therefore potentially leading indicators of ecosystem shifts.

Amazon forests are thought to have maintained similar features at least for the past 55 million years (Morley 2000; Maslin et al. 2005), while the cerrado existed in prototypic form in the Cretaceous (Ratter and Ribeiro 1996). This long time-scale may have been enough to produce unique interactions in the complex contact zone between the two biomes. The overall aim of our research was to understand the ecological interactions in these transitional areas and to use this to improve predictions of the future dynamics of biomass and carbon at the forest/cerrado margins. In particular, by comparing the contemporary dynamics of different vegetation types at this transition we may understand better their sensitivity to climatic conditions and therefore how they may be expected to respond to environmental changes (Malhi et al. 2004; Phillips et al. 2004).

In this study, we explored the hypotheses that: (1) the vegetation formation types at the southern edge of the Amazonian forest were more dynamic in terms of turnover than the core Amazonian tree communities found in less seasonal climates; (2) the diversity and above-ground biomass of the vegetation types of the transition zone have undergone changes due to a recent drought event; and (3) dynamics, including mortality, recruitment, and net biomass change, differed between savanna and forest plots of the transition zone. To address these hypotheses, we analysed new data on stem and biomass dynamics for vegetation. We quantified tree dynamics over a period that included the 2005 drought, and evaluated if dynamics differed by vegetation type and between tree diameter classes.

Materials and methods

Study area

The study areas were located in north-eastern state of Mato Grosso, central Brazil, in the municipality of Nova Xavantina. The vegetation is broadly classified as a mosaic of savanna and forest (Ratter et al. 1973; Ackerly et al. 1989; IBGE 2004; Ivanauskas et al. 2004; Marimon et al. 2006). Seven plots were selected to sample this transition zone, five (one cerrado sensu stricto, one cerradão and three gallery forests) in the Parque Municipal do Bacaba, an ecological reserve (14° 41’ S and 52° 20’ W) and two (one monodominant forest and one semi-deciduous seasonal forest) in the nearby reserve of Fazenda Vera Cruz (14° 50’ 47” S and 52° 08’ 37” W) (Table 1). The climate of all localities was type Aw, according to Köppen’s classification, with a dry season from April to September and a wet season from October to March, and the annual rainfall averaging ca.1400 mm and a mean annual temperature of 25 °C (Marimon et al. 2010; Mews et al. 2011b). The distance between cerrado sensu stricto, cerradão and gallery forest plots was ca. 1.5 km. The monodominant and semi-deciduous forest plots were within 800 m of each other, and less than 25 km from the other plots.

The adjacent cerrado sensu stricto and cerradão grew on Ferralsols (FAO/UNESCO 1994), deep soils with similar fertility but distinct floristic and structural vegetation characteristics (Marimon-Junior and Haridasan 2005; Franczak et al. 2011; Mews et al. 2011a). The three gallery forest plots differed in slope with their soils being predominantly shallow Lithosols (quartzite rocks) and alluvium (Gleysols), with floristic composition strongly similar to Amazonian forests (Marimon et al. 2002, 2010; Miguel et al. 2011). The soils in the monodominant and semi-deciduous seasonal forests were shallow acidic Plinthosols with lateritic outcrops and concretions, with high levels of Fe and exchangeable Al (Marimon 2005) (Table 1).

The cerrado sensu stricto is characterised by a savanna formation with grass understorey and trees and shrubs up to 8–10 m (Oliveira-Filho and Ratter 2002). The cerradão was previously studied and designated as *Hirtella glandulosa* type or dystrophic cerradão (Ratter et al. 1973, 1977; Marimon-Junior and Haridasan 2005). Cerradão has been classified as ‘mesophyllous sclerophyllous forest’ (Rizzini 1979), a transitional forest, characterised by the presence of species from both savanna and forest. The gallery forests are narrow strips of evergreen or semi-deciduous mesophytic forests that occur along water courses in the Cerrado biome (Ratter et al. 1973, 1997; Ribeiro and Walter 2008), and the monodominant and semi-deciduous seasonal forests of this study are typical forests representing the periphery of the Amazon forest (Ratter et al. 1973; Pires and Prance 1985; Marimon et al. 2001; Marimon 2005; Mews et al. 2011b). Trees were identified to species level; a detailed description of the species composition of these plots has been published elsewhere (Marimon et al. 2001, 2002; Marimon 2005; Marimon-Junior and

Table 1. Characteristics of the sample plots in the transition zone between cerrado and Amazonian forest, north-eastern Mato Grosso, Brazil.

Vegetation type	Plot size (ha)	Census dates	Plot description	Dominant species (last inventory, DBH ≥ 5cm)
Cerrado	0.5	2002, 2006 and 2008	Savanna; trees and shrubs with grass understorey. Soil type: Ferrasols, dystrophic and acidic.	*Qualea parviflora* Mart. *Davilla elliptica* A.St.-Hil. *Roupala montana* Aubl.
Cerradão	0.5	2002, 2005 and 2008	Transitional forest (species from both savanna and forest). Soil: Ferrasols, dystrophic and acidic.	*Hirtella glandulosa* Spreng. *Tachigali vulgaris* L.G. Silva & H.C. Lima *Xylopia aromatica* (Lam.) Mart.
Gallery forest-1	0.5	1999 and 2006	Semi-deciduous mesophytic forest. Soil: Lithosols on quartzite bedrock.	*Astrocaryum vulgare* Mart. *Diospyros guianensis* (Aubl.) Gürke *Calophyllum brasiliense* Cambess
Gallery forest-2	0.5	1999 and 2006	Semi-deciduous mesophytic forest. Soil: Lithosols on quartzite bedrock.	*Aspidosperma subincanum* Mart. *Tetragastris altissima* (Aubl.) Swart. *Hymenaea courbaril* L.
Gallery forest-3	0.5	1999 and 2006	Semi-deciduous mesophytic forest. Soil: Gleysols.	*Mauritia flexuosa* L.F. *Astrocaryum vulgare* Mart. *Virola urbaniana* Warb.
Monodominant forest	0.6	1996, 2001, 2004 and 2010	Monodominant forest. Soil: Plinthosols, dystrophic, acidic, shallow with lateritic concretions.	*Brosimum rubescens* Taub. *Amaioua guianensis* Aubl. *Tetragastris altissima* (Aubl.) Swart.
Semi-deciduous forest	0.6	2003 and 2008	Semi-deciduous forest. Soil: Plinthosols, dystrophic, acidic and shallow.	*Cheiloclinium cognatum* (Miers) A.C.Sm. *Amaioua guianensis* Aubl. *Mabea fistulifera* Mart.

Haridasan 2005; Franczak et al. 2011; Mews et al. 2011a, 2011b; Miguel et al. 2011) (Table 1). Voucher specimens were deposited in the Nova Xavantina Herbarium (NX).

The seven forest and savanna plots in this study ranged in size from 0.5 to 0.6 ha and represented in the most recent census a total of 4811 stems with diameter ≥ 5 cm. Trees were measured between 1996 and 2010, with up to four different censuses in each location (Table 1). All plots were lowland (< 250 m a.s.l.) consisting of apparently mature vegetation with low number of pioneer species and no recent direct human impact. For the period reported here there was no fire in any of our plots, although in the cerrado sensu stricto fire historically occurs about every 5 years. For the cerradão, monodominant, and semi-deciduous forests there is no known history of fire or logging (Marimon et al. 2001; Franczak et al. 2011; Mews et al. 2011a, 2011b; Miguel et al. 2011).

Plant inventory

We measured all trees with diameters (*d*) of ≥ 5 cm at 1.3 m (diameter at breast height, dbh) in the forests and 0.3 m (diameter at 0.3 m above the soil level) in the cerrado plots. Measurements were made 2 cm above bole irregularities or 0.5 m above the highest point of buttresses. The first census was made in 1996 and the plots were re-measured during field campaigns in 2001, 2002, 2003, 2004, 2005, 2006, 2008 and 2010, but not all plots in all years (Table 1). The tree data were deposited in the ForestPlots database (Lopez-Gonzalez et al. 2011) as a contribution to the RAINFOR project (www.geog.leeds/projects/rainfor). Based on their species identity, stem wood specific gravity data were derived from the Dryad-Global Wood Density Database (http://datadryad.org/handle/10255/dryad.235), a compilation that contains data for trees from across the Neotropics (Chave et al. 2009; Zanne et al. 2009).

Analyses

Analyses were carried out for the complete datasets ($d \geq 5$ cm), and separately for the smaller ($5 \leq d < 10$ cm) and larger tree ($d \geq 10$ cm) subsets. Tree mortality and recruitment rates were calculated per plot (all) and species (only cerradão) following Sheil et al. (1995). Considering that these rates may be sensitive to census interval length, we applied a generic census interval correction procedure (Lewis et al. 2004b). Stem turnover was estimated as the mean of mortality and recruitment rates over the period, following Phillips and Gentry (1994).

The cerradão has species characteristic of both cerrado and forest that make it of interest to investigate if there exists a difference between the turnover rates of cerrado and forest species in this vegetation formation. We compared species that had ≥15 individuals *(d* ≥ 5 cm) in the first inventory, and sought to identify those taxa that had particularly high rates of mortality or recruitment in the transitional cerradão vegetation.

For forests, above-ground biomass (*B*) was estimated by applying allometric functions of tree diameter (*d*) and wood specific gravity (ρ) developed for Amazon trees by Baker et al. (2004) (online analytic facilities at www.forestplots.net (Lopez-Gonzalez et al. 2011)). Similarly, for cerrado and cerradão we estimated *B* by applying allometric functions of *d* and ρ using the cerrado-based model of Ribeiro et al. (2011). Mortality and recruitment were compared between cerrado and cerradão by using a Mann–Whitney test. Species diversity for each plot, diameter class and census interval was calculated using the Shannon index (*H*') (Magurran 1988). The *H'* and mean plot-level wood specific gravity were compared between the inventories before and after the 2005 drought using a *t*-test.

Results

Recruitment, mortality, diversity and wood specific gravity

Between 1996 and 2010 annual rates of recruitment and mortality varied among sampled areas and among years (Table 2). In general, recruitment was higher than mortality in the two cerrado and cerradão plots (Mann–Whitney test, $d \geq 10$ cm: $z = -2.54$, $P = 0.011$ and $d \geq 5$ cm: $z = 2.78$, $P = 0.005$) and mortality was higher than recruitment in the forest plots ($d \geq 10$ cm: $z = 3.95$, $P = 0.001$ and $d \geq 5$ cm: $z = 2.12$, $P = 0.003$) (Table 2). The highest mortality rates were observed for gallery forests (GF-2 and GF-3) and the highest recruitment rates in the cerrado and cerradão. These same four plots also had the highest turnover (Table 2). For small trees ($5 \leq d < 10$ cm) mortality and recruitment rates did not differ significantly between forest and cerrado types, but in all cases were higher than those observed for the larger trees ($d \geq 10$ cm); in some cases the smaller trees had either mortality or recruitment rates more than five-fold greater than the larger trees in the same plot.

We next examined if species with particularly high mortality and recruitment rates in the transitional cerradão formation were typical of forest or of cerrado. Of the 10 species occurring in the cerradão with high mortality, nine were typical of forests with annual mortality rates as follows: *Guapira noxia* (21.2%), *G. gracilifora* (9.9%), *Erythroxylum daphnites* (8.7%), *Eriotheca gracilipes* (6.0%), *Antonia ovata* (5.8%), *Roupala montana* (4.9%), *Xylopia aromatica* (4.5%), *Tachigali vulgaris* (2.7%), and *Matayba guianensis* (2.6%). Only one species considered to occur preferentially in areas of cerrado sensu stricto in the region had a mortality rate ≥ 2% year^{-1}, *Syagrus flexuosa* (11.4%). Amongst these high-mortality species, only two had annual recruitment rates that exceeded mortality rates: *Matayba guianensis* (recruitment 5.9%) and *Tachigali vulgaris* (13.0%).

For species occurring in the cerradão with high annual recruitment, only one of was typical of cerrado: *Cordiera sessilis* (7.0%). The other species occurred preferentially in forest formations, and those with the highest recruitment rates included: *Siparuna guianensis* (28.4%), *Maprounea guianensis* (16.3%), *Sorocea klotzschiana* (15.5%) and *Tapirira guianensis* (10.3%).

Considering only those plots with at least three different census periods (cerrado, cerradão and monodominant forest), in the monodominant forest stem recruitment of small trees was higher than mortality before the 2005 drought, with this difference being greatly reduced during and after the 2005 drought (Figure 1). For trees with $d \geq 10$ cm, in the monodominant forest, mortality outstripped recruitment in all census periods; in the cerrado and cerradão, recruitment of large trees was always higher than mortality (Figure 1). Evaluating the censuses before and after 2005, the dead individuals were mostly small trees (cerrado, 83%; cerradão, 77%; gallery forests, 67–69%; and seasonal semi-deciduous forest, 51%), except for the monodominant forest where the dead individuals represented by trees with $d \geq 10$ cm were in the majority (66%).

Comparing the first and last censuses per plot, there was a downward trend in species diversity for every plot,

Table 2. Tree stem mortality, recruitment, and turnover rates, for vegetation types in the transition zone between southern Amazon forest and cerrado, north-eastern Mato Grosso, Brazil. Values for each variable are given for three diameter classes.

	Mortality (% year^{-1})			Recruitment (% year^{-1})			Turnover		
Vegetation type	≥5 cm	5–9.9 cm	≥10 cm	≥5 cm	5–9.9 cm	≥10 cm	≥5 cm	5–9.9 cm	≥10 cm
Cerrado	2.00	7.48	1.13	5.96	9.36	8.96	3.98	8.42	5.04
Cerradão	2.77	7.60	1.67	4.92	8.17	5.81	3.85	7.89	3.74
Gallery forest-1	1.96	5.04	1.54	2.16	4.57	2.30	2.06	4.80	1.92
Gallery forest-2	4.08	8.43	2.92	2.71	5.74	2.99	3.40	7.09	2.96
Gallery forest-3	7.03	13.22	5.79	4.71	8.35	7.12	5.87	10.79	6.45
Monodominant forest	2.52	3.93	2.49	2.29	5.49	0.77	2.40	4.71	1.63
Semi-deciduous forest	4.34	6.39	4.04	1.74	3.74	1.50	3.04	5.06	2.77
Mean	3.52	7.44	2.80	3.50	6.49	4.21	3.51	6.96	3.50

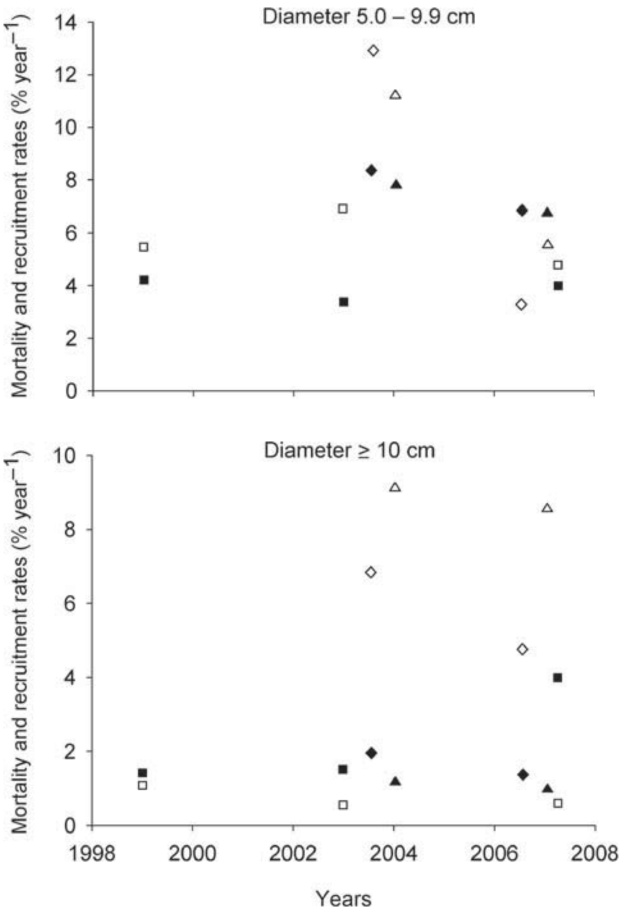

Figure 1. Annual stem recruitment (open symbols) and mortality (filled symbols) rates in plots with at least three census periods, plotted by mid-point of census interval. ▲ and △, cerrado; ◆ and ◇, cerradão; ■ and □, monodominant forest.

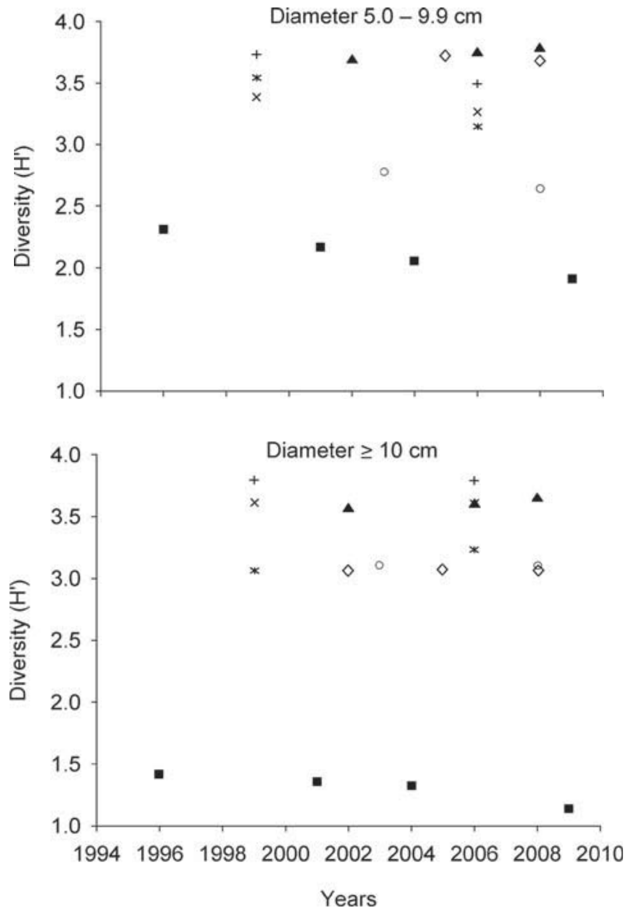

Figure 2. Species diversity (H') for all plots and inventory years. ▲, cerrado; ◇, cerradão; **x**, gallery forest-1; +, gallery forest-2; ж, gallery forest-3; ■, monodominant forest; ○, semi-deciduous forest.

except the cerrado (Figure 2). Considering all plots together there was a significant difference between the initial and final diversity values for the individuals with $d \geq 5$ cm ($t = 2.07$, $P = 0.04$), and for small trees ($t = 2.56$, $P = 0.02$). When cerrado was excluded from the analysis, these diversity declines became even more evident, both for all trees with $d \geq 5$ cm ($t = 4.25$, $P = 0.004$) and for the subset of small trees ($t = 3.43$, $P = 0.009$). For larger trees ($d \geq 10$ cm) there was no significant difference between initial and final species diversity values.

Changes in plot-level mean wood specific gravity potentially provides important information on shifts in tree functional type. When all diameter classes and plots were included, mean plot-level wood specific gravity did not differ significantly between the first and last inventories (i.e. before and after the 2005 Amazon drought) (Table 3). However, once the cerrado plot was excluded from the analysis, then the wood specific gravity of the small trees was observed to decline from the first to last inventories ($t = 2.38$, $P = 0.03$).

Estimated above-ground biomass

For the small trees, considering all vegetation formation types and taking mean values across the various censuses, mean above-ground biomass ranged from 6.6±0.6 Mg ha^{-1} (monodominant forest) to 12.2±0.7 Mg ha^{-1} (cerrado) (Table 4). For larger trees ($d \geq 10$ cm), the pattern was reversed, with the lowest values observed for cerrado and the largest for the monodominant forest (Table 4).

Biomass change

There were changes in biomass stocks over time (Figure 3). For larger trees ($d \geq 10$ cm), the cerrado, cerradão and gallery forest plots in general gained above-ground biomass, while the forest sites tended to lose biomass (Figure 3).

For small trees a net gain of biomass was observed for all vegetation formation types over the sampling period (Figure 3). In plots with three or more inventories, net gains increased from the first to the second intervals in the cerradão, but declined in the cerrado. The monodominant forest gained biomass in all intervals, but this was only marginal in the final interval, that is, that which spanned the drought period (Figure 3).

Considering all individuals with diameters $\geq$ 10 cm (Figure 3), cerrado, cerradão and gallery forests all gained biomass between successive inventories. In cerrado and

Table 3. Average wood specific gravity (g cm^{-3}) of trees in the sampled plots in the transition zone between cerrado and Amazonian forest, north-eastern Mato Grosso, Brazil. Values for each year are given for three diameter classes. Standard deviation between parentheses.

	Wood specific gravity				Wood specific gravity		
Vegetation type	≥5 cm	5–9.9 cm	≥10 cm	Vegetation type	≥5 cm	5–9.9 cm	≥10 cm
Cerrado				Cerradão			
2002	0.652 (0.13)	0.647 (0.13)	0.663 (0.12)	2002	0.675 (0.16)	0.653 (0.15)	0.710 (0.17)
2006	0.642 (0.13)	0.643 (0.14)	0.663 (0.12)	2005	0.667 (0.16)	0.646 (0.14)	0.705 (0.17)
2008	0.652 (0.13)	0.651 (0.13)	0.653 (0.13)	2008	0.667 (0.16)	0.644 (0.15)	0.703 (0.16)
Gallery forest-1				Gallery forest-2			
1999	0.659 (0.11)	0.643 (0.12)	0.674 (0.11)	1999	0.657 (0.13)	0.641 (0.12)	0.676 (0.13)
2006	0.657 (0.11)	0.645 (0.12)	0.617 (0.11)	2006	0.660 (0.12)	0.643 (0.12)	0.686 (0.12)
Gallery forest-3							
1999	0.547 (0.14)	0.568 (0.13)	0.512 (0.14)				
2006	0.546 (0.13)	0.545 (0.13)	0.548 (0.13)				
Monodominant forest				Semi-deciduous forest			
1996	0.725 (0.11)	0.657 (0.10)	0.763 (0.09)	2003	0.665 (0.12)	0.655 (0.11)	0.673 (0.12)
2001	0.713 (0.11)	0.648 (0.10)	0.762 (0.09)	2008	0.663 (0.12)	0.643 (0.12)	0.690 (0.11)
2004	0.709 (0.11)	0.641 (0.10)	0.765 (0.09)				
2010	0.703 (0.11)	0.644 (0.10)	0.777 (0.08)				

Table 4. Mean above-ground biomass (AGB ± standard deviation) in the sampled plots in the transition zone between cerrado and Amazonian forest, north-eastern Mato Grosso, Brazil.

	AGB (Mg ha^{-1})	
Vegetation type	5–9.9 cm	≥10 cm
Cerrado	12.2 ± 0.7	54.9 ± 14.3
Cerradão	10.3 ± 0.7	120.2 ± 25.1
Gallery forest-1	9.6 ± 0.4	197.2 ± 18.2
Gallery forest-2	8.7 ± 0.4	231.0 ± 3.9
Gallery forest-3	14.1 ± 3.0	150.8 ± 28.3
Monodominant forest	6.6 ± 0.6	478.7 ± 35.0
Semi-deciduous forest	10.1 ± 0.5	238.4 ± 14.3

cerradão the net biomass gain increased between the first and second sampling intervals while in the monodominant and semi-deciduous forests, located in an area close to the cerrado and cerradão under the same climatic conditions, there was a decrease, with the net change becoming negative in the final interval (Figure 3).

Discussion

Comparisons with core Amazon and Cerrado biome stands

The forests and savannas of this study, located at the transition between the two largest biomes in tropical South America, were found to be highly dynamic with mortality and recruitment rates substantially greater than the long-term values typically reported for Amazonian forests, including a group of forest plots in western Amazonia known to be particularly fast-growing and dynamic (Table 5). The stem dynamics reported in the present study were also greater than those in central Amazonian plots in a period that spanned a strong ENSO drought (1997–1998), for which mortality and recruitment rates ranged from 1–2% $year^{-1}$ (Laurance et al. 2009). Not only were the mortality and recruitment rates for the ZOT forests greater than those from core Amazonian forests (Table 5), but they were also greater than those in gallery forests, typical and climax vegetation formation types of central Brazil (Table 5). Mortality rates in the *Brosimum*-monodominant forest of our study were also higher than those of a monodominant forest in northern Amazonia sampled over a 20-year period (Nascimento et al. 2014). Other low-diversity forests in Amazonia are also less dynamic than our *Brosimum*-dominated plot, including a monodominant swamp forest in south-western Amazonia (site T1 in Phillips 1996).

Together, these results are consistent with the hypothesis that vegetation types in the transition zone between cerrado and Amazonian forest in Mato Grosso are intrinsically hyperdynamic environments. This high dynamism may result both from the major within-year (seasonality) and between-year variation in climate, and/or from the contact tensions between different vegetation types (Ackerly et al. 1989; Marimon et al. 2006), described by Clements (1949) as "an environmentally stochastic stress zone". The southern edge of Amazonia lies in the range of transition between climatic zones, with highly seasonal rainfall (dry season > 5 months), a situation more typical for the cerrado than for Amazonian forest (Ratter et al. 1973; Furley et al. 1992). Ecosystems in such transitional areas between very distinct vegetation types and climate with strong seasonality are subject to double exogenous stress: climatic variability and contact with 'invading' vegetation. Thus, we hypothesise that (1) the high precipitation seasonality (Furley et al. 1992) at forest–savanna boundaries

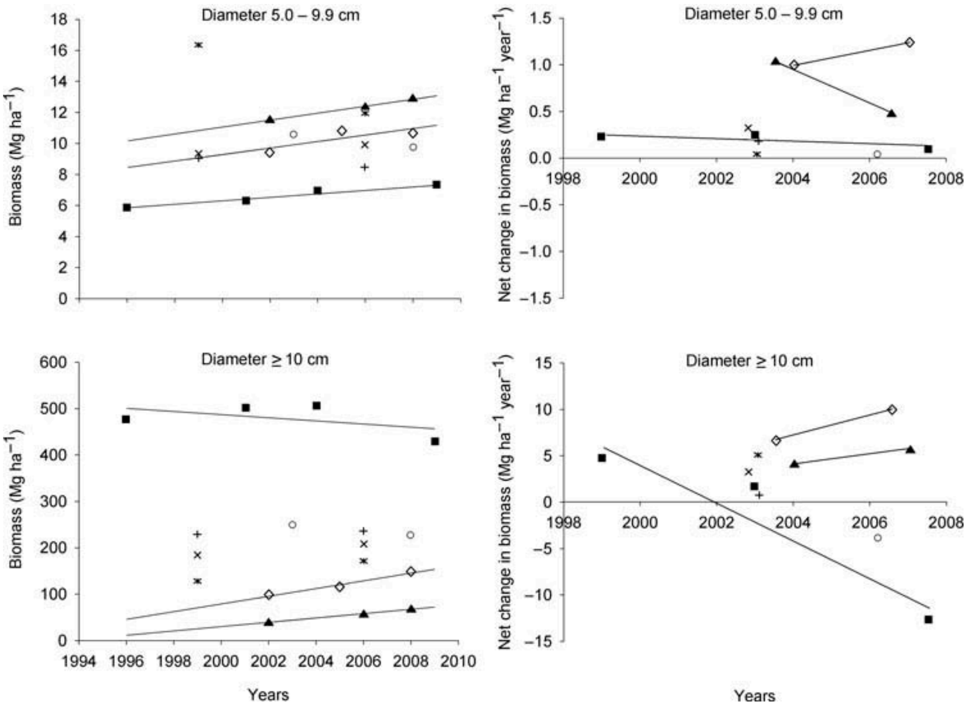

Figure 3. Above-ground biomass (Mg ha^{-1}) in two diameter classes and biomass net gain (Mg ha^{-1}year^{-1}) in each sampled period and vegetation type in the transition zone between southern Amazonian forest and Cerrado, north-eastern Mato Grosso, Brazil. Note that the scale for trees $5 \leq d < 10$ cm is an order of magnitude smaller than the scale for trees ≥ 10 cm diameter. Forest biomass has been static or fallen, while tree biomass in savannas and gallery forests has increased. Regression lines were fit to plots with a minimum of three or two inventories. ▲, cerrado; ◇, cerradão; **x**, gallery forest-1; +, gallery forest-2; ж, gallery forest-3; ■, monodominant forest; ○, semi-deciduous forest.

Table 5. Mean rates of mortality and recruitment of tree stems across tropical forest and the Brazilian cerrado. Values shown reflect the minimum diameter adopted in these studies.

Area	Author	Mortality (% year^{-1})	Recruitment (% year^{-1})
Pan-Amazonian – 96 plots	Phillips et al. (2004)	1.6	1.7
Pan-Amazonian – 12 plots	Phillips et al. (1994)	1.9	1.8
Amazon Basin – 50 plots	Lewis et al. (2004a)	1.5–1.7	1.6–2.0
Central Amazon forest	Laurance et al. (1998	1.27	–
Amazon terra firme forest	Higuchi et al. (2004)	0.4–1.0	0.18–1.58
Amazon terra firme forest	Silva et al. (1995)	2.5	2.0
Amazon terra firme forests	Korning and Balslev (1994)	0.5–2.0	–
Tropical forests	Swaine et al. (1987)	1.0–2.0	1.0–2.0
Costa Rica forests	Lieberman et al. (1985)	1.8–2.2	–
Gallery forest, central Brazil	Pinto and Hay (2005)	2.2	3.2
Gallery forest, central Brazil	Appolinário et al. (2005)	3.7	2.0
Gallery forest, central Brazil	Lopes and Schiavini (2007)	2.85	1.98
Gallery forest, central Brazil	Oliveira and Felfili (2008)	2.87	2.08
Cerrado sensu stricto	Henriques and Hay (2002)	1.3	1.6
Cerrado sensu stricto	Aquino et al. (2007)	2.7	3.2
Cerrado sensu stricto	Roitman et al. (2008)	1.9	3.7

and episodic intense droughts are important driving forces shaping vegetation dynamics in this region, and (2) that the rapid population dynamics of trees in the ZOT is also a consequence of the long history of advance (e.g. Ratter et al. 1973; Ratter 1992; Marimon et al. 2006) and retreat of the forest into and out of the cerrado region (Ab'Saber 1982; Pessenda et al. 1998; Behling 2002), with this process driving near-constant successional changes in both forest and savanna.

Across eastern and western Amazonia tree turnover rates have tended to increase through time (Phillips et al. 2004). Conceivably this could lead to a change in the functional composition of forest trees, favouring species with lower wood density (Phillips and Gentry 1994; Baker et al.

2009), and to significant changes in ecosystem properties (Suding et al. 2008). However, in the present study, despite the high turnover rates, we could not detect differences between mean plot-level initial and final wood specific gravity values other than a downward trend for small trees. Furthermore, the fact that mean plot-level wood specific density did not differ between the inventories before and after the 2005 drought also indicates that dry periods – at least in the short term – do not select for denser-wooded trees here, in apparent contrast to observations of a weak effect for Amazonian central and western areas (Phillips et al. 2010).

The mortality rates recorded in the forests of this study were similar to those encountered in the fastest-growing and most dynamic forests of the Amazon Basin (Phillips et al. 2004). However, those forests usually occur on relatively young soils which, although generally fertile, are also often of a poor physical structure which can lead to the promotion of high stand-level turnover rates (Quesada et al. 2012). This is not the case for the soils analysed in our study (Table 1; Marimon et al. 2001, 2010; Marimon 2005; Marimon-Junior and Haridasan 2005). Therefore, the drivers of high turnover in our plots are likely to be substantially different from those in western Amazonia; in particular, the mechanisms controlling forest dynamics in the transition zone between Cerrado and Amazonian forest appear to be unrelated to edaphic conditions. Since the 1950s, forest turnover has increased in tropical forests worldwide, with one possibility being that tropical climate change had contributed to the trend (Phillips and Gentry 1994). These authors also speculated that as the acceleration in turnover coincided with accelerating build-up of atmospheric CO_2 concentrations, it might be that turnover increases have been driven by increased growth and recruitment. Lloyd and Farquhar (2008) also argued that increases in forest dynamics across Amazonia over recent decades were consistent with a CO_2-induced stimulation of tree growth. Conceivably, such changes could be occurring more intensely in the water-limited zone, with the more variable climate also driving stronger episodic pulses of recruitment and mortality. Regardless of the drivers of the high turnover we report, there is little evidence for equilibrium in the recent stand dynamics of the ZOT vegetation.

Studies evaluating the dynamics of Amazonian forests have shown that smaller woody plants typically have faster mortality and recruitment than large ones (Bierregaard et al. 1992; Silva et al. 1995), but small-tree dynamics also vary greatly within and between species and environmental conditions, especially in relation to canopy height (Welden et al. 1991; Kobe 1996). One reason for smaller plants to have faster dynamics, and a potentially greater proportional response to environmental change, may be that understorey plants are often close to carbon deficit due to shading (Phillips et al. 2008). In all our plots turnover was faster for small trees ($5 \leq d < 10$ cm) than larger ones, confirming the high dynamics of this class. With their faster turnover and potentially greater environmental sensitivity, these small trees may be particularly useful leading indicators of change in the wider forest.

Comparisons among the transition zone plots

This work provides results that are consistent with the hypotheses that the diversity and above-ground biomass of the vegetation types of the transition zone have undergone changes due to recent drought events, and that dynamics differ between savanna and forest plots of the transition zone. In our plots that were sampled at least three times, mortality and recruitment varied widely between years, being greater in cerrado and cerradão than in the forest. Cerradão of the dystrophic type can be considered a 'tall closed woodland' (Torello-Raventos et al. 2013) and typical of the ecotone between Amazonian forest and cerrado, and at least in some cases being in a successional stage according to the observations of Ratter et al. (1973, 1977) and Ratter (1992), this potentially explaining the rapid dynamics of this vegetation. The higher number of dead individuals of forest species compared with typical cerrado species recorded in the cerradão after the 2005 drought might conceivably indicate a climate-driven short-term response in composition. However, this ecotonal vegetation also showed higher recruitment of forest species, confirming the faster dynamics and resilience of this vegetation formation type, and supporting the notion that seasonal ecosystems in Amazonia may be resilient to seasonal drought (Malhi et al. 2009).

One possible explanation for the higher mortality than recruitment after 2005 in the monodominant forest – which lacks cerrado species – is that forest trees are more drought sensitive, while cerrado species are more resilient due to deeper roots (Oliveira et al. 2005) or other physiological adaptations (Lloyd et al. 2009). One recent study suggested that across tropical forests the impacts of drought may tend to lag the moisture deficit, as mortality rates on average remained elevated up to 2 years after the meteorological event ended (Phillips et al. 2010). Temporal patterns of above-ground biomass and biomass net gain in our study are consistent with this finding, as they remained positive throughout for cerrado, cerradão and gallery forests in all diameter classes, but in the monodominant and seasonal forests the biomass net gain turned to net loss after the year 2005. Forests away from local sources of water (rivers, and topographic depressions) may be expected to be the most drought-susceptible vegetation types.

In our plots species diversity decreased over time, with lower values recorded after the 2005 drought, especially in forested areas. Within southern Amazonian forests, there is a well-defined relationship between tree species distribution, and forest hydrology and soil drainage (Feldpausch et al. 2006; Jirka et al. 2007), suggesting that some species may be at greater risk to widespread drying. Interestingly, the reduction in species diversity in our study was consistent across all forest plots, reinforcing the apparent greater susceptibility of forests to drought in relation to the cerrado. The trend to decreasing species diversity could also be partly a result of fragmentation and isolation from neighbouring areas. Our plots are located in protected areas; however, across the landscape as a whole the native transitional vegetation has been reduced due to agricultural development since the early 1970s. Thus, the historical context of human occupation in the region may represent a long-term significant impact on species diversity (Santos et al. 2010).

Conclusion

The natural vegetation in the ZOT between forest and savanna represents a unique and complex set of vegetation types, and it is in rapid decline due to land-use change. Our study shows that tree population dynamics in the ZOT are more rapid than those in core Amazonian forests. While mortality here may also have been boosted by the 2005 drought, comparison with other Amazon and tropical forests that also experienced recent drought indicates that the ZOT is intrinsically hyperdynamic. The leading hypotheses to explain this phenomenon are the extreme seasonality of the region, and the notion that growth and mortality of trees at the climate boundary between forest and savanna are especially sensitive to shifting precipitation patterns. While we anticipate that high dynamics are a general property of ZOT vegetation, until wider sampling in space is achieved it remains conceivable however that our results are a result of other, special conditions in our north-eastern Mato Grosso sampling domain.

In our plots there was evidence for directional change (e.g. decline in diversity, decline in some forest taxa), particularly in smaller trees. To evaluate the dynamics of these transitional systems it is particularly important to assess smaller individuals, since they may respond more quickly to environmental changes and be leading indicators of ecosystem shifts. Nevertheless, rapid ecological change does not necessarily imply vulnerability. For example, in core western Amazon forests a recent study (Butt et al. 2014) has shown a possible shift in forest composition to tree taxa affiliated to drier habitats, suggesting potential for increased forest persistence under projected drier conditions in the future. The vegetation in the ZOT is, however, already on the edge in climate terms, and thus maybe more sensitive than core Amazonian forests to changing climate. The ZOT therefore merits special attention, not only because of the direct anthropogenic threat but also in light of recent regional droughts and projections for further significant drying and warming across the region.

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Notes on contributors

Beatriz Schwantes Marimon is a professor. Her current work focuses on ecology and management of forests in the transition zone between cerrado and Amazon forest biomes to understand changes in tropical plants communities as a result of climate change.

Ben Hur Marimon-Junior is a professor. He has experience in forest ecology, studying biogeochemical cycles, carbon stocks, pyrogenic carbon in mineral nutrition of plants, biodiversity and ecosystem functions.

Ted R. Feldpausch is a lecturer of tropical ecology. His research focuses on the ecology and effects of global change on tropical forests and savannas.

Claudinei Oliveira-Santos is a biologist and conducted his M.Sc. research on the dynamics of the monodominant *Brosimum rubescens* forest.

Henrique A. Mews is a biologist who conducted his M.Sc. research on the dynamics of the semi-deciduous seasonal forest of this study.

Gabriela Lopez-Gonzalez is an ecologist who specialises in eco-informatics. She has led the development of ForestPlots.net, a new data management application for the tropics.

Jon Lloyd is Professor of Earth System Science at the University of Leeds (UK) and Research Professorial Fellow at James Cook University (Cairns, Australia).

Daniel D. Franczak is a biologist and conducted his M.Sc. research on the dynamics of the cerrado and cerradão of this study.

Edmar A. Oliveira is a biologist and conducted his M.Sc. research on the dynamics of the lianas in all plots of this study.

Leandro Maracahipes is a biologist. His main interest is forest ecology and dynamics of flooding forests.

Aline Miguel is a biologist and conducted her M.Sc. research on the dynamics of the gallery forests of this study.

Eddie Lenza is a professor. He works with floristic, structure and phenology of different vegetation communities of the central plateau and southern Amazon boundaries in Central Brazil.

Oliver L. Phillips is professor of tropical ecology at the University of Leeds. He leads the RAINFOR network of scientists in Amazonian forests.

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