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Tree diversity and above-ground biomass in the South America Cerrado biome and their conservation implications

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Abstract Less than half of the original two million square kilometers of the Cerrado vegetation remains standing, and there are still many uncertainties as to how to conserve and prioritize remaining areas effectively. A key limitation is the continuing lack of geographically-extensive evaluation of ecosystem-level properties across the biome. Here we sought to address this gap by comparing the woody vegetation of the typical cerrado of the Cerrado-Amazonia Transition with that of the core area of the Cerrado in terms of both tree diversity and vegetation biomass. We used 21 one-hectare plots in the transition and 18 in the core to compare key structural parameters (tree height, basal area, and above-ground biomass), and diversity metrics between the regions. We also evaluated the effects of temperature and precipitation on biomass, as well as explored the species diversity *vs.* biomass relationship. We found, for the first time, both that the typical cerrado at the transition holds substantially more biomass than at the core, and that higher temperature and greater precipitation can explain this difference. By contrast, plot-level alpha diversity was almost identical in the two regions. Finally, contrary to some theoretical expectations, we found no positive relationship between species diversity and biomass for the Cerrado woody vegetation. This has implications for the development of effective conservation measures, given that areas with high biomass and importance for the compensation of greenhouse gas emissions are often not those with the greatest diversity.

Key words: Diversity-biomass; Richness; Carbon stocks; Core area; Transition; Neotropics

Introduction

As many as two hundred studies recognize the South American Cerrado savannas as a global center of diversity, largely on the basis of its 12,000-plant species which include many endemics (e.g. Mendonça et al. 2008; Brazilian Flora 2016). A likely driver of this high species richness is the heterogeneity of landscapes found within this region (Felfili et al. 2005a; Mendonça et al. 2008). While the importance of this biodiversity has been recognized for at least two decades (e.g., Ratter et al. 1997; Silva and Bates 2002; Klink and Machado 2005; Kier et al. 2005; Silva et al. 2006; BFG 2015), the importance of the Cerrado for ecosystem services such as carbon storage and hence climate mitigation is less appreciated (Grace et al. 2006), and the number and size of conservation units are still insufficient to avoid biodiversity losses (Françoso et al. 2015). In addition to establishing a more complete network of conservation areas covering the whole region, Bridgewater et al. (2004) also recommended a complementary regional focus to guarantee the adequate protection of geographical variations in species. Less than half the two million square kilometers originally occupied by the Cerrado are now intact (Sano et al. 2010; Lahsen et al. 2016); thus, understanding the distribution of remaining species diversity and carbon stocks within this region represents an urgent challenge for its conservation.

Most biodiversity and ecosystem ecology work in the Cerrado has focused on the core region, often relatively close to major population and academic centers such as Brasília (Federal District). The greatest research deficits lie well to the north and west of here (Miranda et al. 2014). In particular, while an extensive and complex transition exists between the Cerrado and the Amazon Forest (Ratter et al. 1973; Marimon et al. 2006, 2014), no study has yet compared the transitional vegetation with that of the core region using the standardized, fixed-area and quantitative inventory protocols required for a robust analysis of most ecosystem properties. Indeed, there has been little large-scale evaluation of structural ecosystem-level properties at all across the Cerrado. In particular, for the key parameters of tree size, basal area and biomass—and hence above-ground carbon storage—the only studies we are aware of that included transition zone sites were based on only one or two sites. Yet, taking the published evidence together (Felfili et al. 1992; Castro and Kauffman 1998; Marimon-Junior and Haridasan 2005; Kunz et al. 2009; Marimon et al. 2014), it appears that the trees of the savanna formations in the Cerrado-Amazonia Transition might have greater basal area or biomass than similar formations in the core region of the Cerrado. Understanding how above-ground biomass varies among different areas of Cerrado and how this parameter responds to environmental and geographic factors will help reduce uncertainties in estimating carbon stocks and may contribute to greater reliability in conservation policies formulation. Forest biomass, for example, may be partly driven by climatic factors, such as precipitation and temperature (Silvertown et al. 1994; Larjavaara and Muller-Landau 2011), and topography, through its effects on water table levels (Fonseca and Silva Júnior 2004). Yet, this correlation may sometimes be weak and dependent on vegetation type (Stegen et al. 2011), while for the Cerrado core region the above-ground biomass of typical cerrado species may even be negatively correlated with precipitation (Miranda et al. 2014).

More generally, there are reasons to expect transition and core regions to differ ecologically beyond considerations of mean climate conditions. For example, the transition can have suboptimal environmental conditions relative to the core of the adjacent ecosystems, potentially reducing species richness (van der Maarel 1990). For similar reasons, the center-periphery hypothesis predicts that, due to harsher environmental conditions, peripheral populations should be smaller, less abundant and more fragmented, resulting in reduced demographic performance and genetic variation (Pironon et al. 2016). This would lead to the communities at the core being more stable and structurally distinct, while the more unstable and fluctuating environments at the transition select for species and genotypes able to tolerate more variable conditions (Hardie and Hutchings 2010). Alternatively, Kark and van Rensburg (2006) suggested that precisely because populations in transitional regions are likely to include a wide range of taxa adapted to environmental instability, this would in fact result in them having greater species richness, and the potential to become centers for speciation.

These intriguing but conflicting viewpoints emphasize the potential existence of different patterns of diversity within the same biome, which need to be considered to develop effective conservation measures. In the specific case of the Cerrado, the picture remains unclear with respect to large-scale diversity patterns. Some studies have suggested that the core region of the Cerrado has relatively high species richness, due to its proximity to the center of species dispersal, whereas more peripheral regions are likely to be poorer in species despite the influence of adjacent biomes (Eiten 1972; Fernandes and Bezerra 1990; Rizzini 1997; Castro et al. 1999). However, others have taken the view that the Cerrado-Amazonia Transition should have greater species richness than the core region, driven by their proximity to Amazonia (Ratter et al. 1973, 2003; Felfili et al. 2002; Marimon et al. 2006, 2014). In parallel to the gap in Cerrado center–periphery studies noted above, what has been lacking so far is an evaluation of basic patterns of tree diversity using adequately replicated and fully standardized quantitative inventories across the biome.

While a better understanding of the distribution of plant diversity and biomass, and their environmental drivers across the Cerrado is necessary for adequate conservation planning, evaluating the diversity-biomass relationship itself is also important, both for the mitigation of climate change and for biodiversity conservation. A positive diversity-biomass relationship would indicate useful synergies between the goals of biodiversity protection and climate protection, while a negative one implies that difficult trade-offs become necessary

(Gardner et al. 2012). Several experimental studies elsewhere show that enhanced plant diversity can promote higher productivity and biomass, via mechanisms that include niche partitioning and species interactions that allow diverse communities to exploit resources more efficiently (e.g. Cardinale et al. 2012; Ruiz-Benito et al. 2014). However, within savanna ecosystems the covariation between ecosystem diversity and carbon properties is largely unstudied. Therefore, whether such mechanisms and relationships matter in the Cerrado, and any possible implications for conservation strategies, remains unknown.

Here, to help address these uncertainties in the geographical pattern, environmental drivers, and potential associations between Cerrado diversity and biomass, we conduct a large-scale analysis of these properties using distributed and standardized fixed-area quantitative ecological sampling plots. First, we investigate whether or not the structure and diversity of arboreal vegetation of the typical cerrado physiognomy (sensu Ribeiro and Walter 2008, a mixed arboreal-shrub vegetation with cover up to 50%) varies significantly between the Cerrado-Amazonia Transition and the core region. We then set out to evaluate the effects of potential climate drivers on typical cerrado structure, and the potential interaction between biomass and diversity. Our working hypotheses are (i) that the typical cerrado vegetation of the Cerrado-Amazonia Transition has greater basal area, biomass, and species diversity than at the core region, (ii) that biomass is influenced by climatic factors, such as precipitation and temperature, and (iii) that biomass is positively associated with diversity, independently of the potential influences of climate on biomass.

Material and methods

Study areas

We used data from standardized floristic and phytosociological surveys conducted across the central portion of the Cerrado (core area – CA) and the Cerrado-Amazonia Transition (TR), i.e., the ecotone between the two largest biomes in South America (Fig. 1, Table S1). We used a zone of 150 km from the line that delimits the Cerrado and Amazonia to define the TR (IBGE 2004; Ivanauskas et al. 2008). We analyzed data from 39 permanent one-hectare plots installed in typical cerrado (cerrado stricto sensu) vegetation, 21 located in the TR and 18 in the CA (Fig. 1). We established plots in conservation units or in legal reserves of private properties in the Brazilian Federal District (CA), the Brazilian states of Mato Grosso (TR), Tocantins (CA), Bahia (CA), Goiás and Minas Gerais (CA), and in the Noel Kempff National Park in Bolivia (TR) (Fig. 1; Table S1). At each site, we selected the largest and best-preserved remnants of natural vegetation, within which we established plots randomly. In these areas, mean annual precipitation varied almost two-fold from 1043 mm to 1951 mm, and mean temperatures also ranged widely, from 19.3 ºC to 26.9 ºC (WorldClim 1.4; Hijmans et al. 2005).

Data collection

We identified and measured the diameter and total height of all woody plants with a diameter of at least 10 cm at a height of 30 cm from the ground, following standard protocols used in the Amazon forest (Phillips et al. 2010) and Cerrado (Felfili et al. 2005b). We identified species through comparison with voucher material available in herbaria, and consultation with specialists. The nomenclature was based on APG III (2009) and we confirmed the species names and synonymies using the Brazilian Flora (2016), with the flora package in the R environment (R Core Team 2018). We deposited botanical specimens in the permanent collections of Herbário NX (UNEMAT – Nova Xavantina campus, MT), Herbário UB (University of Brasília), Herbário IBGE (Brazilian Institute of Geography and Statistics), Herbário CEN (Embrapa Recursos Genéticos e Biotecnologia, Brasília, DF) and Herbario del Oriente Boliviano (USZ).

For each plot we calculated tree density (individuals/ha), mean tree height (m), mean tree diameter (cm), total basal area ($m^2.ha^{-1}$) and total above-ground biomass ($Mg.ha^{-1}$), which were used as structural parameters of the vegetation. We estimated tree height from tree diameter for 10 of the TR plots using the model:

$$H = a \times \left(1 - e^{-b \times D^{c}}\right),$$

where a, b and c are parameters of model and D is the tree diameter (Feldpausch et al. 2012). To assess the adequacy of this model, we compared height measurements from 3657 trees collected in the field with their estimated heights. The correlation between the field data and estimated heights was significant ($r = 0.59$, $p < 0.01$). We calculated above-ground biomass (hereafter biomass) from tree diameter using the Schumacher-Hall model:

$$Y = \beta_0 D^{\beta_1} H^{\beta_2} \varepsilon,$$

where β_0, β_1, β_2 are model parameters, D is tree diameter (at 30 cm from the ground), H is tree height and ε is the random error term (Schumacher and Hall 1933), with parameter values developed specifically for species of the typical cerrado physiognomy ($\beta_0 = 0.03047$, $\beta_1 = 2.27159$, $\beta_2 = 0.89748$; Rezende et al. 2006).

For each plot, we calculated species richness, Shannon information index (H') (Shannon 1948), Fisher's log series α (Fisher et al. 1943) and Pielou's evenness (J') (Pielou 1969), which were used as diversity parameters (Magurran 2004). We also calculated, for each plot, the species richness rarefied to the same number of individuals in the smallest sample, i.e., 169 individuals based on the plot with the smallest number of trees (Hurlbert 1971). All diversity parameters were calculated with the package vegan (Oksanen et al. 2017).

Statistical analyses

To evaluate associations within structural and diversity parameters, we used the Pearson correlation coefficient. We assessed differences between CA and TR in structural and diversity parameters of the vegetation using boxplots and t-tests and, when such differences existed, we used Bayesian model averaging to identify the most important predictors of the two regions. In this analysis, structural and diversity parameters were used as explanatory variables and region (CA and TR) as the response variable. Bayesian model averaging, an extension of the usual Bayesian inference methods, models both parameter and model uncertainty using Bayes' theorem to produce parameter and model posteriors and, thus, allows for model selection by full enumeration of the model space when the number of predictors is not large (Hoeting et al. 1999; Fragoso et al. 2018). We conducted Bayesian model averaging with the BMS package (Zeugner and Feldkircher 2015).

To assess differences in the total (regional) pool of species between CA and TR, we built individual-based and sample-based species accumulation curves (Gotelli and Colwell 2001). Further, to account for unseen species in our collection of sampled plots, we used abundance-based and incidence-based non-parametric estimators of species richness (Colwell and Coddington 1994; O'Hara 2005). Abundance-based estimators (Chao1 and ACE) were applied to the total counts of species in each region (CA vs. TR), while incidence-based estimators (Chao, Jacknife1, Jacknife2 and Bootstrap) were applied to the species frequencies in the plots for each region. Species accumulation curves and non-parametric estimators were calculated with the vegan package (Oksanen et al. 2017).

To investigate the relationships between biomass, diversity and climate, we used a modification of Bayesian model averaging to address model uncertainty in the presence of spatial autocorrelation, due to the inherent spatial dependencies among the observations (Legendre 1993). In this analysis, the spatial dependencies among observations are removed through a semiparametric spatial filtering approach based on selected eigenvectors extracted from the spatial weight matrix (Tiefelsdorf and Griffith 2007). Considering the important effects that uncertainty in the type of spatial weight matrix (neighborhood relationships) can have on model parameter estimates, the spatial Bayesian model averaging method addresses both the uncertainty over model specification and the uncertainty regarding the choice of neighborhood relationships in the spatial regression model (Cuaresma and Feldkircher 2013). We implemented spatial Bayesian model averaging using package spatBMS (Feldkircher 2010), using 10^6 iterations, 10^5 burn-in draws, the reversible-jump model-sampler algorithm, and default settings for the other parameters. We used eight different spatial weight matrices—k nearest-neighbors (k = 1, 2, 4 and 6), Delaunay's triangulation, Gabriel graph, relative neighbor graph, and sphere of influence graph—built with package spdep (Bivand et al. 2013, Bivand and Piras 2015). To assess the adequacy of the spatial filtering, we compared P-values of the Moran's I (Moran 1950ab) test for spatial autocorrelation obtained from the 100 best models versus 100 ordinary least-squares models using the same predictors.

In the spatial Bayesian model averaging analysis, we used biomass as the response, and diversity and climate parameters as predictors. Prior to analysis, we selected diversity parameters based on a variance inflation factor (VIF) maximum threshold score of 4 (Quinn and Keough 2002), using package usdm (Naimi et al. 2014). This resulted in only species richness and Pielou's evenness being retained for analysis (results not shown). Further, we incorporated tree density and the distance from each plot to the line separating Amazonia from the Cerrado (IBGE 2004) as additional predictors, to control for any effects these parameters might have on biomass. We also ran a bivariate regression for both regions combined (CA and TR) to evaluate the relationship between biomass and climate parameters. The climate parameters consisted of temperature and precipitation, obtained from WorldClim

1.4, with a resolution of 30 s (Hijmans et al. 2005) and edited in the raster package (R Core Team 2018).

One TR plot (TR16 – Table S1), located within a protected area, had exceptionally high biomass (outlier) possibly due to the long-term protection from disturbances such as fire. The vegetation in this area is becoming denser and shifting from a savanna-like into a woodland physiognomy (Morandi et al. 2016), even though the habitat is still clearly consistent with that of the typical cerrado (Marimon-Junior and Haridasan 2005; Marimon et al. 2014). We retained this plot because it demonstrates the importance and effect of the establishment of protected areas but, to avoid potentially undesirable effects, we removed it from all regression analyses involving biomass.

Results

Vegetation structure

Summaries of vegetation structure parameters from each plot are in Table S2. Overall, the strongest correlations were between tree basal area vs. biomass, followed by density vs. biomass (Fig. S1). Tree height and total biomass were significantly higher in TR plots (Table 1, Fig. S2). There were no differences between CA and TR plots in tree density, diameter and basal area (Table 1, Fig. S2). Bayesian model averaging indicated that, by and large, tree height was the best predictor of CA and TR plots: it had the largest standardized coefficient, with a 95% credibility interval that did not include zero, and the largest posterior inclusion probability (Table 2). Further, in all models containing height its coefficient was positive, indicating larger values in the TR, and the top model, including just height, concentrated 26% of the posterior model probabilities (Fig. 2). The remaining predictors had much lower standardized coefficients and posterior inclusion probabilities. The second-best model, including height and diameter, concentrated an additional 21% of the posterior model probabilities, with the contribution of remaining models being much smaller (Fig. 2). In all but one model containing diameter, its coefficient was negative. Biomass, which had the second largest standardized coefficient, behaved similarly with a negative coefficient in all but one model (Table 2, Fig. 2). This indicates that, after accounting for differences in height, tree diameter and biomass are smaller in TR plots.

Vegetation diversity

We recorded 233 species in all plots combined, with 177 in the CA plots and 172 in the TR plots. Summaries of vegetation diversity parameters from each plot are in Table S2. The individual-based and sample-based species accumulation curves indicated that the CA has a larger species pool than the TR (Fig. 3). Likewise, all abundance-based and incidence-based non-parametric estimators indicated larger species richness in the CA (Table S3). Except for Pielou's evenness (*J'*), the correlations between all diversity parameters were high (Fig. S3). There were no differences between CA and TR plots in tree diversity parameters (Table 1, Fig. S4). Overall, these results indicate higher regional diversity in the CA, but no differences in local (plot) diversity between CA and TR.

Relationships between biomass, diversity and climate

The spatial Bayesian model averaging analysis indicated that the spatial weight matrix based on the Gabriel graph had the highest posterior model probability (48.3%). By and large, tree density was the single best predictor of plot biomass: it had the largest standardized coefficient, with a 95% credibility interval that did not include zero, and the largest posterior inclusion probability (Table 3). In all models containing density, its coefficient was positive and the top model, including just density, concentrated 21% of the posterior model probabilities (Fig. 4). The remaining predictors had much lower standardized coefficients and posterior inclusion probabilities. The second-best model, including density, richness, and evenness, concentrated an additional 17% of the posterior model probabilities, with the contribution of remaining models being much smaller (Fig. 4A). In all models containing species richness, the second-best predictor, its coefficient was negative (Table 3, Fig. 4A). The importance of the remaining predictors was much smaller. The incorporation of eigenvectors in the analysis successfully removed the spatial autocorrelation from the regression residuals (Fig. 4B). Summing up, the results indicate that after accounting for differences in density, species richness and biomass tend to be negatively correlated in the study plots. The results of bivariate regression indicated that, when evaluated separately, temperature is a good positive predictor of the biomass ($r^2 = 0.21$, $p < 0.01$; Fig. S5).

Discussion

We found that plots in typical cerrado vegetation of the Cerrado-Amazonia Transition (TR) had much greater biomass (58% more) than those of the core area (CA) of the Cerrado. By contrast, species richness and diversity are similar between the TR and CA. We also find that for typical cerrado trees there is no systematic relationship between species diversity and biomass. Thus, our first hypothesis, which suggested that the cerrados of the TR have greater tree size and ecosystem biomass and greater species diversity than the CA cerrados, was partly corroborated, given that only the structural variables differed as predicted. Our second hypothesis was supported, given that the climatic variables predict biomass. The species diversity-biomass relationship was weak and, if anything, negative, meaning that the third hypothesis was rejected. These findings are discussed in more detail below, together with an assessment of the implications for conservation.

Structure

The biomass and tree height in typical cerrado plots in the transition (TR) were all significantly greater than those recorded in the core area (CA) and in previous studies spread in the Cerrado biome (Castro and Kauffman 1998; Vale and Felfili 2005; Rezende et al. 2006; Paiva et al. 2011; Miranda et al. 2014). Several small-scale (1 hectare) local studies in single sites within the TR had already indicated that the cerrados of this zone may have greater basal area than those of the more central regions of the Cerrado biome (Felfili et al. 2002; Marimon-Junior and Haridasan 2005; Kunz et al. 2009; Marimon et al. 2014). However, this is the first time that a biome-scale study, which compares different regions directly with multiple, replicated plots, has detected such a pattern. The factors that affect the variation in biomass are discussed below.

From a conservation perspective, the clear structural differences between TR and CA cerrados are a new find, which has important implications. While the vegetation is defined as typical cerrado (Ribeiro and Walter 2008) in both cases, the unique structural characteristics found in each region should be considered for the development of habitat management practices. In other words, a conservation unit that protects typical cerrado in the core area will likely not be representative of the same physiognomy in the Cerrado-Amazonia Transition. This reinforces the position of Primack and Rodrigues (2001), who argued that conservation units should encompass physiognomies that are representative of environments on a wide geographic scale. In the specific case of the Cerrado-Amazonia Transition, the region also coincides with that of the ‘arc of deforestation’ (Fearnside 2005; Marimon et al. 2014), where the landscape is dominated by agricultural frontiers, reinforcing the urgent need for the establishment of conservation units in this big region. In this context, the maintenance of private reserves is also an important strategy to conserve portions of cerrado along its wide geographic distribution.

The maps available on the site of the Mato Grosso State Environment Secretariat (SEMA: http://www.sema.mt.gov.br/) show that the unique state conservation unit of the TR that include Cerrado vegetation are all part of Mortes-Araguaia river basin, which is subject to seasonal flooding (Marimon et al. 2015). In the Araguaia State Park for example, the predominant physiognomy is the murundus grassland, in which patches of typical cerrado are found only on the higher terrain, which is free of seasonal flooding. Throughout the state there is no fully protected area within a 200 km distance of the established limit between the Cerrado and Amazon biomes (IBGE 2016) in which the predominant vegetation is typical cerrado not subject to seasonal flooding (SEMA 2016). Given that TR cerrados are structurally different from those found in the CA, it is important to establish typical cerrado conservation units within the non-flooded areas of the TR.

Species diversity

While several previous studies have indicated that the typical cerrados of the TR have greater species diversity per unit area (alpha diversity) than those of the core area (Felfili et al. 2002; Ratter et al. 2003; Bridgewater et al. 2004), this was clearly not the case in our study in which well replicated, quantitative ecological sampling was conducted across both TR and CA. We conclude that tree species diversity does not vary notably between the central and outer regions of the Cerrado, even in the TR, where the contribution of the Amazonian flora increases (Eiten 1972; Ratter et al. 1973, 2003; Castro et al. 1999; Felfili et al. 2002; Bridgewater et al. 2004; Marimon-Junior and Haridasan 2005).

In a recent study it was stated that there is a greater overlap of species in the central portion of the Cerrado, which is reflected in higher species richness in the core area than in the border (Françoso et al. 2016). However, that study may have been influenced by sampling gaps, as the TR was under-represented. In addition, the above study was based on binary presence-absence data, which may not be sufficiently robust given that population size is an important aspect of species diversity, and a fundamental parameter for the development of conservation measures (Felfili et al. 2005a; Mews et al. 2014).

While our results indicate that alpha diversity did not vary between the CA and TR, there is a suggestion that beta diversity was higher in the CA, possibly due to the more stable climate in this area (Werneck et al. 2012) which would be reflected in increased niche specialization (Moldenke 1975). Even so, neither our study nor previous work using different methods (Eiten 1972; Fernandes and Bezerra 1990; Rizzini 1997; Castro et al. 1999) strongly suggests that the TR is relatively species-poor or less diverse than the central area of the Cerrado. Marimon et al. (2014) observed that the vegetation of the transition zone, in addition to being hyperdynamic, is in disequilibrium, and Werneck et al. (2012) suggested that the lower diversity in the transition zone may reflect this instability. However, the instability normally observed in ecotones (e.g. van der Maarel 1990; Werneck et al. 2012; Pironon et al. 2016) does not appear to have affected tree species richness and diversity in the TR. For all these reasons, it is essential to consider both the TR and CA when designing conservation units, to guarantee the preservation of intrinsic vegetation properties of each region. As agricultural frontiers are still rapidly advancing within the TR (Marimon et al. 2014), the complete absence of conservation units in typical cerrados is a significant concern.

Determinants of biomass variation

In our study, tree density was the most important predictor of biomass variation. In other studies, precipitation and temperature were determinants of biomass in South African savannas (Scholes et al. 2002). In contrast with our results, however, Miranda et al. (2014) found a negative correlation between biomass and precipitation levels, albeit in an analysis in which the TR was under-represented. Moreover, none studies referred here has used density as predictor of biomass.

Miranda et al. (2014) however suggest that biomass was greater in areas with reduced seasonality, which may also be relevant to the present study, given that TR cerrados are located in a region where the mean annual precipitation (1659 mm) is approximately 200 mm (14% – Table S1) higher than that in the CA (1446 mm), and seasonality is less pronounced (Keller-Filho et al. 2005; Alvares et al. 2013). This reinforces the effect of its proximity to the Amazon Forest (Felfili et al. 2002; Marimon-Junior and Haridasan 2005; Torello-Raventos et al. 2013), which may impact tree growth. Additionally, if we consider the results of the bivariate regression models, temperature and precipitation have a direct effect on biomass, with the TR contributing most to this tendency.

Diversity-biomass relationships and implications for conservation

We observed no positive diversity vs. biomass relationship across all plots. It is notable that the lack of correlation between biomass and diversity metrics remains despite the fact that only biomass is associated with temperature and to precipitation, and this clearly argues against their being a positive effect of tree species diversity on carbon storage within the Cerrado. It is interesting to note that these findings parallel a recent report from across the tropical moist forest biome (i.e., Amazonia, Africa, Southeast Asia), for which there is also no detectable relationship between community diversity and carbon storage except at the very smallest scales (0.04 ha) (Sullivan et al. 2017). Torello-Raventos et al. (2013), analyzing the structural and floristic data from three continents, observed that there is not necessarily a congruence between floristic and structural groupings for vegetation types in the forest-savanna transition zone. Therefore, to the extent that positive diversity-function mechanisms and relationships might exist, within the two largest tropical biomes on Earth they do no translate into a significant effect on carbon storage.

As a practical consequence, it cannot be assumed that efforts made to conserve the diversity of typical cerrado will have clear co-benefits (cf. Day et al. 2013) for climate protection, since the areas with higher diversity do not necessarily coincide with those with highest biomass. According to Gardner et al. (2012), when this relationship is inverse or nonexistent, as in the case of the Cerrado, then decisions on the conservation of carbon stocks or species diversity will imply difficult trade-offs for institutions responsible for the conservation of biodiversity and the reduction of greenhouse gases. For the Cerrado the implications seem clear—it is necessary to carefully design a biome-wide conservation network that can protect both high levels of species diversity and also store large stocks of carbon, and not assume that protection for one purpose automatically guarantees the other.

As we have already argued, there is clearly now a deeply concerning gap in the protection of TR cerrado. Furthermore, the similar tree species richness and diversity observed in the typical cerrado of the CA and TR, together with the greater tree heights and biomass in the TR, are consistent with the notion that populations of transition zones may be better adapted to environmental instability and impacts, and would be more capable of persisting through periods of climate change (Kark and van Rensburg 2006), were they to survive direct removal as part of Brazil's agricultural revolution. While the high environmental heterogeneity of the Cerrado (Felfili et al. 2005a; Mendonça et al. 2008; BFG 2015) cannot be overlooked in the planning of the network of conservation units (Bridgewater et al. 2004), it is clearly vital to increase protection of the TR, threatened as it is by intense anthropogenic pressures that may provoke the disappearance of this unique and valuable environment.

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Figure Captions

Fig. 1 Geographic location of 39 one-hectare plots of typical cerrado in the core area of the Cerrado (brown circles) and at the Cerrado-Amazonia Transition (green circles) in South America. Shading indicates the ranges of Cerrado and Amazonia. Lines represent country boundaries

Fig. 2 Bayesian model averaging of vegetation structure parameters for 39 one-hectare plots of typical cerrado in the core region of the Cerrado and at the Cerrado-Amazonia transition. The Y-axis contains the predictors of core vs. transition plots, while the X-axis is scaled by the posterior model probabilities. Colors indicate predictor inclusion in each of the 32 models assessed (the full set of possible models). Positive coefficients are indicated by blue, negative coefficients by red, and white indicates non-inclusion of the respective predictor

Fig. 3 Individual-based (top) and sample-based (bottom) species accumulation curves for trees from 39 one-hectare plots of typical cerrado in the core region of the Cerrado and at the Cerrado-Amazonia transition. The continuous lines represent the mean and the shaded areas the 95% confidence interval

Fig. 4 Spatial Bayesian model averaging of tree above-ground biomass, diversity and climate parameters for 39 one-hectare plots of typical cerrado in the core region of the Cerrado and at the Cerrado-Amazonia transition. Above-ground biomass represents plot totals. Distance to transition boundary represents linear distance from each plot to the line separating Amazonia from the Cerrado (IBGE 2004). The Y-axis contains the predictors of total tree above-ground biomass in plots, while the X-axis is scaled by the posterior model probabilities. Colors indicate predictor inclusion in each of the 32 models assessed. Positive coefficients are indicated by blue, negative coefficients by red, and white indicates non-inclusion of the respective predictor

Table 1 Summary statistics of vegetation structure and diversity parameters for 39 one-hectare plots of typical cerrado in the core region of the Cerrado and at the Cerrado-Amazonia transition. Values indicate mean ± one standard deviation and t-test statistics. Tree height and diameter represent plot means, whereas basal area and above-ground biomass represent plot totals. n: number of plots sampled

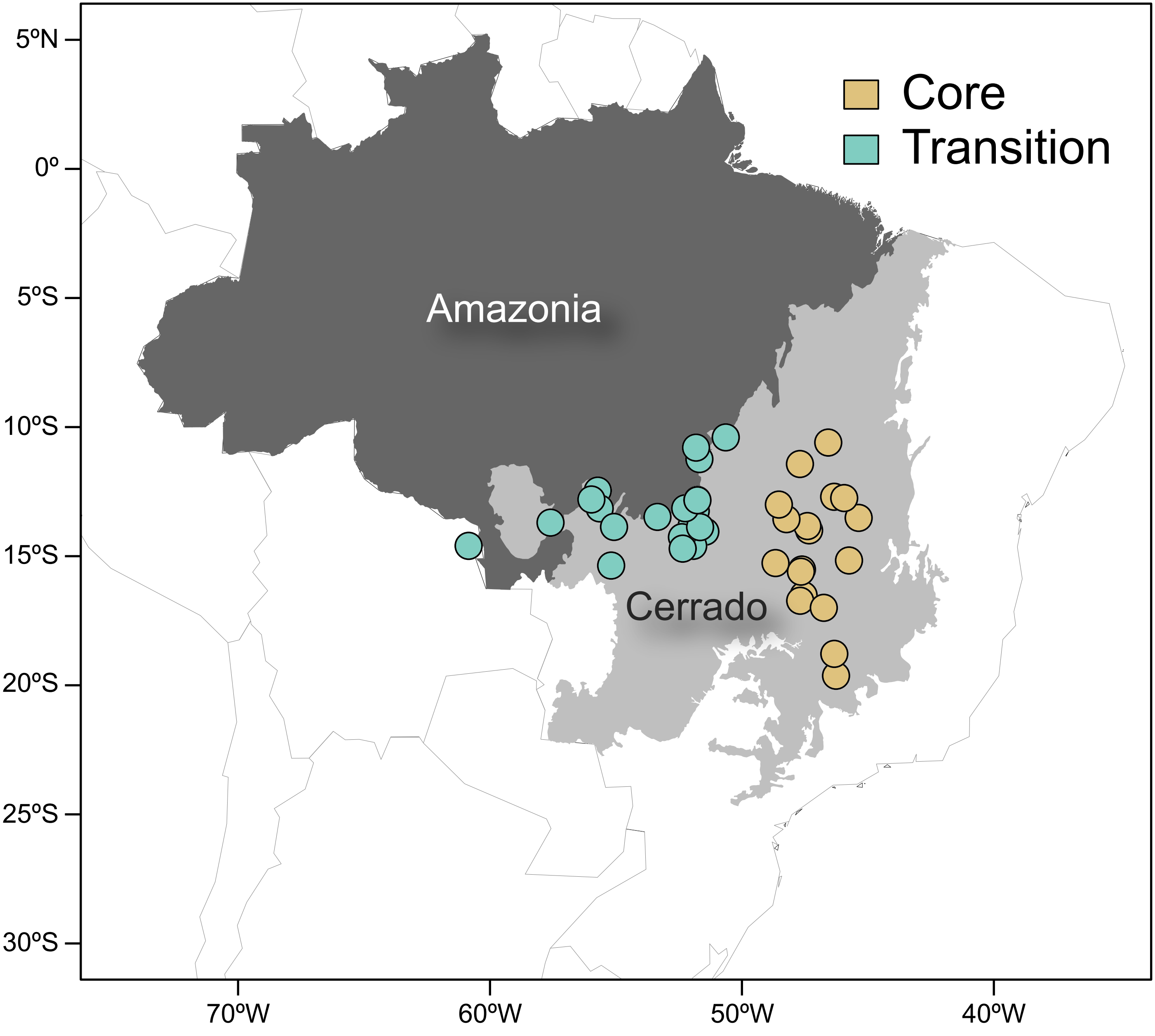
Parameter	Core area (n= 18)	Transition (n= 21)	t	P
Vegetation structure				
Density (individuals.ha^{-1})	304.3 ± 71.7	355.5 ± 152.3	-1.372	0.181
Height (m)	4.5 ± 0.5	5.8 ± 0.5	-8.454	< 0.001
Diameter (cm)	14.4 ± 0.7	14.9 ± 1.6	-1.155	0.258
Basal area (m^{2}.ha^{-1})	5.6 ± 1.7	6.9 ± 3.1	-1.590	0.122
Above-ground biomass (Mg.ha^{-1})	20.4 ± 6.5	32.4 ± 16.5	-3.052	0.005
Vegetation diversity				
Species richness	45.6 ± 11.4	45.6 ± 12.0	-0.004	0.997
Rarefied species richness	37.4 ± 7.3	37.0 ± 8.3	0.162	0.872
Shannon information index (*H'*)	3.0 ± 0.4	3.1 ± 0.4	-0.945	0.351
Fisher's log-series α	15.3 ± 4.5	14.4 ± 4.3	0.641	0.525
Pielou's evenness (*J'*)	0.80 ± 0.07	0.83 ± 0.05	-1.606	0.117

Table 2 Bayesian model averaging of vegetation structure parameters for 39 one-hectare plots of typical cerrado in the core region of the Cerrado and at the Cerrado-Amazonia transition. PIP: posterior inclusion probabilities, i.e., sum of posterior model probabilities for all models wherein a predictor was included; PostMean: standardized coefficients averaged over all models; PostSD: standard deviations of standardized coefficients; CondPosSign: sign certainty, i.e., posterior probability of a positive coefficient expected value conditional on inclusion; 95% PostCI: 95% credibility interval of the posterior probability distribution. Tree height and diameter represent plot means, whereas basal area and above-ground biomass represent plot totals

Parameter	PIP	PostMean	PostSD	CondPosSign	95% PostCI
Height (m)	1.000	0.874	0.161	1.000	0.3691 – 0.7576
Diameter (cm)	0.386	-0.067	0.129	0.067	-0.1642 – 0.0798
Density (individuals.ha^{-1})	0.301	0.094	0.222	1.000	-0.0005 – 0.0038
Above-ground biomass (Mg.ha^{-1})	0.274	-0.142	0.395	0.136	-0.0743 – 0.0088
Basal area (m^{2}.ha^{-1})	0.235	0.035	0.365	0.520	-0.1935 – 0.3599

Table 3 Spatial Bayesian model averaging of tree above-ground biomass versus diversity and climate parameters for 39 one-hectare plots of typical cerrado in the core region of the Cerrado and at the Cerrado-Amazonia transition. PIP: posterior inclusion probabilities, i.e., sum of posterior model probabilities for all models wherein a predictor was included; PostMean: standardized coefficients averaged over all models; PostSD: standard deviations of standardized coefficients; CondPosSign: sign certainty, i.e., posterior probability of a positive coefficient expected value conditional on inclusion; 95% PostCI: 95% credibility interval of the posterior probability distribution. Above-ground biomass represents plot totals. Distance to transition boundary represents linear distance from each plot to the line separating Amazonia from the Cerrado (IBGE 2004).

Parameter	**PIP**	**PostMean**	**PostSD**	**CondPosSign**	**95% PostCI**
Density (individuals.ha^{-1})	1.000	0.697	0.111	1.000	0.4914 – 0.9210
Species richness	0.462	-0.133	0.171	0.000	-0.5038 – 0.0910
Pielou’s evenness (*J’*)	0.273	0.037	0.084	0.916	-0.0628 – 0.2583
Temperature (ºC)	0.198	0.026	0.079	1.000	-0.1237 – 0.2532
Precipitation (mm)	0.174	0.009	0.052	0.816	-0.1109 – 0.1772
Distance to transition boundary (km)	0.148	0.002	0.057	0.485	-0.1660 – 0.2192


5ºN
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25ºS
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50ºW
40ºW
Core
Transition
Amazonia
Cerrado

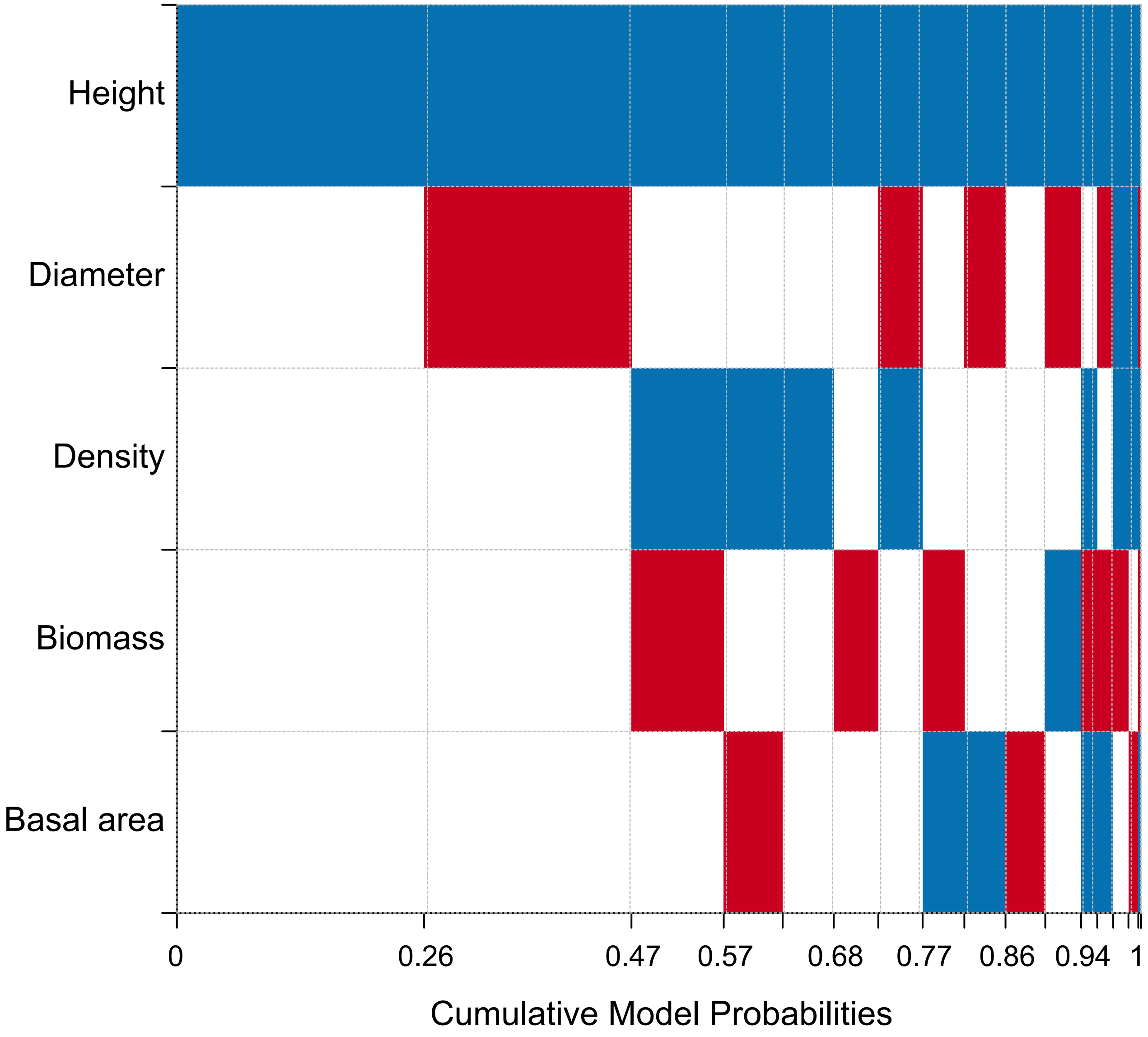
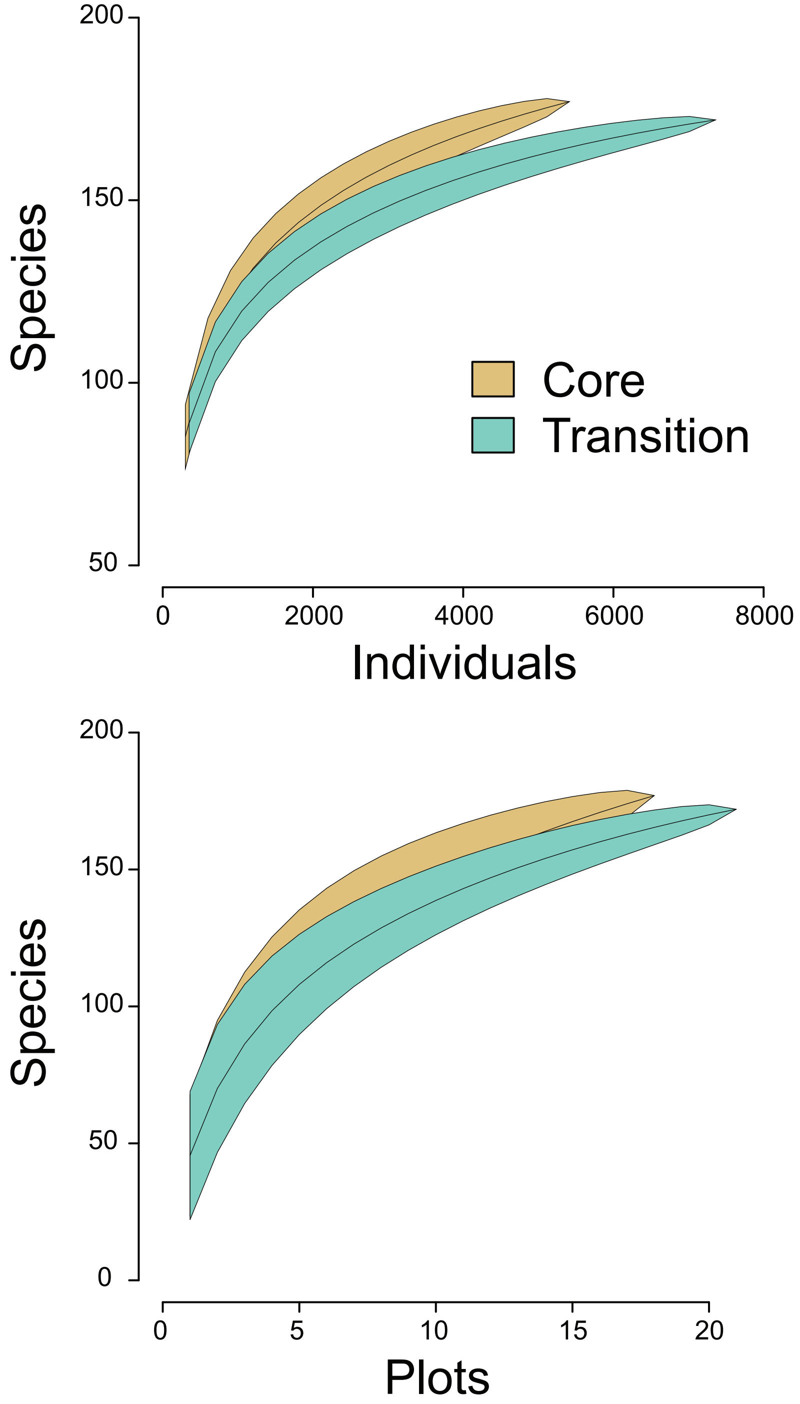
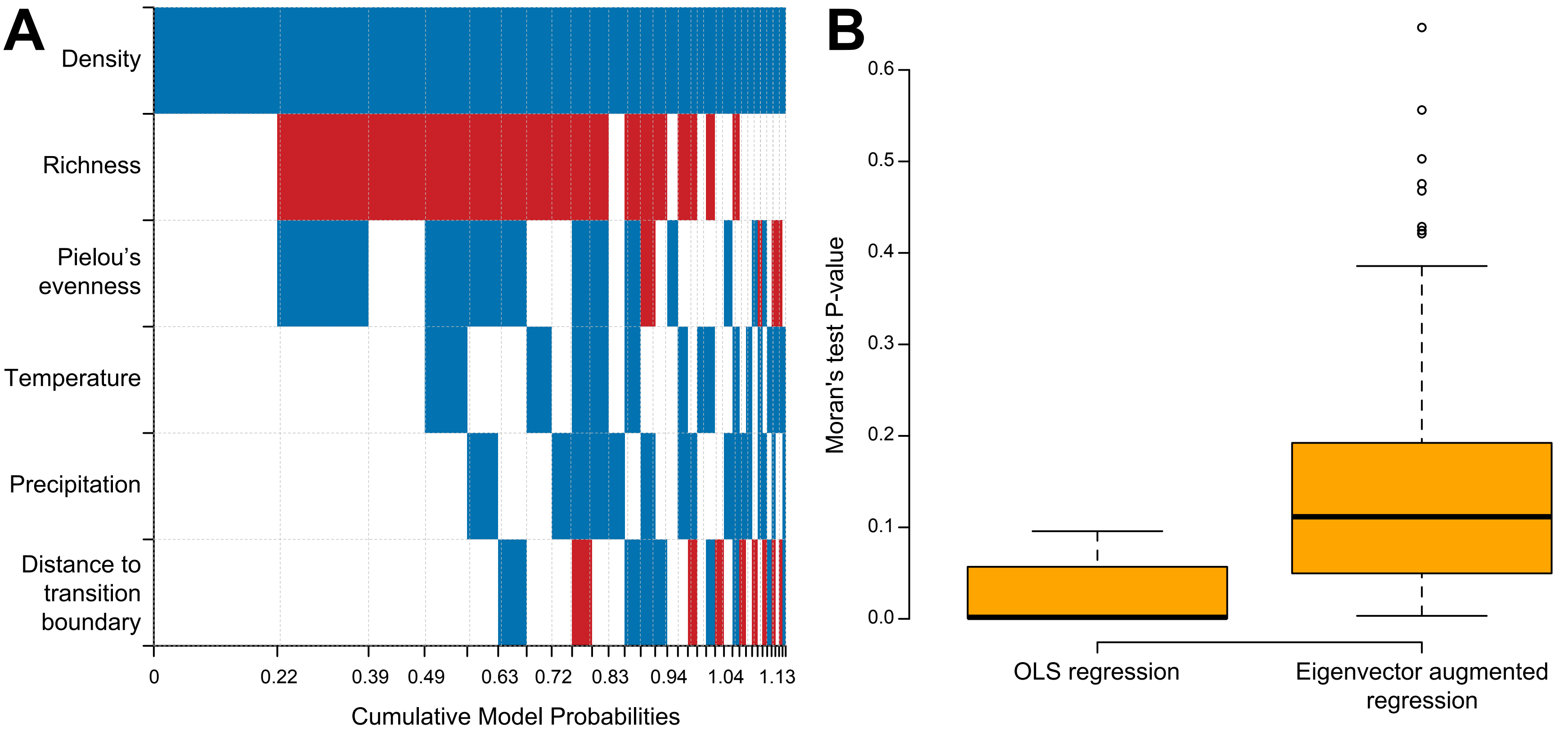

Height
Diameter
Density
Biomass
Basal area
0
0.26
0.47
0.57
0.68
0.77
0.86
0.94
1
Cumulative Model Probabilities

Figure 3


200
150
100
50
Species
Core
Transition
0
2000
4000
6000
8000
Individuals
200
150
100
50
0
Species
0
5
10
15
20
Plots


A
Density
Richness
Pielou's evenness
Temperature
Precipitation
Distance to transition boundary
0
0.22
0.39
0.49
0.63
0.72
0.83
0.94
1.04
1.13
Cumulative Model Probabilities
B
Moran's test P-value
0.0
0.1
0.2
0.3
0.4
0.5
0.6
OLS regression
Eigenvector augmented regression