



Taxonomic distinctness and diversity of a hyperseasonal savanna in central Brazil

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ABSTRACT

Savannas are characterized by a sharp seasonality, in which the water shortage defines the community functioning. Hyperseasonal savannas, however, experience additionally waterlogging in the rainy season. Since waterlogging may cause local extinctions of intolerant species, we asked whether waterlogging constricts the phylogenetic structure of a hyperseasonal savanna. We studied a hyperseasonal cerrado, comparing it with a nearby seasonal cerrado, never waterlogged, in Emas National Park, central Brazil. In each vegetation form, we sampled all vascular plants by placing fifty 1-m² quadrats in five surveys. We compared the phylogenetic structure of both vegetation forms, calculating their taxonomic distinctness, taxonomic diversity, expected taxonomic distinctness, and species, genus, and family similarities. The taxonomic distinctness of both cerrados was similar and the values of similarities were high, but taxonomic diversity and expected taxonomic distinctness were lower in the hyperseasonal cerrado than in the seasonal one. Assuming that phenotypic attraction is the major process organizing local communities, the waterlogging in hyperseasonal cerrado assembles phylogenetically unrelated species that have converged on similar habitat use. As a consequence, the habitat use of hyperseasonal cerrado species is a trait widespread in the phylogeny of seasonal cerrado. Waterlogging constrains the phylogenetic structure of the hyperseasonal cerrado, especially by reducing species diversity. In more ecological terms, we can only fully assess the phylogenetic structure of a community if we consider the species abundance.

Keywords

Cerrado, expected taxonomic distinctness, phylogenetic structure, taxonomic distinctness, taxonomic relatedness, waterlogging.

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INTRODUCTION

Waterlogging is an important determinant of species distribution and ranks alongside water shortage, salinity, and extreme temperatures as major abiotic stresses (Visser *et al.*, 2003). The consequences of waterlogging to terrestrial plants can be fatal, because, as aerobic respiration ceases, levels of energy-rich adenylates drop rapidly, causing a dramatic decline in ion uptake and transport (Huang *et al.*, 2003; Vartapetian *et al.*, 2003). Even if a short period of waterlogging does not kill vegetation, it has considerable long-term effects on plant growth (Malik *et al.*, 2002), reducing the competitive abilities of species (Jackson & Drew, 1984). Wherever waterlogging causes local extinctions of intolerant species, it may shape the composition of the local assemblages (Nicol *et al.*, 2003; Visser *et al.*, 2003).

The current composition of an assemblage is thought to be the result of different historical sequences of species entering the locality and ecological constraints acting as environmental

filters (Chase, 2003). Their relative influence on assemblage composition has been the subject of much debate (Gentry, 1988; Kinzig *et al.*, 1999; Chase, 2003). However, since theoretical models (e.g. Law & Morton, 1996) and controlled experiments (e.g. Tilman *et al.*, 1986; Sommer, 1991) often find little or no effect of history, even when the history in which species invade a community is highly variable, environmental constraints should play the major role in determination of communities.

The most practical way for summarizing the processes that structure the community is through a measure of diversity (Magurran, 2004; Hooper *et al.*, 2005). Nevertheless, it has become clear that simple estimation of species diversity is a very crude estimation of community structure (Ricotta, 2005). Consequently, responses of assemblages to environmental constraints are better understood, when the entire taxonomic hierarchy is considered (Warwick & Clarke, 1995; Rogers *et al.*, 1999; Ricotta *et al.*, 2005). For example, if an environmental filter acts replacing a community in which most species belong to the

same genus by others with similar abundances but from different genera, small-scale analyses of specific diversity or abundance will not reveal the constraint effects of environment on community (Ricotta *et al.*, 2005). Also, specific diversity or richness is difficult to relate to community disturbance, because the diversity–productivity relationship remains controversial (Grace, 1999; Mackey & Currie, 2001; Hooper *et al.*, 2005). Thus, contemporary ecological processes that structure community composition may be better understood, when a measure of phylogenetic distance of the species (phylogenetic relatedness) within the community is used (Webb, 2000; Webb *et al.*, 2002).

Clarke & Warwick (1998) proposed a method to measure the taxonomic distinctness and taxonomic diversity of a community that was shown to be very sensitive to perturbation, robust with respect to differences in sampling methods, and appropriate to assess differences among communities (Warwick & Clarke, 1995; Rogers *et al.*, 1999; Magurran, 2004). Whereas taxonomic distinctness is purely a measure of phylogenetic relatedness of species, taxonomic diversity mixes phylogenetic relatedness with the evenness properties of abundance distribution (Clarke & Warwick, 1998). Another diversity measure that seems very adequate to capture the changes in community structure is the ‘expected taxonomic distinctness’, which combines species relative abundances with their taxonomic distinctiveness and allows one to set the index sensitivity to differences in the domain of rare species (Ricotta, 2004; Ricotta *et al.*, 2005). The taxonomic distinctiveness refers to the distinctiveness of a particular species in relation to the rest of the community and differs from taxonomic distinctness, which is a property of the community as a whole (Warwick & Clarke, 2001).

Species are usually treated as equivalent units, with independent functional traits (Petchey & Gaston, 2002; Hooper *et al.*, 2005). Nevertheless, because of the conservatism of many species traits in the evolution of a lineage, there is, in general, a positive relationship between a measure of the phylogenetic relatedness of two species and a measure of their overall life history and ecological similarity (Harvey & Pagel, 1991; Silvertown *et al.*, 1997). Congeners generally occupy similar ecological niches, and the competition by the same resources may lead to a local extinction of species in a genus (Webb, 2000). For these reasons, analyses involving phylogenetic relationships of species (phylogenetic structure) within communities also provide insight into their ecological similarity (Webb, 2000; Webb *et al.*, 2002).

Seasonal savannas are characterized by a sharp seasonality, in which the pronounced rainless season defines the community functioning (Sarmiento, 1983). In hyperseasonal savannas, however, the seasonality is reinforced by a period in which the soil remains waterlogged for some months in the rainy season (Sarmiento *et al.*, 2004). As a consequence of the wide range between the limits at both extremes of soil moisture — water shortage and water excess, waterlogging determines the species abundance in hyperseasonal savannas (Sarmiento, 1983, 1996; Batalha *et al.*, 2005; Cianciaruso *et al.*, 2005), but does it limit the phylogenetic structure as well?

We related the first occurrence of a hyperseasonal cerrado in Emas National Park (ENP), central Brazil, flooded by the

accumulation of rainwater, with fewer species and less diverse than the seasonal cerrado (Batalha *et al.*, 2005; Cianciaruso *et al.*, 2005). Our aim was to study the phylogenetic structure of this hyperseasonal cerrado, comparing it with a nearby seasonal cerrado. We used a simple logical framework to infer mechanisms of contemporary coexistence (Leibold, 1998; Webb *et al.*, 2002): a clumped phylogenetic distribution of taxa (phylogenetic attraction) indicates that habitat use is a conserved trait within the pool of species in the community and that phenotypic attraction dominates over repulsion. However, phylogenetic overdispersion can result either when closely related taxa with the most similar niche use are being locally excluded (phenotypically repulsed) or when distantly related taxa have converged on similar niche use and are phenotypically attracted. Taking into account that plant communities present a limited taxonomic diversity in unfavourable environments and the role of environment filtering on determination of community is more important than the local competitive exclusion of similar species, that is, phenotypic attraction dominates over repulsion (Webb, 2000; Enquist *et al.*, 2002; Webb *et al.*, 2002), we tried to answer the following questions: Are the phylogenetic structures of a hyperseasonal and a seasonal cerrado different? Is phylogenetic relatedness in the hyperseasonal cerrado higher than in the seasonal one, indicating a habitat-use filtering of waterlogging? Are species, genus, and family similarities low between hyperseasonal and seasonal cerrados?

METHODS

We carried out this study in ENP, which is one of the largest and most important reserves in the cerrado region. It comprises 132,941 ha and is located in the Brazilian Central Plateau, south-western Goiás State (17°49′–18°28′ S; 52°39′–53°10′ W). The ENP was recently included by UNESCO (2001) in the World Natural Heritage List as one of the sites containing fauna, flora, and key habitats that characterize the cerrado. Regional climate is classified as Aw according to Köppen (1931), being humid tropical with wet summer and dry winter. Annual rainfall varies from 1200 mm to 2000 mm, concentrated from October to March, and mean annual temperature lies around 24.6 °C (Ramos-Neto & Pivello, 2000).

We studied two sites, one covered by hyperseasonal cerrado and other covered by seasonal cerrado. Both sites are physiognomically similar: grasslands, with few scattered shrubs and dwarf trees. The hyperseasonal cerrado, in the south-western portion of ENP, covers c. 300 ha and its most abundant species is the grass *Andropogon leucostachyus* Kunth. (Batalha *et al.*, 2005). At the end of the rainy season (from February to April), the water table rises up to 0.2 m above soil level, whereas, at the dry season (from June to August), there is a water shortage in the upper soil layers. In the seasonal cerrado, the grass *Tristachya leiostachya* Nees is the most abundant species (Batalha *et al.*, 2005). Both cerrados are on nutrient-poor soils, with aluminium saturation higher than 50%, base saturation lower than 50%, high percentage of sand and low values of pH, organic matter, and phosphorus (P.K. Amorim & M.A. Batalha, 2006).

To sample the plants that could be present in some season as an unseen dormant form (for example, therophytes or geophytes), we sampled the hyperseasonal cerrado (approximately, 18°18'07" S, 52°57'56" W) and a nearby seasonal cerrado (approximately, 18°17'34" S, 52°58'12" W) in all seasons: February 2003, at mid-rainy season, when the hyperseasonal cerrado was waterlogged; May 2003, at late rainy season; August 2003, at dry season; November 2003, at early rainy season; and February 2004, again at mid rainy season. In each survey, we placed randomly ten 1-m² quadrats, in which we sampled all vascular plants except seedlings. The total sampling effort, thus, was 50 quadrats in each vegetation form. We counted the number of individuals belonging to each species. In the case of cespitose grasses and sedges, we considered as an individual the whole tuft. We identified the species by comparing the collected material to vouchers, mainly the ENP's reference material collected by Batalha & Martins (2002), lodged at the São Paulo State Botanical Institute herbarium, but also vouchers lodged at Brazilian Institute of Geography and Statistic and University of Brazilia herbaria. We lodged the collected material at the Federal University of São Carlos herbarium.

We used data from all surveys to construct the phylogenetic tree and compute the taxonomic distinctness (Δ^*), the taxonomic diversity (Δ), and the expected taxonomic distinctness ($T(m)$) of both cerrados. We excluded some species that we could not identify to genus level from the analyses. We constructed the phylogenetic trees based on recent ordinal classification of angiosperms (Judd *et al.*, 2002; APG II, 2003), considering the major clades within the four angiosperm groups (see Appendix S1 in Supplementary Material).

We determined Δ^* and Δ as defined by Clarke & Warwick (1998) and confidence intervals using the PAST software (Hammer *et al.*, 2001); Δ is the expected path length between any two randomly picked individuals from the sample (Clarke & Warwick, 1998); Δ^* is modified to remove some of the overt dependence of Δ on the species abundance and is the expected 'weighted' path length between any two randomly picked individuals from the sample, conditional on they being from different species (Clarke & Warwick, 1998). The confidence intervals with a range corresponding to a 95% were computed by bootstrapping from 200 random replicates on total sampled individuals (Hammer *et al.*, 2001). We entered the taxonomic information on five levels: species, genus, family, order, and angiosperm major groups (APG II, 2003).

We computed $T(m)$, following the procedure described by Ricotta (2004) and Ricotta *et al.* (2005). First, we calculated the values of $N(m)$ with the equation:

$$N(m) = \sum_{i=1}^N (1 - (1 - p_i)^m),$$

where p_i is the proportion of individuals belonging to the i th species and m is the sensitivity to rare species. By increasing the value of the parameter m , one can enhance the sensitivity of this index to the least abundant species, and the expected species diversity will be more and more sensitive to the abundances of a

wider range of species and not only the most abundant ones (Ricotta *et al.*, 2005).

Then, we computed the pairwise species distances (d_{ij}) based on the topological distance (i.e. the number of edges) between the i th and the j th species in the taxonomic tree of each vegetation form, obtaining a species distance matrix. After that, we computed the taxonomic distinctiveness w_i of each species, adding all d_{ij} elements along row i of this matrix and dividing the result by the number of non-zero distances $K - 1$. Finally, we determined the expected taxonomic distinctness, by increasing values of the parameter m through the equation:

$$T(m) = \frac{\sum_{i=1}^N w_i (1 - (1 - p_i)^m)}{N(m)}$$

We arbitrarily selected m values that were equally spaced on a log₂ scale ranging from $m = 1$ (log₂ $m = 0$) to $m = 32,768$ (log₂ $m = 15$), as suggested by Ricotta *et al.* (2005). To check whether the $T(m)$ from the cerrados were different, we compared their $N(m)$ against log₂ m profiles.

We also calculated species, genus, and family similarities between the hyperseasonal and seasonal cerrados with the abundance-based Chao estimator for Sørensen index (Chao–Sørensen), which reduces undersampling bias by estimating and compensating for the effects of unseen, shared species (Chao *et al.*, 2005). We calculated the Chao–Sørensen index and its standard deviation (SD) using the EstimateS 7.5 software (Colwell, 2005). We obtained confidence intervals (CI) of each Chao–Sørensen index by multiplying the standard deviation value by the upper 2.5% limit of the t -distribution with $n - 1$ degrees of freedom (Manly, 1997).

RESULTS

We sampled 2377 individuals, belonging to 64 species, in the hyperseasonal cerrado, and 3360 individuals, belonging to 120 species, in the seasonal cerrado (see Appendix S2 in Supplementary Material). We excluded from the analyses eight unknown species found in hyperseasonal cerrado (comprising 24 individuals or 1.0% of the total sampled) and 12 unknown species found in seasonal cerrado (comprising 55 individuals or 1.6% of the total sampled).

The taxonomic distinctness of hyperseasonal and seasonal cerrados was not different from a random distribution of values: the Δ^* values of hyperseasonal and seasonal cerrados were, respectively, 4.056 and 4.065, and the bootstrapped CI ranged from 3.956 to 4.072. However, the taxonomic diversity of hyperseasonal cerrado was lower than expected by chance: the Δ values of hyperseasonal and seasonal cerrados were, respectively, 2.940 and 3.635, and the bootstrapped CI ranged from 3.565 to 3.637. The expected taxonomic distinctness was higher in the seasonal cerrado than in the hyperseasonal cerrado (Fig. 1). The Chao–Sørensen similarity values \pm CI between the hyperseasonal and seasonal cerrados were 0.769 ± 0.286 at species level, 0.956 ± 0.014 at genus level, and 0.866 ± 0.202 at family level.

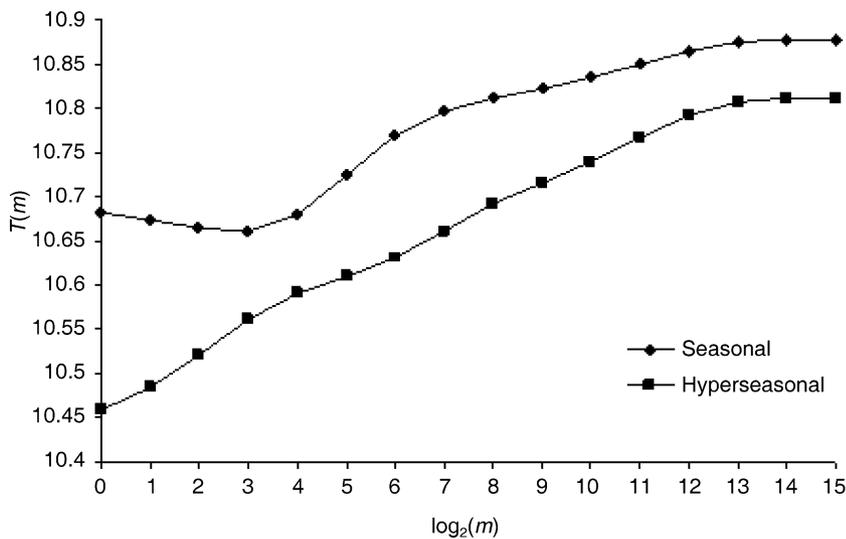


Figure 1 Expected taxonomic distinctness ($T(m)$) vs. $\log_2 m$ profiles of the hyperseasonal and seasonal cerrados, Emas National Park, central Brazil (approximately, 18°18'07" S, 52°57'56" W).

DISCUSSION AND CONCLUSIONS

The hyperseasonal cerrado is a subset of the species of the seasonal cerrado, because its richness is almost exactly half of the seasonal cerrado richness and the similarity between them is high. However, the analysis of taxonomic distinctness, as well as those of genus and family similarities, showed that the temporary waterlogging in the hyperseasonal cerrado does not clump phylogenetically related species. The habitat use of hyperseasonal cerrado species is, thus, a trait widespread in the phylogeny of seasonal cerrado. Where the environment situations are spatiotemporally heterogeneous, as in savannas, species are adapted to dynamism and evolve strategies for responding to shifting opportunities (Fjeldsa & Lovett, 1997). Consequently, the interaction and occurrence of several environmental factors in savannas should have favoured species able to withstand many ecological restrictions (Sarmiento & Monasterio, 1975; Lopes & Cox, 1977), even the environmental constraints resulting from drought and waterlogging.

Analyses of genus and family similarities also support that waterlogging in the hyperseasonal cerrado may not be stressful enough to clump phylogenetically related species, since most of the genera and families were found in both cerrados. However, local communities are characterized by fewer higher taxa than would be expected by chance, because the abiotic features that influence the ability of species to colonize and survive consistently regulate taxa composition (Leibold, 1998; Webb, 2000; Enquist *et al.*, 2002). Thus, local processes in the hyperseasonal cerrado must be very similar to those in the seasonal one, and waterlogging may not be strong enough to constrain its phylogeny.

Although phylogenies have a non-overlapping structure whereas functional groups tend to have an overlapping one (Von Euler & Svensson, 2001), the similar taxonomic distinctness between both cerrados suggests that waterlogging does not reduce the number of functional groups in hyperseasonal savannas. The diversity of functional groups is important to

maintain the resilience of community structure and function (Walker *et al.*, 1999). High functional group diversity is expected for communities with high taxonomic diversity (Petchey & Gaston, 2002), because related species share more functional traits than unrelated ones (Harvey & Pagel, 1991; Silvertown *et al.*, 1997). As correlations between phylogenetic structure and the structure of functional groups in species assemblages have also been found (Warwick & Clarke, 1998; Von Euler & Svensson, 2001), we may postulate that functional groups in hyperseasonal savannas are maintained even under physiological restrictions due to waterlogging. If so, community level process of seasonal savannas should be retained in hyperseasonal ones.

Taking into account the taxonomic diversity and the expected taxonomic distinctness, waterlogging modifies the phylogenetic structure of the hyperseasonal cerrado. The lower Δ and $T(m)$ values of the hyperseasonal cerrado pointed out that its phylogenetic structure is taxonomically more homogeneous than that of the seasonal cerrado. However, taxonomic diversity is an extension of Simpson diversity and incorporates information on taxonomic relationships into an index measuring species dominance (Clarke & Warwick, 1998). As the taxonomic distinctness was equal and higher taxa were shared by both cerrados, low taxonomic diversity of the hyperseasonal cerrado indicated that waterlogging affects species diversity rather than phylogeny. In accordance with this interpretation were also the outcomes of expected taxonomic distinctness, which is a parametric diversity index (Ricotta, 2004; Ricotta *et al.*, 2005). Since, for any degree of index sensitivity to the least abundant species, we found lower values of $T(m)$ in the hyperseasonal cerrado than in the seasonal one, waterlogging decreased species diversity in the former. As long as cerrado species are commonly dryland ones (Ratter *et al.*, 1997), the major consequence of waterlogging is hence to limit the number of species able to grow in such a condition (Sarmiento, 1996; Batalha *et al.*, 2005; Cianciaruso *et al.*, 2005). Accordingly, waterlogging modifies the phylogenetic structure of the hyperseasonal cerrado by decreasing the number

and the abundance of those cerrado species that are less tolerant to water excess, but not constraining the phylogenetic tree of its community.

Whereas we observed substantial differences between the phylogenetic structure of hyperseasonal and seasonal cerrados, as long as each vegetation form is unreplicated, caution should be taken when extrapolating our findings to other hyperseasonal savannas. Moreover, since we could not classify the unidentified 20 species into any taxonomic level lower than angiosperm, our conclusions are based on an incomplete phylogenetic tree of the studied communities. Nevertheless, these 20 unidentified species comprised proportionately few individuals and our conclusions should hold even when they are included.

It is worth noticing that $T(m)$ is closely related to others measures. Whereas Δ^* does not take into account the species abundance, Δ have an explicit dependence on the species abundance (Clarke & Warwick, 1998). However, because we can set the index sensitivity to differences in the domain of rare species (Ricotta, 2004; Ricotta *et al.*, 2005), Δ is closely related to $T(0)$ and Δ^* is identical to $T(\infty)$. Considering that we found the higher difference between the two cerrados in $T(0)$ rather than in $T(15)$ (Fig. 1), as well as a significant difference only between Δ values, a better comprehension of phylogenetic structure arises only when the species abundance is considered.

Finally, assuming that phenotypic attraction is the major process organizing the local communities (Webb, 2000; Enquist *et al.*, 2002; Webb *et al.*, 2002), the waterlogging in hyperseasonal cerrado assembles phylogenetically unrelated species that have converged on similar habitat use. As a consequence, the habitat use of hyperseasonal cerrado species is a trait widespread in the phylogeny of seasonal cerrado. The waterlogging constrains the phylogenetic structure of hyperseasonal specially by reducing species diversity. In more ecological terms, we can only fully assess the phylogenetic structure of a community if we consider the species abundance.

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SUPPLEMENTARY MATERIAL

The following material is available online at www.blackwell-synergy.com/loi/ddi

Appendix S1. Taxonomic relation among all angiosperm species sampled.

Appendix S2. List of species and number of individuals sampled.