



Patterns of species diversity in different spatial scales and spatial heterogeneity on beta diversity

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ABSTRACT

Patterns of species diversity are essential to understand community structure. We aimed to determine species diversity and patterns of beta diversity in different spatial scales. We sampled three thousand individuals between the coordinates 22°10'S to 22°16'S and 47°47'W to 48°00'W to assess species diversity in three spatial scales (maximum distances of 80 m, 1,400 m, and 12,000 m), using the point-centered-quarter method. We partitioned gamma diversity into alpha and beta components. Beta diversity was partitioned into dissimilarities produced by spatial species turnover and nestedness. The contribution of beta diversity to gamma diversity was greater than that of alpha diversity in all scales, although the patterns of species diversity were similar for the evaluated scales, and was similar to that described for larger spatial scales. The sampled fragments presented means of 15 exclusive species and 47.5 species per fragment, and dissimilarities [$\beta(S\text{Ø}R)=0.7$] almost completely explained (94 %) by spatial species turnover. The results indicate that the remnant fragments are residual patches of an originally heterogeneous vegetation. The fragmentation processes could have progressed differently in each portion of the original vegetation, producing the current heterogeneous vegetation. Thus, there is a potential of high local species extinctions if the remnant fragments are deforested.

Keywords: beta diversity, biogeography, disturbance, diversity partition, local spatial scale, nestedness, phytogeography, spatial species turnover

Introduction

Description of patterns of species diversity is a central theme in ecology. Understanding patterns of species diversity is useful for conservation planning and sustainable management of natural ecosystems. Patterns of species diversity is a tool to evaluate impacts of fragmentation (Arroyo-Rodríguez *et al.* 2013) and invasion by exotic species (Marini *et al.* 2013), and to select priority fragments for conservation (Eken *et al.* 2004). Studies applying this

information have evaluated diversity distribution on different spatial scales (Gering & Crist 2002; Crist *et al.* 2003) and spatial compartments: alpha, beta, and gamma diversity (Whittaker 1972). The alpha component is defined as the local richness, gamma is the regional diversity, and beta is the extension of dissimilarities that separates alpha from the gamma component (Whittaker 1972).

Baselga (2010) proposed an approach in which species diversity and beta diversity information could lead to two distinct ecological processes: species turnover and nestedness. Species turnover is the simultaneous

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deletion and addition of species from one place to another ordination imposed by different environmental conditions or biogeographical histories (Leprieur *et al.* 2011). Therefore, a high species turnover rate is expected where physical conditions are very different between two neighbor localities (Gaston *et al.* 2007). Species nestedness indicates that poor species assemblages are subsets of richer assemblages. Nestedness is induced by environmental gradients, variance on inter- and intraspecific tolerance to different conditions, and limitations of species dispersal (Leprieur *et al.* 2009).

Considering the available information, beta diversity has proven to be more affected by species turnover than nestedness in high-diversity ecosystems, while nestedness is commonly described for ecosystems with relatively high compositional and environmental homogeneity among communities (Gibson *et al.* 2012; Sfenthourakis & Panitsa 2012). However, regarding aquatic ecosystems, species nestedness has been described as the most important factor affecting beta diversity of freshwater fishes, mainly due to interactions between harsh climatic events of the past and latitudinal gradients of abiotic aquatic conditions (Leprieur *et al.* 2011).

Information on patterns of species diversity is important in the context of fragmentation and habitat loss (Tabarelli *et al.* 1999), since tropical ecosystems have been largely transformed from continuous habitats to sets of small fragments surrounded by human-modified matrices (Gardner *et al.* 2009). Thus, understanding how patterns of species diversity respond to fragmentation disturbances—such as edge effects and collapse of animal-plant interactions—is essential for a proactive conservation planning (Lôbo *et al.* 2011; Tabarelli *et al.* 2012). The approach of Baselga is useful for addressing questions about biotic homogenization driven by fragmentation, such as those raised by Lôbo *et al.* (2011) and Arroyo-Rodríguez *et al.* (2013).

Beta diversity is also highly affected by spatial scale. Some vegetation types, such as Seasonally Dry Tropical Forests (Pennington *et al.* 2009), Atlantic Ombrophilous Dense Forest (Scudeller *et al.* 2001), and Cerrado (Felfili & Felfili 2001) have high compositional dissimilarities between regions on wide geographical scales. Thus, the contribution of beta diversity to gamma diversity is higher than that of alpha diversity. Moreover, species diversity is characterized by few widespread and many spatially restricted species. Therefore, the contribution of alpha and beta to gamma diversity and the patterns of species diversity at local scales in these vegetation types are little known.

The present study addresses the following questions: Are the species diversity patterns described for different communities occurring at large geographic scales (2 million km²)—high beta diversity, with few widespread and many spatially restricted species—different from the patterns found in communities occurring at local spatial scales (200 km²)? II. How is diversity partitioned between alpha, beta, and gamma components at local spatial scales? III. At which

spatial scale beta diversity starts to contribute more to gamma diversity than alpha? IV. Is beta diversity at local scales more affected by species turnover than by nestedness?

We expected a lower contribution of beta diversity than that of alpha diversity to gamma diversity at local spatial scales. Studies on intermediate and larger spatial scales in Cerrado vegetation—a neotropical savanna with the highest overall species richness (Kier *et al.* 2005)—have shown that large scales are needed to promote significant increases in species richness (Felfili & Felfili 2001; Bridgewater *et al.* 2004; Felfili & Fagg 2007). Thus, we expected a low beta diversity at local spatial scales because of the relative homogeneity of environmental conditions (types of soil and climate) at that scale, in which spatial scale beta diversity is higher than alpha due to the greater heterogeneity of environmental conditions over larger scales.

Materials and methods

Study area

The study was carried out in six Cerrado vegetation fragments in the state of São Paulo, Brazil (22°10'–22°16'S; 47°47'–48°00'W); two of them were sampled in the Itirapina Ecological Station (a full-protection conservation area), two in the Itirapina Experimental Station (a sustainable-use conservation area), and two in private properties near those conservation areas (Fig. 1). The longest distance between the sampled fragments was 12 km, while the distance between the closest fragments was 0.8 km.

Cerrado fragments in the region are currently immersed in a matrix of pastureland, sugar cane and *Pinus elliottii* L. plantations, and urban areas. The climate of the region is temperate (Cwa), according to the Köppen-Geiger classification, presenting average annual temperature of 22 °C, average annual precipitation of 1,459 mm (Silva 2005), and altitudes of 700 to 827 m, with most of these Cerrado fragments at 760 m of altitude (Silva 2005).

The Cerrado biome has several physiognomies, from grasslands to forests. It can be recognized based on density and basal area of shrubs and trees, canopy openness, and vertical stratification (Coutinho 1978). The physiognomies of the sampled fragments were classified, according to Ribeiro & Walter (2008), as Campo Sujo (grassland interspersed with sparse shrubs and short trees), Cerrado Ralo (savanna with low-density short trees), Cerrado Típico (typical savanna), Cerrado Denso (savanna with high-density trees), and Cerradão (savanna woodland with dense canopy). These six fragments will be treated thereafter, respectively as A, B, C1, C2, D, and E, following the crescent order of woody biomass.

The soil of all fragments is classified as arenosol, showing a highly sandy texture, high porosity, and hydric deficit (Dalla-Nora & Santos 2011). The sampled fragments also have different disturbance histories. Fragments A and B





Figure 1. Location of study fragments (A-E) of Cerrado vegetation (gray patch) and conservation areas (ESEC –Estação Ecológica de Itirapina; ESEX –Estação Experimental de Itirapina) in the state of São Paulo, Brazil. A. Campo Sujo; B. Cerrado Ralo; C. Cerrado Típico; D. Cerrado Denso; and E. Cerradão.



were extensively exploited as cattle pasture before 1984; C1 is the closest to an urban area and is used as garbage dump; C2 and D have exotic invader species, mainly *Pinus elliottii* and *Urochloa spp.*; and E is surrounded by highways and sugar-cane plantations, but was the most preserved sampled fragment.

Data survey

Data was collected between October 2013 and April 2014, using the point-centered quarter method (Cottam & Curtis 1956). The sampling points were distributed within transects (transect scale) located inside blocks (block scale). Each transect was 80 m long and was composed by five points (20 individuals per transect) with 20 m between points; this distance was established after pilot surveys were conducted in A and B fragments, which are those with the lowest tree densities. Each block contained five transects arranged in parallel to each other and separated by 20 m. Five blocks were randomly allocated in each fragment (b1, b2, b3, b4, and b5), the larger spatial scale were sampled, with a minimum distance of 120 m between them (the distance determined by the smallest fragment, C2) and a maximum distance of 1400 m. We avoided sampling points at distances less than 15 m from any fragment edge in areas with high density of exotic species (e.g., *Pinus elliottii* or *Urochloa spp.*) and in overly disturbed sites. Therefore, we sampled 500 individuals per sampling fragment, totaling 3,000 sampled individuals, which were distributed into three spatial scales (transects, blocks, and fragments).

Cerrado trees commonly have root expansions—xylopodium or cork accumulations; thus, we measured their stem diameters at 30 cm from the soil surface to avoid overestimation (Moro & Martins 2011). Only individuals with stem diameter greater than 3 cm were included in the sampling. The exotic species *Pinus elliottii* was disregarded.

Data analysis

The diversity organization within the study area (200 km²) was evaluated by the contributions of alpha and beta diversities to total shrub and tree diversity at three spatial scales: transects, blocks, and fragments. Alpha, beta, and gamma diversities were calculated for each spatial scale as described by Jost (2006; 2007). Alpha and beta diversities are independent and determined by additive (Lande 1996) and multiplicative partitions (Whittaker 1960; 1972). These approaches (additive and multiplicative) allowed the evaluation of patterns of species diversity at different spatial scales, although the results showed different aspects of the communities evaluated (Chao *et al.* 2012). Additive partitioning estimates alpha diversity as the mean number of species found in each sample, whereas beta diversity is estimated as the mean number of species that cannot be found in each sample; so, both parameters are calculated

using the same units (Lande 1996). The multiplicative approach estimates alpha diversity as the effective number of species per sample, and beta diversity as the number of samples completely different among a set of communities (Whittaker 1972; Jost 2007; Chao *et al.* 2012).

The effective number of species depends on the weight attributed to each species (indicated by “q”) using the decomposition of Hill numbers (Hill 1973). This calculation can be synthesized as: $q = 0$, where all species have the same weight (species richness; S); $q = 1$, where each species’ weight is proportional to its relative abundance ($\exp(H')$); and $q = 2$, where the weights of rare species are almost insignificant when compared to dominant species ($1/D$).

According to Chao *et al.* (2012), the only “q” value that allows multiplicative beta diversity to be interpreted as the number of different samples among a set of communities is ‘ $q = 1$ ’, which was the value that we used for multiplicative diversity partition. The additive partition of diversity can be used, in addition to the contributions of alpha and beta diversity, to evaluate the mean number of exclusive species in each sample (when additive beta diversity is divided by $N-1$, where “N” is the number of samples) (Chao *et al.* 2012).

Null parameters were obtained through 1,000 randomizations of the data to test when the observed parameters differed from those expected by chance (Veech & Crist 2009). The partition results and null parameters were obtained using the Partition software (version 3.0, www.users.muohio.edu/cristto/partition.htm).

We estimated beta diversity among the samples simultaneously, on the three spatial scales, as “dissimilarity among multiple samples”, using $\beta(SOR)$, a metric conceived by Baselga (2007; 2010). We used presence/absence matrices and the Sørensen index, calculated for all samples simultaneously at each spatial scale. The beta diversity value obtained was partitioned to show the proportions of the dissimilarities among the samples that were affected by species turnover [$\beta(SIM)$] and by species nestedness [$\beta(NES)$], using the equation $\beta(SOR) = \beta(SIM) + \beta(NES)$ (Baselga 2010). The partitioning of beta diversity was performed using Betapart package (version 1.3. <http://CRAN.R-project.org/package=betapart>) in the R environment (R Development Core Team 2012).

Results

We found a gradual increase of the contribution of each spatial scale to gamma diversity. Additive beta diversity was significantly higher than that expected by chance on the fragment scale ($P < 0.01$; Fig. 2). Beta diversity contributed more to gamma diversity than alpha component in all evaluated scales, but only in the fragment scale this difference was strong (Tab. 1).

According to the additive partition estimate, each sampled fragment had a mean of 15 exclusive species.



The results for multiplicative partition of diversity ($q=1$) had higher values of beta diversity than those expected by chance for the block and fragment spatial scales. The values of beta diversity for blocks and fragments were 1.6 and 2.2, respectively (Tab. 2). These values can be interpreted as the mean number of samples that present completely dissimilar sets of species. Thus, there were approximately two communities completely different among the six sampled fragments, and 1.6 communities among the 30 blocks. The beta diversity for fragment scale was higher than that for block scale.

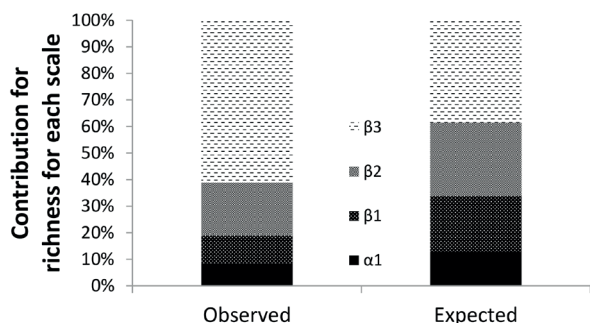


Figure 2. Observed and expected contribution to gamma diversity on each sampled spatial scale in the Cerrado vegetation. α_1 = Alpha diversity on transect scale; β_1 = Beta diversity on transect scale; β_2 = Beta diversity on block scale; and β_3 = Beta diversity on fragment scale.

Table 1. Values of alpha (α), beta (β^+), and gamma (γ) for additive partition of diversity ($q = 0$) on transect, block, and fragment spatial scales in the Cerrado vegetation (maximum distance of 80 m, 1400 m, and 12.000 m, respectively). (*) Values that were different from those expected by chance ($P < 0.01$) after 1,000 data randomizations.

Spatial scale	A	β^+	$\gamma (\alpha+\beta^+)$
Transects	10.3	12.9	23.2
Blocks	23.2	24.3	47.5
Fragments	47.5	74.5*	122

Table 2. Values of alpha (α), beta (β^*), and gamma (γ) for multiplicative partition of diversity ($q = 1$) on transect, block, and fragment spatial scales in the Cerrado vegetation (maximum distance of 80 m, 1400 m, and 12.000 m, respectively). (*) Values that were different from those expected by chance ($P < 0.01$) after 1,000 data randomizations.

Spatial scale	A	β^*	$\gamma (\alpha\beta^*)$
Transects	8.1	1.7	13.6
Blocks	13.7	1.6*	21.8
Fragments	21.8	2.2*	47.9

The dissimilarity among multiple blocks inside all six fragments was much more affected by species turnover than by nestedness (Fig. 3). Blocks in the fragment A had the highest dissimilarity among each other, and had the highest proportions of dissimilarity explained by nestedness. Therefore, besides blocks of this fragment had

great compositional heterogeneity, they had a set of species distributed according to some environmental gradient.

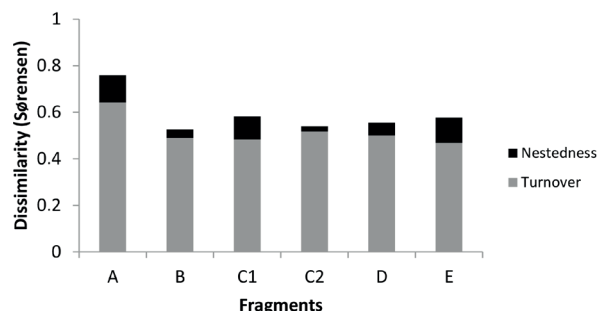


Figure 3. Partition of beta diversity in the block scale to each fragment of the Cerrado. A. Campo Sujo; B. Cerrado Ralo; C1. Cerrado Típico 1; C2. Cerrado Típico 2; D. Cerrado Denso; and E. Cerradão.

The fragments B and C2 had the lowest dissimilarity among blocks, and the lowest proportion of the dissimilarity was explained by species nestedness. Thus, for megadiverse vegetation types, such as the Cerrado, even samples with relative homogeneous composition of species have their differences more affected by species turnover than by nestedness.

The pattern of low nestedness and high species turnover was found for all evaluated spatial scales (Fig. 4). The rate of species nestedness decreased as the spatial scale became more locally restricted, with almost total absence of nestedness in the transect scale. Moreover, an increase of dissimilarity among multiple samples was found as the spatial scales became more locally restricted (fragments to transects), whereas fragment scale had the lowest compositional dissimilarity among samples (Fig. 4).

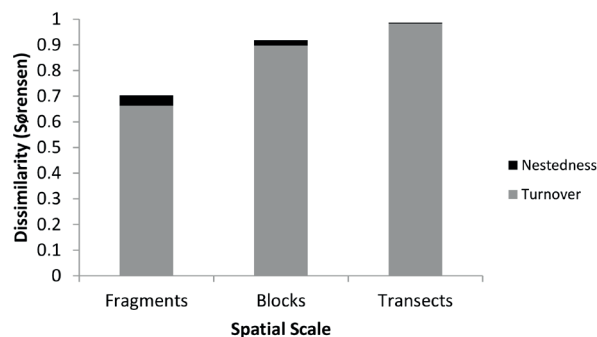


Figure 4. Partition of beta diversity on fragment, block, and transect spatial scales of Cerrado vegetation.

We founded a total of 122 species. Many species (79 spp, 65 %) were found exclusively in only one or two fragments (Fig. 5), and five species (4%) were found in all fragments (*Byrsonima coccolobifolia*, *Dalbergia miscolobium*, *Handroanthus ochraceus*, *Pouteria ramiflora* and *Qualea grandiflora*).



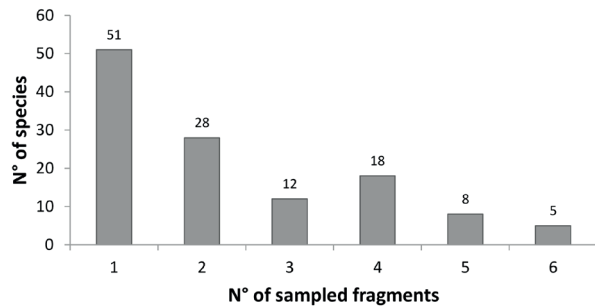


Figure 5. Species frequency in the sampled Cerrado vegetation fragments, at local scale.

Discussion

The pattern of species diversity on wide scale does not occur uniformly, but is characterized by few widespread species and several species occurring in few or even in only one region of tropical forests in general (Scudeller *et al.* 2001; Milliken *et al.* 2010; Moro *et al.* 2014) and also of the Cerrado vegetation (Castro & Martins 1999; Ratter *et al.* 2003; Bridgewater *et al.* 2004). Thus, the contribution of beta diversity to gamma diversity is higher than the contribution of alpha diversity in such wide scale. Here, we show that this pattern of woody species diversity repeats, even for locally restricted spatial scales, indicating that there is no specific scale in which alpha diversity has high contribution to gamma than beta diversity. This result is directly applied to biodiversity management and selection of priority conservation areas in these domains.

The pattern of species diversity that we found in an area of 200 km² was also found for a spatial scale of 2 000 000 km², with many rare and spatially restricted species and few frequent and widespread species (Ratter *et al.* 2003). Even in small portions of the Cerrado biome, only 4% of the species were found in all sampled fragments, whereas 65% of species were much less frequent, which were found in only one or two localities. The increase in the mean number of species that does not occur in a sample (additive beta diversity) was higher than that expected by chance for the fragment scale, including distances between 0.8 and 12 km; thus, indicates that the vegetation can have relevant compositional heterogeneity on the fragment scale.

The five species common to all sampled fragments are included in the list of most frequent species of the Cerrado domain (Bridgewater *et al.* 2004). This result evidences that not only the pattern of species diversity at local spatial scales—such as fragment scale—is the same of larger spatial scales, but the more widespread species are the same for both spatial scales (Bridgewater *et al.* 2004).

Few studies have evaluated patterns of species diversity at local spatial scale in the Cerrado biome and found low beta diversity due to low environmental heterogeneity among sampled fragments (Bridgewater *et al.* 2004; Neri *et al.* 2007). Bridgewater *et al.* (2004) analyzed floristic data

of 13 Cerrado fragments (comprising 5748 km²) and found high compositional similarity among samples. Considering the short geographical distances, climate similarities, and similar soil types of the sampled fragments, we expected to find low beta diversity; however, it was not supported by the results. Therefore, the history of disturbance of the studied landscape should have limited the species establishment, generating plant communities with different vertical structure and floristic composition (Foster 1988; Chapin III *et al.* 2011).

The process that contributed the most to the high beta diversity found in the present study was the spatial species turnover and not the nested pattern of species diversity. The same result was found for megadiverse dry forests in the Northeast region of Brazil (Apgaua *et al.* 2014). The high contribution of species turnover to beta diversity supports our conclusion that the compositional heterogeneity among fragments is generated by some ordination or restriction promoted by environmental biotic or abiotic conditions, or, alternatively, a filtering associated with the colonization history of the sampled fragments that generated different biotic arrangements (Foster 1988; Gaston *et al.* 2007; Baselga 2010; Chapin III *et al.* 2011; Leprieur *et al.* 2011). The same pattern was recently described for other domains with great biodiversity. Gibson *et al.* (2012) found high beta diversity in the arid vegetation of southeastern Australia and reported that the high compositional dissimilarity was produced by species turnover due to environmental heterogeneity. Sfenthourakis & Panitsa (2012) found that the plant species dissimilarity among Greek islands was better explained by species turnover, but for those pairs of communities that presented low dissimilarity, they explained that low beta diversities were produced by nestedness. Because of the non-occurrence of species nestedness, we suggest that the history of disturbance or colonization is the greatest responsible for Cerrado community structuring at local scales. However, further studies should assess which process have more effect on community structuring at local scale.

High beta diversity and high effect of species turnover process were found in all evaluated scales, even in the transect scale. This result may have been affected by the occurrence of different microenvironmental conditions among the evaluated fragments (e.g. fine differences in soil fertility, microtopography, proximity to water courses, natural or anthropogenic disturbance level, and physic factors determined by vegetation structure) and even among transects of the same fragment. It is unlikely that these microenvironmental conditions often occur in a spatially restrict scale (Arrhenius 1921; Levin 1992; Rahbek 2005). Contrastingly, it is likely that some conditions repeat at some points in a larger spatial scale; thus, transects or even entire blocks can have similar species composition in more than one fragment. This pattern of beta diversity is dependent on the spatial scale, as shown in other studies (Arrhenius 1921; Rahbek 2005). However, as far as we know, there are

no other studies evaluating the partition of beta diversity on different scales.

There are two explanations to the patterns of species diversity found in the present study. The first is that current fragments are residual patches of an original heterogeneous vegetation type, which was established under colonization and biogeographical processes, such as dispersal limitation of species, resulting in a great heterogeneity. When this heterogeneous vegetation became fragmented, fragments with different sets of environmental conditions and different floras were produced (Lôbo *et al.* 2011; Tabarelli *et al.* 2012; Arroyo-Rodríguez *et al.* 2013). The second possibility is that the processes of degradation and fragmentation could have occurred differently in each portion of the original vegetation, producing the current set of remnant fragments with heterogeneous vegetation. In this case, the history of disturbance would be the main responsible for the vegetation structuring on spatially restrict scales (Foster 1988; Chapin III *et al.* 2011; Vranken *et al.* 2015). This last possibility has great support because of the different types of disturbance found in the evaluated fragments, such as pasture, fire, domestic waste deposition, forestry, and agriculture. In addition, the two possibilities could be complementary to each other. When the original vegetation had environmental heterogeneity, a random fragmentation process contributes to generate a set of fragments with different environmental conditions and floristic compositions.

Based on our results and the patterns of species diversity described by other authors (Castro & Martins 1999; Ratter *et al.* 2003; Bridgewater *et al.* 2004), it is possible to draw a very challenging scenario for the conservation of the Cerrado biome. The diversity component that contributes the most to the entire diversity of this domain, even at local spatial scales, is the beta diversity—the extension of the dissimilarity among samples. This beta diversity is produced by spatial species turnover, generating a pattern in which most species are restricted to some location and few species are widespread, with each fragment having a distinct set of exclusive species. Thus, any remnant fragments, even the little and disturbed ones, should have their species composition carefully evaluated before any management intervention in the landscape because of the high risk of local species extinction if the vegetation suffers a conversion to productive systems.

These results denote the importance of conserving Cerrado remnant fragments, and the magnitude of the impact on biodiversity if the actual deforestation rate continues, as previously described by other authors (Durigan *et al.* 2003; Ratter *et al.* 2003; Bridgewater *et al.* 2004). Selecting large and less disturbed fragments for the creation of conservation units is not enough to conserve biodiversity. It is necessary to promote an extensive conservation of remnant fragments distributed across the entire Cerrado domain, regardless of their size or disturbance level, since even small fragments can have high conservation value

(Santos *et al.* 2007). This conservation strategy is applicable to the Cerrado, but also to other megadiverse domains, which have high beta diversity on wide scale, such as Tropical Dry Forests, and Atlantic Forests.

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References

- Apgaua DMG, Santos RM, Pereira DGS, *et al.* 2014. Beta-diversity in seasonally dry tropical forests (SDTF) in the Caatinga Biogeographic Domain, Brazil, and its implications for conservation. *Biodiversity and Conservation* 23: 217-232.
- Arrhenius O. 1921. Species and area. *Journal of Ecology* 9: 95-99.
- Arroyo-Rodríguez V, Rös M, Escobar F, *et al.* 2013. Plant β -diversity in fragmented rain forests: testing floristic homogenization and differentiation hypotheses. *Journal of Ecology* 101: 1449-1458.
- Baselga A. 2007. Disentangling distance decay of similarity from richness gradients: response to Sojininen *et al.* 2007. *Ecography* 30: 838-841.
- Baselga A. 2010. Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography* 19: 134-143.
- Bridgewater S, Ratter JA, Ribeiro JF. 2004. Biogeographic patterns, β -diversity and dominance in the Cerrado biome of Brazil. *Biodiversity and Conservation* 13: 2295-2318.
- Castro AAJF, Martins FR. 1999. Cerrados do Brasil e do Nordeste: caracterização, área de ocupação e considerações sobre a sua fitodiversidade. *Pesquisa em Foco* 7: 147-178.
- Chao A, Chiu CH, Hsieh T. 2012. Proposing a resolution to debates on diversity partitioning. *Ecology* 93: 2037-2051.
- Chapin III FS, Matson PA, Vitousek P. 2011. Principles of terrestrial ecosystem ecology. New York, Springer Science & Business Media.
- Cottam G, Curtis JT. 1956. The use of distance measures in phytosociological sampling. *Ecology* 37: 451-460.
- Coutinho LM. 1978. O conceito de Cerrado. *Revista Brasileira de Botânica* 1: 17-13.
- Crist TO, Veech JA, Gering JC, Summerville KS. 2003. Partitioning species diversity across landscapes and regions: A hierarchical analysis of α , β , and γ diversity. *The American Naturalist* 162: 734-743.
- Dalla-Nora EL, Santos J E. 2011. Dinâmica ambiental da zona de amortecimento de áreas naturais protegidas. *Ambiência (UNICENTRO)* 7: 279-293.
- Durigan G, Siqueira MF, Franco GADC, Bridgewater S, Ratter JA. 2003. The vegetation of priority areas for cerrado conservation in São Paulo state, Brazil. *Edinburgh Journal of Botany* 60: 217-241.
- Eken G. 2004. Key biodiversity areas as site conservation targets. *BioScience* 54: 1110-1118.
- Felfili MC, Felfili JM. 2001. Diversidade alfa e beta no Cerrado *sensu stricto* da Chapada Pratinha, Brasil. *Acta Botanica Brasílica* 15: 243-254.
- Felfili JM, Fagg CW. 2007. Floristic composition, diversity and structure of the “cerrado” *sensu stricto* on rocky soils in northern Goiás and southern Tocantins, Brazil. *Revista Brasileira de Botânica* 30: 375-385.
- Foster DR. 1988. Disturbance history, community organization and vegetation dynamics of the Old-Growth Pisgah Forest, South-West, New Hampshire, U.S.A. *Journal of Ecology* 76: 105-134.
- Gardner TA, Barlow J, Chazdon R, *et al.* 2009. Prospects for tropical forest biodiversity in a human-modified world. *Ecology Letters* 12: 561-582.



- Gaston KJ, Davies RG, Orme CDL, Olson VA, Thomas GH, Ding TS. 2007. Spatial turnover in the global avifauna. *Proceedings of Royal Society Biological Sciences* 274: 1567-1574.
- Gering JC, Crist TO. 2002. The alpha-beta regional relationship: providing new insights into local regional patterns of species richness and scale dependence of diversity components. *Ecology Letters* 5: 433-444.
- Gibson N, Meissner R, Markey AS, Thompson WA. 2012. Patterns of plant diversity in ironstone ranges in arid south western Australia. *Journal of Arid Environments* 77: 25-31.
- Hill MO. 1973. Diversity and evenness: a unifying notation and its consequences. *Ecology* 54: 427-432.
- Jost L. 2006. Entropy and diversity. *Oikos* 113: 363-375.
- Jost L. 2007. Partitioning diversity into independent alpha and beta components. *Ecology* 88: 2427-2439.
- Kier G, Mutke J, Dinerstein E, *et al.* 2005. Global patterns of plant diversity and floristic knowledge. *Journal of Biogeography* 32: 1107-1116.
- Lande R. 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos* 76: 5-13.
- Leprieur F, Olden JD, Lek S, Brosse S. 2009. Contrasting patterns and mechanisms of spatial turnover for native and exotic freshwater fish in Europe. *Journal of Biogeography* 36: 1899-1912.
- Leprieur F, Tedesco PA, Beauchard BHO, Dürr HH, Brosse S, Oberdorff T. 2011. Partitioning global patterns of freshwater fish beta diversity reveals contrasting signatures of past climate changes. *Ecology Letters* 14: 325-334.
- Levin SA. 1992. The problem of pattern and scale in ecology. *Ecology* 73: 1943-1967.
- Lôbo D, Leão T, Melo FPL, Santos AMM, Tabarelli M. 2011. Forest fragmentation drives Atlantic forest of northeastern Brazil to biotic homogenization. *Diversity and Distributions* 17: 287-296.
- Marini L, Bertolli A, Bona E, *et al.* 2013. Beta-diversity patterns elucidate mechanisms of alien plant invasion in mountains. *Global ecology and Biogeography* 22: 450-460.
- Milliken W, Zappi D, Sasaki D, Hopkins M, Pennington RT. 2010. Amazon vegetation: how much don't we know and how much does it matter? *Kew Bulletin* 65: 691-709.
- Moro MF, Martins FR. 2011. *Métodos de levantamento do componente arbóreo-arbustivo*. In: Felfili JM, Eisenlohr PV, Melo MMR, Andrade LA, Meira Neto JAA. (eds.) *Fitossociologia no Brasil: métodos e estudos de caso*. Viçosa, Editora da Universidade Federal de Viçosa. p. 174-212.
- Moro MF, Lughadha EN, Filer DL, Araújo FS, Martins FR. 2014. A catalogue of the vascular plants of the Caatinga phytogeographical domain: a synthesis of floristic and phytosociological surveys. *Phytotaxa* 160: 1-118.
- Neri AV, Meira Neto JAA, Silva AF, Martins SV, Saporetti Junior AW. 2007. Composição florística de uma área de Cerrado *sensu stricto* no município de Senador Modestino Gonçalves, Vale do Jequitinhonha (MG) e análise de similaridade florística de algumas áreas de Cerrado em Minas Gerais. *Revista Árvore* 31: 1109-1119.
- Pennington TP, Lavin M, Oliveira-Filho A. 2009. Woody plant diversity, evolution, and ecology in the tropics: Perspectives from seasonally dry tropical forests. *Annual Review of Ecology and Systematics* 40: 437-457.
- R Development Core Team. 2012. R: a language and environment for statistical computing. Vienna, R Foundation for Statistical Computing. <http://www.R-project.org>
- Rahbek C. 2005. The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology Letters* 8: 224-239.
- Ratter JA, Bridgewater S, Ribeiro JF. 2003. Analysis of the floristic composition of the Brazilian cerrado vegetation III: Comparison of the woody vegetation of 376 areas. *Edinburgh Journal of Botany* 60: 57-109.
- Ribeiro JF, Walter BMT. 2008. As principais fitofisionomias do bioma Cerrado. In: Sano SM, Almeida SP, Ribeiro JF.(eds.) *Cerrado: ecologia e flora*. Brasília, Embrapa Informação Tecnológica. p. 151-199.
- Santos K, Kinoshita LS, Santos FAM. 2007. Tree species composition and similarity in semideciduous forest fragments of southeastern Brazil. *Biological Conservation* 135: 268-277.
- Scudeller VV, Martins FR, Shepherd GJ. 2001. Distribution and abundance of arboreal species in the Atlantic Ombrophilous Dense Forest in southeastern Brazil. *Plant Ecology* 152: 185-199.
- Sfenthourakis S, Panitsa M. 2012. From plots to islands: species diversity at different scales. *Journal of Biogeography* 39: 750-759.
- Silva DA. 2005. Levantamento do meio físico das Estações Ecológica e Experimental de Itirapina, São Paulo, Brasil. *Revista do Instituto Florestal* 17: 113-128.
- Tabarelli M, Mantovani W, Peres CA. 1999. Effects of habitat fragmentation on plant guild structure in the Montane Atlantic Forest of southeastern Brazil. *Biological Conservation* 91: 119-127.
- Tabarelli M, Peres CA, Melo FPL. 2012. The 'few winners and many losers' paradigm revisited: emerging prospects for tropical forest biodiversity. *Biological Conservation* 155: 136-140.
- Veech JA, Crist TO. 2009. PARTITION: software for hierarchical partitioning of species diversity, version 3.0. <http://www.users.muohio.edu/cristto/partition.htm>
- Vranken I, Baudry J, Aubinet M, Visser M, Bogaert J. 2015. Landscape ecology: heterogeneity, unpredictability, scale dependence and their links with thermodynamics. *Landscape Ecology* 30: 51-65.
- Whittaker RH. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* 30: 279-338.
- Whittaker RH. 1972. Evolution and measurement of species diversity. *Taxon* 12: 213-251.

