Space and time in Brazilian savannas: 14 years of spatio-temporal dynamics

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ABSTRACT – (Space and time in Brazilian savannas: 14 years of spatio-temporal dynamics)**.** Patterns in the relationships among the geographic range, abundance, and distribution of species within a biome are of fundamental interest in ecology and conservation. We studied the spatial and temporal patterns of species distribution in a Brazilian seasonal savanna. We used a data set consisting of 14 years of vegetation collection realized in a permanent plot located in a cerrado area at southeastern Brazil. The species abundance distribution did not fit the bimodal distribution predicted by the core-satellite species hypothesis. The species showed a unimodal distribution across all the years analyzed. 26 species from the 110 species we registered along the 14 years of collection were present in all the 14 years and were considered persistent. These persistent species were also the most locally abundant. From the 26 species considered persistent in our study, 17 of them are reported as commom (or abundant) and widespread considering the entire cerrado biome area. Two of them are reported as being commom (or abundant) only in the cerrados of São Paulo state, and 5 species considered persistent in our data set are assigned as not abundant nor widespread for the biome. We argue that the high alpha and beta diversity exhibited by some megabiodiverse tropical ecosystems, including the cerrados, leads to the unimodal distribution observed in our study area because these communities are often structured by a great number of low density and abundance species and a small number of high density and abundance species.

Keywords: core-satellite species hypothesis, local abundance, geographic range.

Introduction

The commonness and rarity of species in natural communities are recurrent topics in ecology and biogeography and are related to the species susceptibility to extinction, thus the understanding of these patterns has important implications to conservation biology.

Although the spatial component of natural communities and populations has been long studied, the temporal aspects of such a relationship have been rarely explored. There are some studies about the spatial structure assumed by populations and its implications on the community assembly (Hubbell 2001; McGill 2003a,b; Volkov *et al.* 2003; Connolly *et al.* 2005; Dornelas *et al.* 2006; McGill *et al.* 2006) but there are few studies that consider the temporal component of species distribution and there are even fewer that relate these temporal trends with the community spatial structure.

Many ecological patterns that are expressed over space are also observed over time (Blackburn *et al*. 1998) and this might also be true for abundance-distribution relationships (Hanski 1982; Brown 1984). In this case, the question would be: is the species frequency distribution bimodal and do abundant species occur frequently and less abundant species (or rare species) occur infrequently over time as well as over space? (Guo *et al.* 2000).

Several sets of data indicate that the average local abundance is positively correlated with regional distribution (Hanski 1982; Brown 1984; Gotelli & Simberloff 1987; Collins & Glenn 1990, 1991; Maurer 1990; Nee *et al*. 1991; Gaston 1996; Hanski & Gyllenberg 1993, 1997; Guo *et al*. 2000) and other studies demonstrated that plant communities exhibit a group of a few abundant species and another group composed by species with low population densities (Bock 1987; Gaston & Lawton 1989).

The Brazilian savanna-like ecosystem, also known as “Cerrado” biome, covers approximately 2 million km^2 in the central Brazil (about 22% of the country’s surface area) and is currently one of the most threatened biomes of South America due to the rapid agriculture expansion which converted about 35% of its total natural cover into planted pastures and crops (Oliveira & Marquis 2002).The biome has several physiognomies, changing from open grasslands with sparse shrubs and treelets, called “campo limpo” (clean field), to dense stratified forms with high trees and forest structure, named “cerradão” (woody savanna)and the overall biodiversity for the “Cerrado” biome, including all its physiognomic forms, is estimated at 160,000 species of plants, animals, and fungi. Endemicity of “cerrado” higher plants has recently been estimated at 4,400 species, representing 1.5% of the world’s total vascular plant species (Oliveira & Marquis 2002).

The spatial heterogeneity of plant populations and communities exerts great influence on the ecological theory and there are several models created to explain the variation in species abundance distribution in plant communities. One of them, called the “core-satellite species hypothesis” (hereafter CSS hypothesis) predicts a bimodal distribution in the species abundance rank (Hanski 1982).

The opportunity to assess abundance-distribution patterns over space and time is limited by the availability of consistent data sets. In this paper we investigate the temporal and spatial patterns of woody species distribution in the Brazilian savannas focusing on the relationships among their persistence over time, their local population abundances, and their distribution along the whole geographic space occupied by the biome to check whether the species abundance rank for our data fits the bimodal distribution predicted by the core-satellite species hypothesis and whether abundant species are more widely distributed in both space and time than rare ones.

We specifically aimed to answer the following questions: (i) Does the species abundance rank distribution for the Itirapina cerrado permanent plot fits the bimodal distribution predicted by the core-satellite species hypothesis ? (ii) are there persistent species over time in the Brazilian savannas ? (iii) These persistent species are the species with the greater geographic range over the entire biome ? (iv) These persistent species are the ones with the greater local abundance?

Materials and methods

We studied cerrado woody species distribution over time and space using two data sets. The first consisting of 14 years of vegetation data embracing a temporal series of 16 years realized in a permanent plot located at the Itirapina Experimental Station located at Itirapina municipality in São Paulo state at southeastern Brazil (FIGURE 1). The plot has 40 x 40 m (0.16 ha) divided into 64 sub-plots of 5 x 5 m. We sampled all individuals with diameter at ground level (DGL) greater or equal to 3 cm from 1994 to 2009 (except 1998 and 2000).

The second data set was compiled from Ratter *et al.* (2003) which analyzed the vegetation of 376 cerrado fragments distributed across all the country. We used those information to assess which species are geographically widespread and abundant across all the biome.

We constructed species abundance rank to assess the species distribution model assumed by the community along the years. We considered persistent a species that is present along the 14 years of sampling and we considered abundance as the fraction of the total sub-plots that the species was recorded. To express the local density we calculated the relative density for each species and then calculated the mean relative density for all the years.

Results

Species abundance distribution - The species abundance distribution for the cerrado permanent plot vegetation data did not fit the bimodal distribution predicted by the core-satellite species hypothesis. The species showed a unimodal distribution across all the years analyzed (FIGURE 2).

Persistence over time - A total of 110 species were registered along the 14 years of collection in the permanent plot. From those 26 species were present in all the 14 years (TABLE 1) and were considered persistent.

Abundant and widespread species - From the 26 species considered persistent in our study, 17 of them are reported as commom (abundant) and widespread by Ratter *et al.* (2003), 2 of them are reported as being commom (abundant) only in the cerrados of São Paulo state, and 5 species considered persistent in our data set are assigned as not abundant nor widespread by Ratter *et al.* (2003).

Persistence and local abundance - We calculated the relative density for each species to assess the relationship between temporal persistence and local abundance. First we calculated the relative density year after year and then we calculated a mean relative density considering all the years. The persistent species were also the most locally abundant (TABLE 3).

Discussion

It is widely reported in the scientific literature the multi-species coexistence phenomenon exhibited by some tropical ecosystems. The cerrado biome is considered a biodiversity hotspot (Myers *et al.* 2001) and may be considered a multi-diverse ecosystem because of its high alpha and beta diversity evidenced in the floristic list compiled by Ratter *et al.* (2003). His list presents us 951 species collected in 376 fragments across all the cerrado area. From those, 334 species (35%) were registered in only a single locality (unicates). Only 300 species (31.5%) occurred in more than 8 sites and surprisingly only 34 species (less than 4%) occurred in more than 50% of the sites considered in his study.

Those tropical communities always harbor a great number of low density (or “rare”) species on its community structure. In other words, the most part of the species in any sample made at any place at any time would consist in a great number of low density and abundance species while only a few would have high density and abundances.

Another explanation for the pattern, according to (Brown 1984), is that each species having a different center of distribution and consisting of a focal site (the center of the distribution) with high density and abundance and assuming consecutively lower density and abundance in the edges of the distribution range. Any sample plotted at any place would be sampling the center of the distribution of one species (the most abundant) and the edge of the distribution of several other species.

We concluded that the persistent species in the permanent plot in Itirapina are the most locally abundant species and are also the most abundant and widely

distributed species across all the cerrado biome.

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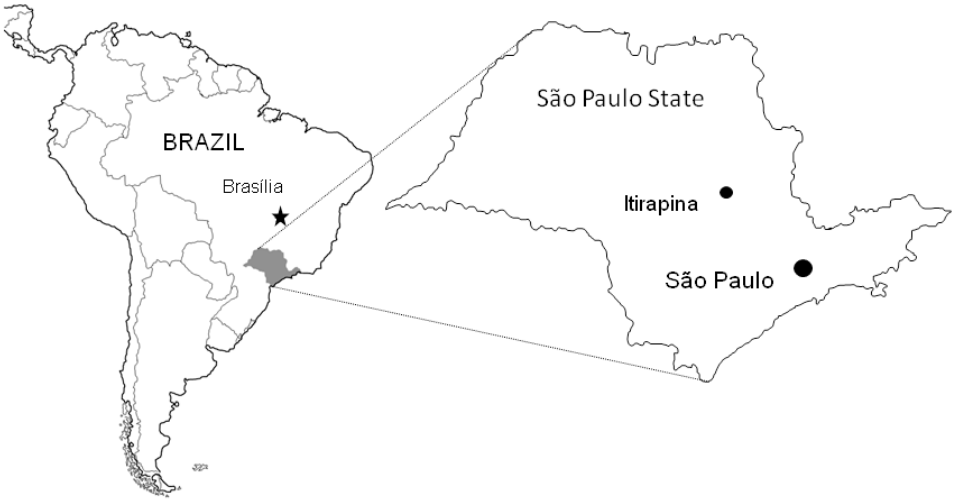

FIGURE 1. Location of the study area

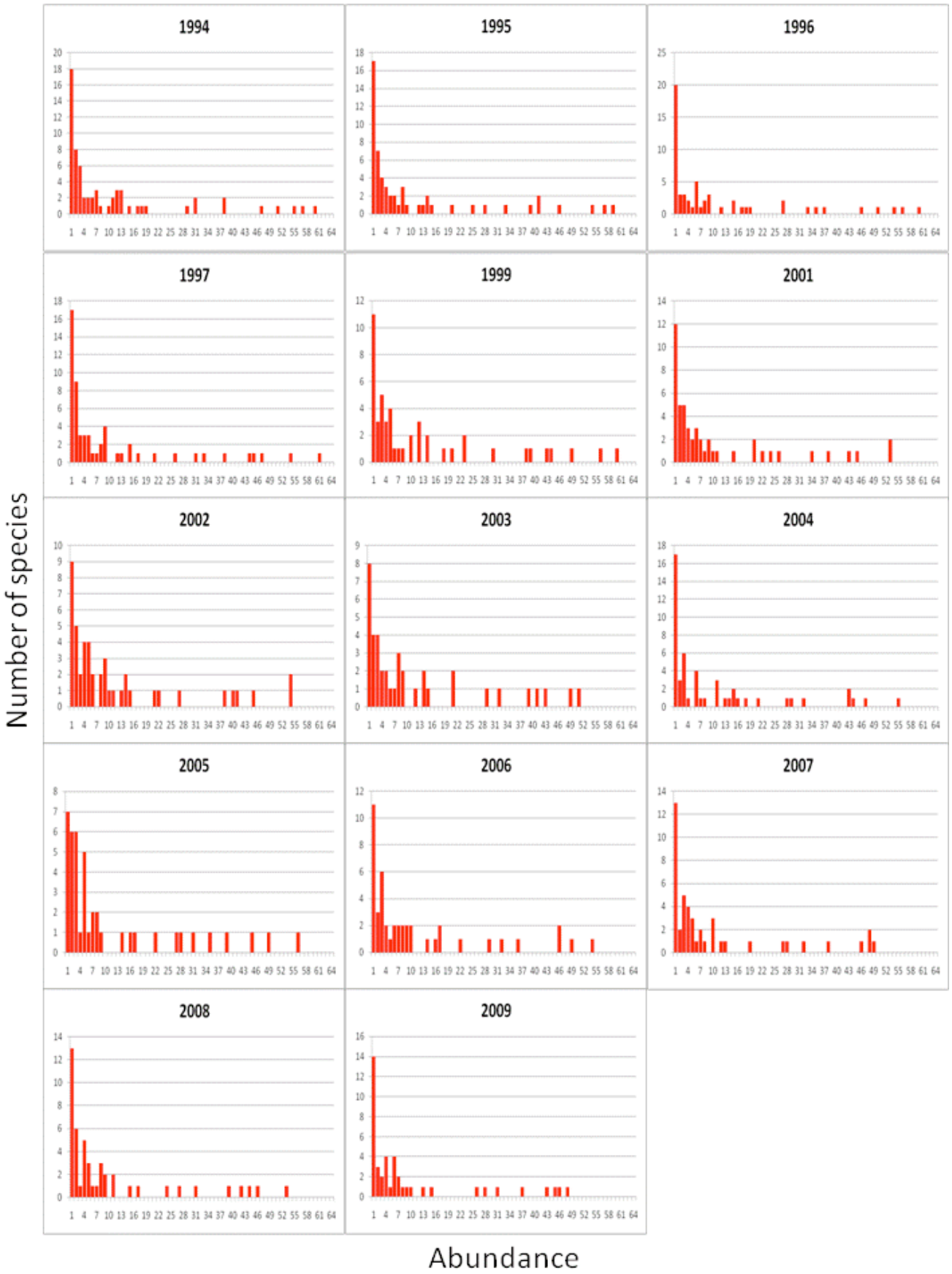

FIGURE 2. Species abundance distribution from 1994 to 2009 (except 1998 and 2000) for the cerrado permanent plot at Itirapina, southeastern Brazil.

TABLE 1. Temporal persistent species in the cerrado permanent plot at Itirapina, southeastern Brazil. Species in bold are reported as abundant and widespread by Ratter *et al.* (2003). * indicates species reported as commom in São Paulo state but not in the entire biome. ** indicates species assigned as not abundant nor widespread by Ratter *et al.* (2003). † indicates species not found in Ratter *et al.* (2003).

Species
Xylopia aromatica
Syagrus petraea †
Erythroxylum deciduum
Pera obovata *
Bauhinia rufa
Acosmium subelegans
Bowdichia virgilioides
Dalbergia miscolobium
Machaerium acutifolium
Anadenanthera falcata †
Ocotea pulchella **
Byrsonima coccolobifolia
Miconia albicans
Rapanea guianensis
Blepharocalyx salicifolius **
Eugenia punicaefolia **
Myrcia lingua **
Myrcia tomentosa
Guapira noxia
Ouratea spectabilis
Roupala montana
Amaioua guianensis *
Pouteria ramiflora
Pouteria torta
Qualea grandiflora
Vochysia tucanorum **

TABLE 2. Mean relative density rank for the 110 species collected in the cerrado permanent plot at Itirapina, southeastern Brazil. The persistent species are in bold. Mrd=mean relative density.

Species	Mrd
Vochysia tucanorum	0.144333519
Myrcia lingua	0.120515863
Roupala montana	0.100694746
Xylopia aromatica	0.070813649
Ocotea pulchella	0.069432190
Qualea grandiflora	0.066204257
Miconia albicans	0.065018493
Dalbergia miscolobium	0.061982364
Pouteria torta	0.044300418
Amaioua guianensis	0.035144301
Acosmium subelegans	0.020229333
Ouratea spectabilis	0.019665146
Syagrus petraea e/ou loefgrenii	0.019433118
Pouteria ramiflora	0.015258255
Anadenanthera falcata	0.014155869
Guapira noxia	0.013211114
Bowdichia virgilioides	0.010833179
Myrcia tomentosa	0.009841146
Aspidosperma tomentosum	0.008402491
Miconia rubiginosa	0.007299457
Bauhinia rufa	0.007192235
Byrsonima coccolobifolia	0.006065441
Eriotheca gracilipes	0.005923704
Tocoyena formosa	0.005391806
Eugenia punicaefolia	0.005389915
Byrsonima crassifolia e/ou pachiphylla	0.00434639
Pera obovata e/ou glabrata	0.003909875
Blepharocalyx salicifolius	0.003774955
Annona coriacea	0.003724012
Rapanea guianensis	0.003720655
Attalea geraensis	0.002965164
Machaerium acutifolium	0.002244212
Erythroxylum deciduum	0.00224389
Dyospiros hispida	0.002238445
Schefflera vinosa	0.002100684
Tabebuia ochracea	0.00157355
Stryphnodendron obovatum (ex polyphyllum)	0.001384351
Austroplenckia populnea	0.001322474
Byrsonima verbascifolia	0.00118031
Miconia pohliana	0.000930953
Ficus citrifolia e/ou guaranitica	0.000890421

Casearia sylvestris	0.000863141
Styrax camporum e/ou ferrugineus	0.000856852
Stryphnodendron adstringens	0.000704865
Asteraceae 1	0.000633714
Licania humilis	0.000618753
Strychnos pseudoquina e/ou brasiliensis	0.000609697
Kielmeyera variabilis e/ou coriacea	0.000553741
Qualea parviflora	0.000547659
Vernonia diffusa	0.00054725
Tapirira guianensis	0.0005122
Plathymenia reticulata	0.000461167
Eugenia bimarginata	0.000407387
Virola sebifera	0.000401794
Annona crassiflora	0.000323982
Erythroxylum tortuosum	0.000296261
Byrsonima crassa	0.0002775
Miconia stenostachya	0.000254107
Campomanesia pubescens	0.000239978
Siparuna guianensis	0.000239331
Eugenia pyriformis	0.000222
Dimorphandra mollis	0.000188552
Erythroxylum suberosum	0.000187518
Alophyllus edulis	0.000186498
Strychnos discolor e/ou bicolor	0.00017573
Palicourea rigida	0.000175626
Eugenia sp.1	0.000173868
Campomanesia sp.	0.000163577
Couepia grandiflora	0.000159767
Tibouchina stenocarpa e/ou stenostachya	0.000150716
Miconia fallax	0.000149833
Myrcia bella	0.000148756
Piptocarpha polymorpha e/ou rotundifolia	0.000146729
Aegiphilla lhotskyana	0.000143287
Ocotea corymbosa	0.000143287
Myrcia albotomentosa	0.000140272
Kielmeyera rubriflora	0.000135796
Eugenia pitanga	0.000127953
Connarus suberosus	0.000123739
Myrcia rostrata	0.000123739
Lacistema hassleriana	0.000123366
Campomanesia cambessedesiana	0.000109051
Eugenia bracteata	0.000109051
Qualea multiflora	0.000109051
Myrcia pallens	0.000103445
Miconia pepericapa	9.32488E-05
Calyptranthes lucida	9.32488E-05
Eugenia uniflora	9.32488E-05

Myrcia fallax	9.32488E-05
Banisteriopsis variabilis	8.2481E-05
Miconia regnelli	8.2481E-05
Eugenia florida	8.2481E-05
Eupatorium inulaefolium	8.06192E-05
Palicourea marcgravii	7.98977E-05
Banisteriopsis campestris	7.95418E-05
Eugenia livida	7.62311E-05
Magonia pubescens	7.16435E-05
Tabebuia aurea	6.92137E-05
Byrsonima intermedia	6.92137E-05
Rudgea viburnoides	6.92137E-05
Campomanesia adamantium	5.55001E-05
Didymopanax macrocarpum	4.97413E-05
Vernonia polianthum	4.97413E-05
Agonandra brasiliensis	4.97413E-05
Erythroxylum ambiguum	4.52653E-05
Miconia ligustroides	4.52653E-05
Calycorectes acutatus	4.52653E-05
Ouratea sp	4.52653E-05
Vochysia cinnamomea	4.52653E-05