Universidade Federal do Rio Grande do Sul
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Dissertação de Mestrado

Padrões funcionais de organização de árvores juvenis em manchas

florestais na Serra do Sudeste do Rio Grande do Sul

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Porto Alegre, fevereiro de 2011

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"O desafio apaixonante da pesquisa, a curiosidade científica cada vez mais aguçada, a interpretação do passado recente e remoto de nossos campos e florestas e, por fim, a constatação humilde de que, em se tratando do estudo da vida, estamos sempre começando."

Inês Bergmann Carlucci

AGRADECIMENTOS

SUMÁRIO

RESUMO

Uma das mais relevantes perspectivas que buscam explicar como as comunidades ecológicas se organizam é a teoria do nicho, que se divide em duas linhas de pesquisa com filosofias opostas. A primeira enfatiza que diferenças nas características funcionais de organismos permitem sua coexistência, enquanto que a segunda avalia até que ponto membros de uma mesma comunidade tendem a exibir similaridade em seus atributos funcionais. Uma variedade de métodos analíticos tem sido desenvolvida para avaliar mecanismos ligados a cada um dos processos. Explorando o padrão de distribuição de atributos de comunidades, a limitação de similaridade resulta em divergência de atributos, enquanto a ação local de filtros ambientais em geral produz convergência de atributos. Nesse sentido, o método para discriminação de padrões de organização por convergência ou por divergência de atributos no contexto de metacomunidades é de grande valor. Nesta dissertação, tal abordagem é utilizada para a avaliação de padrões de convergência e de divergência de atributos de plantas arbóreas juvenis em manchas florestais. Não incluímos informação filogenética ou de espécies a fim de avaliarmos até que ponto uma abordagem plenamente funcional pode explicar padrões de comunidades. O trabalho foi desenvolvido na Serra do Sudeste do RS, que consiste em um mosaico campo-floresta relativamente bem conservado. Algo instigante na Serra do Sudeste é a presença das coníferas *Araucaria angustifolia* (Bertol.) Kuntze e *Podocarpus lambertii* Klotzsch ex Endl. em várias manchas florestais, espécies reconhecidas como características da Floresta com Araucária do Planalto Sul-Brasileiro. Tal ocorrência vem sendo discutida há muitas décadas na literatura, mas nenhum estudo ecológico feito nessas áreas foi publicado ainda. Assim, nesta dissertação, tive como objetivos avançar na teoria relacionada à organização de comunidades e obter dados de qualidade para a avaliação continuada da

dinâmica ecológica por trás dos mosaicos campo-floresta com presença de *A. angustifolia* na Serra do Sudeste. Os resultados encontrados revelaram padrões tanto de convergência quanto de divergência de atributos. A abordagem inteiramente funcional utilizada neste trabalho foi muito útil para a inferência de prováveis mecanismos de nicho envolvidos na organização das comunidades de árvores juvenis. Nós defendemos que a análise de dados de atributos referentes ao nível de indivíduos em um contexto de metacomunidades é a melhor maneira de explorar diretamente como a convergência e a divergência de atributos realmente se comporta ao longo de um dado gradiente. Com relação ao limite austral da distribuição de *Araucaria angustifolia*, caso as áreas da Serra do Sudeste sejam consideradas nativas, haveria uma ocorrência disjunta da espécie e, talvez, do tipo vegetacional Floresta com Araucária. Esse tema é especialmente importante no que concerne a uma possível migração da espécie ou mesmo da flora típica da formação rumo ao sul, ou alternativamente a uma possível evidência remanescente de que a espécie ou mesmo de que a formação tenham ocorrido continuamente até essas latitudes, talvez há centenas de milhares de anos atrás. A resolução desse mistério, entretanto, provavelmente só seja alcançada através de estudos paleopolínicos e genéticos. De qualquer forma, tais áreas devem ser protegidas, já que seu desconhecimento por grande parte da comunidade científica facilita a negligência de sua conservação.

Palavras-chave: Microhábitat; Filtragem ambiental; Regras de montagem; Limitação de similaridade; Partição de nicho; Interação biótica; *Araucaria angustifolia*; Campos sulinos; Serra do Sudeste do Rio Grande do Sul.

ABSTRACT

Ecologists have considered niche theory one of the most relevant perspectives attempting to explain ecological community assembly. It is divided in two research programs with opposed philosophies. The first emphasises that differences in functional attributes of organisms enable their coexistence, whereas the second evaluate to which extent members of a same community tend to exhibit similarity regarding their functional traits. A variety of analytical methods have been developed for assessing mechanisms related to each of these processes. By exploring the trait distribution pattern in communities, it is generally accepted that the local action of environmental filters generates a pattern of trait convergence, whereas limiting similarity leads to trait divergence. In this sense, the method for discriminating trait-convergence and trait-divergence assembly patterns in the metacommunity context is of great value. In this dissertation, such approach is used for evaluating convergence and divergence patterns of tree sapling traits in forest patches in the *Serra do Sudeste* region of *Rio Grande do Sul* state, southern Brazil. We did not include phylogenetic or species identity information in the analysis since we wanted to evaluate to which extent an entirely functional approach could explain community patterns. The study was carried out in *Serra do Sudeste*, which consists of a forest-grassland mosaic relatively well conserved. Something puzzling in *Serra do Sudeste* is the presence of conifers such as *Araucaria angustifolia* (Bertol.) Kuntze and *Podocarpus lambertii* Klotzsch ex Endl. in several forest patches. These species are characteristic of the *Araucaria* forest occurring in the South-Brazilian Plateau. Such occurrence has been matter of a long-lasting debate in the regional literature, but no ecological study done in these areas has been published yet. In this dissertation I aimed at advancing on the theoretical bases of community assembly and at gathering data for

continuously evaluating the ecological dynamics of the forest-grassland mosaics with presence of *A. angustifolia* in *Serra do Sudeste*. The results revealed both trait convergence and divergence patterns, which indicated mechanisms for the assembly of tree sapling communities. The entirely functional approach applied here was very useful to infer probable mechanisms underlying community assembly. We argue that the use of individual-based trait information in a metacommunity context is the best way to directly explore how trait convergence and trait divergence behave along a given gradient. With regard to the austral boundary of *Araucaria angustifolia* distribution, if the patches of *Serra do Sudeste* are considered native, there would be a disjunct occurrence of the species and perhaps of the vegetational type *Araucaria* forest. This issue is especially important regarding a possible migration of the species or even of the typical associated flora southwards, or alternatively, regarding a possible relict evidence that the species had continuously occurred along such latitudes in a remote past. Nonetheless, the resolution of this puzzle probably only will be achieved through genetic and paleopollen studies. Anyway, such areas must be protected as their omission in important scientific studies facilitates the negligence of their conservation.

Key-words: Microhabitat; Environmental filtering; Assembly rules; Limiting similarity; Niche partitioning; Biotic interaction; *Araucaria angustifolia*; *Campos* grassland; *Serra do Sudeste*.

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Introdução geral.

Cápitulo 1.

INTRODUÇÃO GERAL

Apresentação

Desde o início do século XX, ecólogos têm buscado explicar como as comunidades ecológicas se organizam (Tansley 1920; Gleason 1926; Clements 1928). Desde então, duas visões conflitantes têm dominado a discussão sobre a natureza das comunidades (Keddy & Weiher 1999; Hubbell 2001): (i) a perspectiva de que as comunidades são organizadas pelas interações determinadas pelo nicho das espécies que as compõem e (ii) a perspectiva de que as comunidades são organizadas por padrões derivados da dispersão dos indivíduos. Dentro da perspectiva de organização pelo nicho, novamente há uma dicotomia que se originou de duas linhas de pesquisa com filosofias opostas (Grime 2006). A primeira escola tem antecedentes em Darwin (1859) e enfatiza que diferenças nas características funcionais de organismos e, em última análise, diferenças na exploração de recursos em comum pelos mesmos, permitem sua coexistência. Essa visão foi fortalecida com a proposição das teorias de limitação de similaridade (MacArthur & Levins 1967) e das 'regras de montagem' (do inglês *assembly rules*, Diamond 1975). No entanto, alguns autores recentemente afirmaram que apesar de o 'programa da coexistência' ser largamente utilizado em pesquisas de ecologia de comunidades e de ecossistemas, há uma carência de evidências diretas que validem a ocorrência de limitação de similaridade na natureza (Grime 2006; Siepielski & McPeek 2010). Por outro lado, a segunda escola tem raízes nos primeiros estudiosos da biogeogragia, sociologia e fisiologia de plantas [por exemplo, Alexander von Humboldt (1769-1859), Frederic Clements (1874-1945) e Eugenius Warming (1841-1924), respectivamente (ver McIntosh 1985)], e avalia até que ponto membros de uma mesma comunidade frequentemente

tendem a exibir similaridade em seus atributos funcionais (Grime 2006). Essa visão foi consolidada pela teoria de 'filtragem ambiental' (do inglês *environmental filtering*), em que variáveis ambientais funcionam como filtros ecológicos restringindo os tipos e valores de atributos ocorrentes sob sua ação (Keddy & Weiher 1999).

Dentro dessas duas perspectivas de organização de comunidades ecológicas pelo nicho, têm ocorrido avanços importantes representados por uma variedade de métodos analíticos para avaliar mecanismos ligados a cada um dos processos. Explorando o padrão de distribuição de atributos funcionais de comunidades, a divergência de atributos normalmente resulta de limitação de similaridade, enquanto que a convergência de atributos é uma consequência da ação local de filtros ambientais (Grime 2006; Wilson 2007). Nesse sentido, o método proposto por Pillar *et al.* (2009a) para discriminação de padrões de organização por convergência ou por divergência de atributos no contexto de metacomunidades é de grande valor. Nesta dissertação tal abordagem é utilizada para a avaliação de padrões de convergência e de divergência de atributos de plantas arbóreas juvenis em manchas florestais na Serra do Sudeste do Rio Grande do Sul. Mais especificamente, pretendeu-se (1) avaliar como tais padrões se relacionam a gradientes de abertura de dossel e de intensidade de pastejo em uma escala de microhábitat e (2) inferir os mecanismos de nicho potencialmente responsáveis pela organização das comunidades estudadas. Ressalta-se que o presente estudo é pioneiro em avaliar padrões de convergência e de divergência com dados de atributos coletados para todos os indivíduos registrados. Além disso, este é um dos primeiros trabalhos a testar empiricamente a abordagem de Pillar *et al.* (2009a), que é, até onde se sabe, o único método proposto que permite a avaliação simultânea de padrões de convergência e de divergência de atributos em um contexto de metacomunidades, ou seja considerando a

composição de organismos (ou de espécies ou grupos funcionais) e de seus atributos ao longo de comunidades dispostas em gradientes ambientais.

Sistema de estudo

O sul do Brasil é rico em mosaicos de ecossistemas nativos contrastantes, como campos e florestas (Overbeck *et al.* 2009). As florestas encontram-se de maneira geral dispostas ao redor das áreas campestres, criando campos insulares de diferentes tamanhos, bem como em manchas que acompanham cursos d'água ou que se distribuem isoladamente ao longo dos Campos (Rambo 1956). Os principais tipos florestais em contato com Campos são a Floresta com Araucária no Planalto Sul-Brasileiro e a Floresta Estacional na Serra do Sudeste do Rio Grande do Sul e demais regiões geomorfológicas do RS (Overbeck *et al.* 2009). Os Campos são ecossistemas remanescentes de um clima mais frio e seco, e com a tendência de mudança para um clima mais quente e úmido nos últimos três milênios, tem se observado uma progressiva expansão das florestas sobre os mesmos, pelo menos no Planalto Sul-Brasileiro e na Campanha oeste do RS (Behling *et al.* 2009). Há carência de evidência de expansão da vegetação lenhosa sobre a campestre para a região da Serra do Sudeste, mas considerando o padrão em mosaico campo-floresta e a tendência global de expansão da vegetação lenhosa sobre áreas campestres em latitudes subtropicais (Archer *et al.* 1988; Bond 2008), pode-se assumir que o fenômeno também ocorre na região.

O Rio Grande do Sul possui, segundo o Instituto Brasileiro de Geografia e Estatística e o Ministério do Meio Ambiente do Brasil (IBGE & MMA 2004), dois biomas: Pampa e Mata Atlântica. Ultimamente, a atenção conservacionista tem se focado no bioma Pampa (Overbeck *et al.* 2007; Pillar *et al.* 2009b) como resposta à crescente conversão dos campos

sulinos em ecossistemas antropizados como lavouras e plantios de árvores exóticas. Além do conhecimento incompleto da flora e vegetação campestre do sul do RS (Overbeck *et al.* 2009), pouco se sabe sobre a dinâmica e a diversidade das comunidades florestais que assumidamente se expandem nessa região. A Serra do Sudeste do RS (também chamada de Escudo Sul-Riograndense ou Escudo Cristalino), nesse sentido, representa um ótimo sistema para se estudar a dinâmica de organização de comunidades arbóreas, já que consiste em um mosaico relativamente bem conservado de campos manejados principalmente com gado bovino e ovino e de florestas estacionais em manchas insulares, em galeria ou em encostas úmidas.

Algo instigante na Serra do Sudeste é a presença das coníferas *Araucaria angustifolia* (Bertol.) Kuntze e *Podocarpus lambertii* Klotzsch ex Endl. em várias manchas de Floresta Estacional (onde atingem a latitude 31° S), espécies que são amplamente reconhecidas como características da Floresta com Araucária do Planalto Sul-Brasileiro (até a latitude 29.5° S). Tal ocorrência vem sendo discutida há muitas décadas na literatura (Lindman & Ferri 1974). Surpreendentemente, nenhum estudo ecológico feito nessas áreas foi publicado ainda, mas alguns autores pelo menos citam essas manchas (Reitz, Klein & Reis 1983; Leite 2002; Dutra & Stranz 2003). A localidade da Serra dos Pereiras em Santana da Boa Vista (cerca de 30.8°S, 53.1°W) foi escolhida para o estudo por apresentar um mosaico de campo nativo e florestas bem conservado (Fig. 1). Localmente, *A. angustifolia* e *P. lambertii* são as árvores mais evidentes na paisagem, dominando os dosséis da maioria das manchas florestais (Fig. 2), embora em um levantamento rápido tenha se registrado 74 espécies de angiospermas arbóreas (Carlucci & Bergamin, dados não publicados).
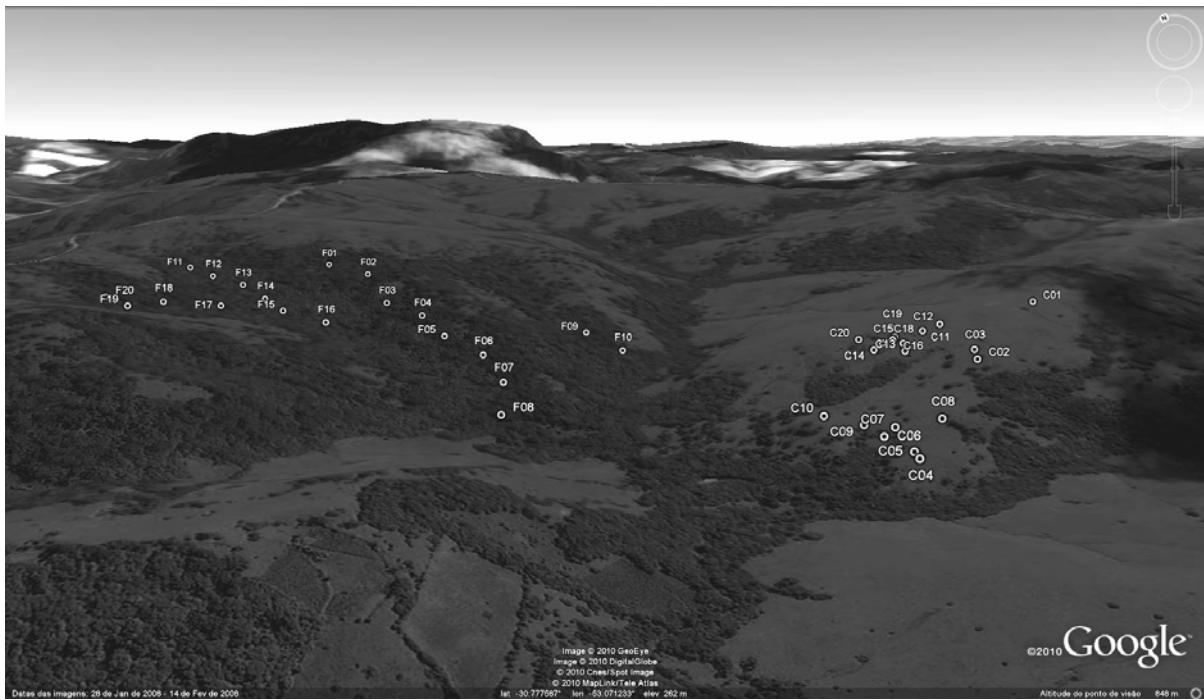
Fig. 1. Floresta Estacional com presença de *Araucaria angustifolia* (Bertol.) Kuntze e *Podocarpus lambertii* Klotzsch ex Endl.em mosaico com campo nativo, Santana da Boa Vista, sul do Brasil.

Fig.2. Paisagem da área de estudo, mostrando manchas florestais com presença de *Araucaria angustifolia* (Bertol.) Kuntze e *Podocarpus lambertii* Klotzsch ex Endl., em contato com campo nativo, Santana da Boa Vista, sul do Brasil.

Portanto, nesta dissertação, tive como objetivos avançar na teoria relacionada à organização de comunidades de plantas arbóreas juvenis e obter dados de qualidade para a avaliação continuada da dinâmica ecológica por trás dos mosaicos de campo e florestas estacionais com presença de *A. angustifolia* na Serra do Sudeste.

CAPÍTULO 1. Individual-based traits of tree saplings reveal convergence and divergence assembly patterns related to gradients in forest patches*

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Running headline

Convergence and divergence of tree sapling traits

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Summary

1. Niche theory is divided in two research programs with opposed philosophies: the first evaluate to which extent members of a same community tend to exhibit similarity regarding their functional traits, whereas the second emphasises that differences in functional attributes of organisms enable their coexistence. By exploring trait distribution pattern in communities, it is generally accepted that the local action of environmental filters generates trait-convergence assembly pattern (TCAP), whereas limiting similarity leads to trait-divergence assembly pattern (TDAP).

2. In this manuscript, we evaluate TCAP and TDAP of tree saplings in forest patches in relation to ecological gradients in a microhabitat scale and infer niche-mechanisms potentially responsible for community assembly.

3. For this, we used individual-based trait information of 1132 tree saplings occurring in 40 plots placed along gradients of canopy openness and grazing intensity in forest patches in southern Brazil. We did not include phylogenetic or species identity information in our analyses to evaluate to which extent an entirely functional approach could explain community patterns.

4. The results revealed both TCAP and TDAP, which indicated niche mechanisms for the assembly of tree sapling communities. Specific leaf area (SLA), leaf area (LA) and relative abundance of toothed leaf margin (TM) maximised TCAP. SLA and TM presented a tendency of increasing under more closed canopies, whereas LA presented higher values in intermediate proportions of canopy openness. SLA and LA maximised TDAP and tended to vary more in more closed canopies, whereas SLA and SP that also maximised TDAP presented higher variation under lower grazing intensity.

5. *Synthesis*. The entirely functional approach we used here was very useful to infer niche mechanisms involved in tree sapling assembly in forest patches. By adopting an individual-based trait approach we assumed that both intra-specific and intra-population trait variability were relevant for revealing the assembly patterns. Therefore, we argue that, besides the great value for interpreting trait convergence, the use of individual-based trait data in a metacommunity framework is the best way to directly explore how trait divergence actually behaves along a gradient and to localise exactly in which part or parts of the gradient higher variation of such trait is occurring.

Introduction

Ecologists have historically developed theories to explain ecological community assembly, which may be divided in two mainstreams (Keddy & Weiher 1999; Hubbell 2001): (i) the perspective that communities are assembled by the interactions determined by the niche of organisms and (ii) the perspective that communities are assembled by patterns derived from organism dispersal. The former approach aims to search for the niche-mechanisms underlying community patterns, both those mediated by the environment and those determined by biotic interactions (Keddy 1992). Basically, starting from a regional or local pool of species (Zobel 1997) carrying different sorts of traits, the action of environmental filters constrains the types and values of traits that will compose local communities (van der Valk 1981; Keddy & Weiher 1999). Considering that only organisms having similar traits will remain in a given site, environmental filtering causes convergence of traits (Weiher & Keddy 1995; Grime 2006; Funk *et al.* 2008). As a contrary force, competition is expected to cause trait divergence since coexisting organisms that present high similarity in ecological requirements are likely to face competitive exclusion (MacArthur & Levins 1967; Wilson 1999). Another mechanism that tends to generate trait divergence is the diverse defence traits plants exhibit when disturbances are common in their habitats (Grime 2006). As a consequence of the two opposing forces, local communities may exhibit both trait-convergence and trait-divergence assembly patterns (Pillar *et al.* 2009). In synthesis, niche theories are based upon the responses of organisms to resource availability, environmental conditions and biotic interactions (Keddy & Weiher 1999; Wilson 1999). Taking into account that these responses vary spatially, niche-based community assembly patterns are in great extent the result of environmental gradients (Ackerly 2003; McGill *et al.* 2006).

In community ecology, functional traits are operationally defined as those traits that respond to the environment and/or have effects on ecosystem functioning (Diaz & Cabido 2001). Since the 1990s, ecologists have done great efforts in compiling species' mean traits for sites around the globe and in comparing functional patterns along regional and macroecological gradients (e.g. Reich, Walters & Ellsworth 1997; Wright *et al.* 2004). Recently, many community ecologists became interested in evaluating mechanisms underlying community assembly in the microhabitat scale (e.g. Ackerly & Cornwell 2007; Cianciaruso *et al.* 2009; Gross *et al.* 2009; Albert *et al.* 2010; Baraloto *et al.* 2010), which may be viewed as a middle way between community ecology and ecophysiology. Indeed, some authors have pointed out the need of using a concept of functional traits closer to the ecophysiological and the evolutionary perspectives (McGill *et al.* 2006; Violle *et al.* 2007). In this sense, the definition of functional traits by Violle *et al.* (2007) is of great value: "the morpho-physio-phenological traits which impacts fitness indirectly via their effects on growth, reproduction and survival". To put such approach in practice, traits must be collected in a proper scale, such as at the individual level or at least at the population level (Lavorel *et al.* 2007; Baraloto *et al.* 2010). Here, we use the Violle and collaborator's functional trait definition (Violle *et al.* 2007) in a context of environmental gradients.

Much effort has been made to explain the assembly of tree sapling communities in a variety of forest ecosystems (e.g. Nicotra, Chazdon & Iriarte 1999; Gilbert *et al.* 2006; Lusk, Chazdon & Hofmann 2006). Light availability is one of the most important factors determining assembly of sapling communities (Wright 2002), having effect on plant survival and growing (e.g. Walters & Reich 1996). Light has been found to impact directly leaf traits such as leaf area (LA) and specific leaf area (SLA) or its inverse, leaf mass per area (Westoby 1998; Lusk & Warton 2007). SLA is one of the most important traits for plant performance

(Diaz *et al.* 2004) as it represents a trade-off between acquiring light for photosynthesis, i.e. having high LA, and building more protected leaf tissues to resist herbivory and water deficit, i.e. having thick leaves (Westoby 1998; Wilson, Thompson & Hodgson 1999) (Table 1). Herbivory and particularly cattle grazing may also play a major role in the distribution of plant functional traits in communities (Blanco *et al.* 2007). For instance, grazing may cause dominance of spiny and/or unpalatable plants, as cattle often avoid eating such plants (Howe & Westley 1988) (Table 1).

In the last years, many important analytical trait-based frameworks have been created for assessing patterns of community assembly (e.g. Ackerly & Cornwell 2007; Gross *et al.* 2009). However, these approaches usually do not encompass simultaneous evaluation of patterns derived both from environmental filtering and from biotic interactions along ecological gradients. In this sense, the method proposed by Pillar *et al.* (2009) for discriminating trait-convergence and trait-divergence assembly patterns in a metacommunity framework is of great value. The approach permits the assessment of such patterns using traits measured at the individual scale. Thereby, in this manuscript, we aimed (1) to evaluate functional trait-convergence and trait-divergence assembly patterns of tree saplings in forest patches in relation to ecological gradients in a microhabitat scale and (2) to infer niche-mechanisms potentially responsible for the assembly of the studied communities by using Pillar and collaborators' framework (Pillar *et al.* 2009). For this, we (1) recorded information on traits that are expected to respond to environmental gradients and also to influence plant fitness (Table 1) for each tree sapling individual in 40 plots located in forest patches and (2) measured variables that are indicators of ecological gradients acting at the plot scale (Table 2). In order to assess to which extent an entirely functional approach can explain community patterns, we did not consider species identity or phylogenetic information. We hypothesised

(1) that sapling communities under more opened canopies tend to present lower SLA and LA values but higher proportion of individuals with leaf trichomes; and (2) that sapling communities under lower grazing intensity tend to have a lower proportion of spiny individuals (Table 2).

Materials and methods

STUDY AREA

Data collection was conducted in a forest-grassland mosaic (ca. 30.8ºS, 53.1ºW) located in Santana da Boa Vista municipality, in the region of *Serra do Sudeste*, a geomorphologic complex located in southernmost Brazil. The local climate between 1950 and 2000 was characterised by mean annual rainfall of 1473 mm and mean annual temperature of 18.3 ºC; during this period, mean precipitation of the wettest quarter of the year was 416 mm and mean precipitation of the driest quarter of the year was 332 mm (Hijmans *et al.* 2005). The bedrock consists of gneiss (Dutra & Stranz 2003). The regional vegetation is a mosaic formed by *Campos* grassland and seasonal forests (Pillar & Quadros 1997; Jurinitz & Jarenkow 2003; Oliveira-Filho, Jarenkow & Rodal 2006; Overbeck *et al.* 2007). Locally, forests spread mainly along valleys and moist slopes, appearing also as isolated small patches scattered in the grassland matrix. The conifers *Araucaria angustifolia* (Bertol.) Kuntze and *Podocarpus lambertii* Klotzsch ex Endl. are the most evident trees in the landscape, dominating the canopies of most patches, although 74 angiosperm tree species were also registered locally (Carlucci & Bergamin, unpublished data). The vast majority of these angiosperms are evergreens (Carlucci *et al.*, unpublished data). The presence of *A. angustifolia* and associated species, which are widely acknowledged to naturally occur in the southern Brazilian plateau (up to latitude 29.5º S), in the forests of *Serra do Sudeste* (up to 31º S) is matter of a regional

scientific debate that has already lasted many decades (Lindman & Ferri 1974). Surprisingly, no ecological study done in these areas has been published yet, although few authors have at least cited these patches (Reitz, Klein & Reis 1983; Leite 2002; Dutra & Stranz 2003). Management of grasslands in the study area has traditionally consisted of extensive grazing by domestic cattle, which use large forest patches for shelter and forage in the colder season (April-August). By the time of data collection, there were no evidences of burning or harvesting done in the previous years. Basically, the study area comprised two slopes, the first (hereafter *grassland slope*) consisted of a grassland matrix containing a great amount of small forest patches (area = 90 ± 23 m^2) and the second (hereafter *forest slope*) was almost totally formed by a single large forest patch of ca. 35 ha.

SAMPLING DESIGN

We collected data on the distribution of tree saplings in forest patches from January to October 2010. We disposed 40 circular plots (4.5 ± 0.1 m^2) along forest patches in different stages of succession in order to capture the highest variation of the environmental gradient. Considering that the small forest patches scattered in the *grassland slope* represented initial stages of forest succession and that the forest interior in the *forest slope* constituted more advanced stages of succession, we placed half of the plots in small patches located in the *grassland slope* and another half in the *forest slope*. We first recorded with a GPS device the geographical coordinates of all existing patches in the *grassland slope*. Next, we selected at random twenty of these patches. In each elected forest patch, we settled one circular plot centered in the largest tree of the patch. For delimiting the circular plot, we used an 1-m radius around the plot focal tree. Since focal trees presented varying basal areas, we registered their perimeters to calculate actual plot sizes *a posteriori*. Our plot areas were then obtained

by subtracting the basal area of the focal tree from the area of the circle having radius equal to the tree radius plus 1 m. In the *forest slope*, we marked two transects for the location of plots using a satellite image, avoiding close proximity with streams. The distance range of each plot to the edge with grassland was 25-142 m. We defined the spatial coordinates of the 20 plots in the satellite image. In the study area, we marked the actual plots in the forest interior using the previously-defined spatial coordinates. Circular plots of the *forest slope* were delimited in the same manner as those of the *grassland slope*, but were centered in the largest tree within a radius of 10 m from the previously-defined spatial coordinate in the forest interior. Minimum distance between two plots of the *forest slope* was 50 m. In each plot, we recorded all tree sapling individuals (15-100 cm tall). Overall, 1132 saplings were sampled in a plot total area of 180 m^2. For the analysis these data were arranged in a binary matrix (**W**) of saplings by plots, in which, by definition, each sapling occurred only once.

TREE SAPLING TRAITS

For each sapling individual, we measured traits (Table 3) expected to respond to gradients of canopy openness (and correlated microclimate conditions) and grazing intensity (Table 2) and to affect sapling performance (Table 1). For each sapling, six expanded leaves without evidence of herbivory were collected; when less than six leaves under this condition were available, all leaves were collected. We considered leaflets as laminar units for compound leaves (Baraloto *et al.* 2010). Since neither area meters nor scanners were available at the field, we proceed the following steps to measure fresh mean leaf areas (LA): in the field (1) placing a white paper over the plant leaves to be drawn, and (2) drawing with a wax-pencil the area exactly on the plant leaf to obtain the precise leaf counter-print; in the lab (3) cutting with scissors the leaf draws to obtain precise leaf replicates, (4) scanning leaf draws and (5)

measuring LA using the software ImageJ (by W. Rasband, v1.43u available at http://rsb.info.nih.gov/ij). We compared areas obtained from the actual plant leaves and their correspondent draws; the correlation between values generated from the methods was very high and significant ($r = 0.999$ and $P = 0.0001$), showing that the draw method of measuring LA is accurate. After proper drying, the collected leaves were weighed for SLA calculation. Since the study area was distant ca. 300 km from the laboratory, we maintained all leaves in silica gel from the time of collection until the time of weighing. In the laboratory, we oven-dried the collected leaves under 60^oC during 96 h. For obtaining mean SLA of a sapling s, we divided total area of the collected leaves of s by the total dry mass of the collected leaves of s. Studies have found that ontogeny may influence SLA of juveniles, especially of deciduous plants (Lusk & Warton 2007). We decided not to remove the influence of ontogeny on SLA and LA from our analyses, since the vast majority of our individuals were evergreens and ontogeny explained a low and negligible portion of SLA and LA variation (linear regressions of SLA and LA on sapling height generated $R^2 = 0.07$ and $R^2 = 0.02$, respectively). The data for the other sapling traits, namely presence of trichomes, compound leaves, toothed leaf margins and spines, were recorded in the field. We regarded trichomes or toothed margins as present when they could be easily seen or felt by touch. These binary traits together with the two quantitative traits, SLA and LA (Table 3), composed a matrix describing sapling individuals by their traits (matrix **B**).

ENVIRONMENTAL GRADIENTS

For describing environmental gradients acting at the sapling microhabitat scale, we measured proxy environmental variables related to gradients of light availability, grazing intensity and microclimate (Table 2). For obtaining canopy openness data, we took hemispheric photos

using a digital camera (Nikon CoolPix 995[®], Tokyo, Japan) with fisheye lens (Nikon FC-E8[®], Tokyo, Japan) in each plot. Canopy openness was calculated using the software GapLight Analyzer v. 2.0 by Frazer, Canham and Lertzman (Simon Fraser University, Burnaby, British Columbia, Canada, and the Institute of Ecosystem Studies, Millbrook, New York, USA; available at http://www.ecostudies.org/gla/). The data for canopy openness proportions in the plots were arranged in a univariate matrix $\mathbf{E_C}$. We used density of cattle faeces near plots as an indication for intensity of habitat use by cattle. Assuming that intensity of habitat use by cattle and grazing intensity are positively correlated, we used the density of cattle faeces around each plot (number of faeces . m^{-2}) as a proxy for grazing intensity. Data of grazing intensity were arranged in a univariate matrix $\mathbf{E_G}$. Microclimate variables were measured during few days for differentiating very contrasting plots and for evaluating correlations between microclimate and canopy openness (Table 2). We used 20 dataloggers (Novus LogBox-RHT[®], Novus Produtos Eletrônicos Ltda, Porto Alegre, Brazil) to measure microclimate variables (maximum and minimum air temperature and relative moisture) in two periods of three days (one in March 2010 and another in April 2010). In each period, we arranged the dataloggers along 10 plots of the *grassland slope* and 10 plots of the *forest slope*. After, we statistically removed the influence of period on the microclimate variables by using the residuals of regressions of each microclimate variable on period (as dummy variables). The residuals were used as microclimatic variables of the plots.

DATA ANALYSES

 We used the method proposed by Pillar *et al*. (2009) for discriminating trait-convergence and trait-divergence assembly patterns in a metacommunity framework (hereafter generically referred to as 'functional analysis'), which is synthetically explained below. In each step of

functional analysis, matrices **B** (sapling individuals described by their traits), **W** (sapling occurrence in communities, after standardisation by plot totals) and each of the **E** matrices describing environmental gradients (canopy openness, grazing intensity) were used. A matrix of similarities between saplings (matrix $\mathbf{S_B}$) was obtained from matrix **B** (for this we adopted the Gower index, Gower 1971). After the standardisation by row totals of $\mathbf{S_B}$, such similarities defined degrees of belonging of each sapling i in the fuzzy sets defined for each sapling $j = 1$ to s saplings (matrix **U**). **U** is thus a matrix of fuzzy sets defined by the trait similarities between saplings. Next, matrices were multiplied as follows: **B'W**, generating a matrix **T** composed of mean traits by communities, and **U'W**, resulting in a matrix **X** containing communities described by the saplings taken as fuzzy sets. Using each of the matrices **T**, **X** and **E**, we computed pairwise resemblance matrices between communities: $\mathbf{D_T}$, $\mathbf{D_X}$ and $\mathbf{D_E}$, respectively. For this we adopted chord distances for $\mathbf{D_X}$, and Euclidean distances for $\mathbf{D_T}$ and $\mathbf{D_E}$ (after proper standardisation of traits by unit length in matrix **T**). The correlation $\rho(\mathbf{TE})$ between matrices $\mathbf{D_T}$ and $\mathbf{D_E}$ is a measure of trait convergence related to the variation in **E**, whereas the correlation $\rho(\mathbf{XE})$ between matrices $\mathbf{D_X}$ and $\mathbf{D_E}$ indicates both convergence and divergence of traits related to the variation in **E**. To disclose how much of trait divergence is expressed in **X**, the trait-convergence component involved in the correlation between $\mathbf{D_X}$ and $\mathbf{D_E}$ is removed by partial Mantel correlation ($\rho(\mathbf{XE.T})$). For more details on the method, see Pillar *et al*. (2009).

We performed separated functional analyses for the canopy openness gradient and for the grazing intensity gradient; i.e. by using matrix $\mathbf{E_C}$ or $\mathbf{E_G}$ as the environmental matrix. Before each of these, by using the iterative method developed by Pillar & Sosinski (2003), we searched for traits maximising (1) trait-convergence ($\rho(\mathbf{TE})$) and (2) trait-divergence ($\rho(\mathbf{XE.T})$). Then, for each gradient we used only the trait set that maximised the concerning

pattern (convergence or divergence). The statistical significances of convergence and divergence patterns were tested against null models (Pillar *et al.* 2009). Functional analyses were carried out using the software SYNCSA (by V. Pillar, v. 2.6.9 available at http://ecoqua.ecologia.ufrgs.br).

We performed PCA ordination on the six environmental variables, namely canopy openness, grazing intensity, maximum and minimum air temperature and relative moisture, in order to explore the structure of environmental gradients. We tested for the stability of the first PCA axis through bootstrap resampling (Pillar 1999). We also tested for correlations between pairs of environmental variables. Correlation *P*-values were obtained using randomisation tests. We applied PCoA ordination to matrix **T** for interpreting convergence patterns related to the concerning ecological gradient. We also used linear regressions of the community mean traits maximising convergence and linear regressions of the functional diversity (Rao entropy) of trait sets maximising divergence on the concerning ecological gradient. Regression *P*-values were obtained using randomisation of the response variable (Manly 2007). To better visualise both convergence and divergence patterns, we plotted SLA values of all saplings against the ecological gradient. PCA, PCoA, correlations and regressions were performed using statistical software MULTIV (by V. Pillar, v. 2.67β available at http://ecoqua.ecologia.ufrgs.br).

Results

Minimum air relative moisture was related to more closed canopies, whereas maximum air temperature and grazing intensity were related to more opened canopies (Fig. 1). The environmental variables that were significantly correlated with canopy openness were (Table

2): grazing intensity ($r = 0.51$, $P = 0.001$), maximum temperature ($r = 0.75$, $P = 0.001$) and minimum moisture ($r = -0.77$, $P = 0.001$).

We found both convergence and divergence patterns of sapling traits related to the canopy openness gradient (Table 4). SLA and LA as well as the proportion of individuals presenting toothed leaf margin (hereafter TM relative abundance) were the traits responsible for maximisation of the convergence pattern related to canopy openness (Table 4, Fig. 2). Higher values of SLA and TM relative abundance were related to more closed canopies, whereas lower values of these traits were related to more opened canopies (Fig. 2). Indeed, there was a clear tendency of decreasing community-level averaged SLA and TM relative abundance with increasing canopy openness (Fig. 3a, c). Alternatively, higher community-level averaged LA seemed to be related to intermediate proportions of canopy openness (Fig. 2) so that a quadratic regression was the best model to represent its pattern in relation to the gradient (Fig. 3b).

All measured traits were important in maximising the divergence of sapling traits related to the canopy openness gradient (Table 4). Other trait sets also generated high values of TDAP and were composed of three or more traits but did not add information in relation to the first maximising trait set (all traits) (Appendix 1). In order to better explore patterns and facilitate understanding of TDAP, we chose two maximising sets with TDAP Mantel correlation ($\rho(\mathbf{XE.T})$) higher than 0.20 and containing as fewer traits as possible (Appendix 1). Such trait sets were: SLA, SP ($\rho(\mathbf{XE.T}) = 0.36$) and SLA, LA ($\rho(\mathbf{XE.T}) = 0.23$). Taking all traits, a divergence pattern was evident from closed to opened canopies as indicated by functional diversity (Fig. 4a), that is, functional diversity decreased along this gradient. Considering the maximising set composed by SLA and SP, there was a slight tendency of

decreasing functional diversity with increasing canopy openness (Fig. 4b). For the SLA and LA trait set, there was a clear tendency of divergence along the canopy gradient (Fig. 4c).

Open forest patches presented only saplings with low SLA, typically lower than ca. 350 $cm^2.g^{-1}$ (Fig. 5). This pattern consists of a clear convergence for low SLA under highly opened canopies, i.e. more than ca. 18 % of canopy openness. On the other hand, both low and high values of SLA were found under more closed canopies (Fig. 5). Although it seems to there be high variation of SLA within communities under shade, which would result in divergence along the gradient, this is not true, as SLA alone did not maximise TDAP ($\rho($**XE.T**$) = -0.03$, $P = 0.94$). Rather, SLA alone maximised TCAP (Fig. 3).

We found no significant pattern of trait convergence or divergence related to grazing intensity gradient (Table 4).

Discussion

CONVERGENCE AND DIVERGENCE PATTERNS AT THE METACOMMUNITY SCALE

Overall, trait-convergence and trait-divergence assessment along environmental gradients permits simultaneous evaluation of the several mechanisms explaining community assembly (Grime 2006). Specifically, effects of environmental variables as ecological filters are expected to lead to trait convergence, whereas effects of environmental-structured biotic interactions and of disturbance mechanisms may lead to trait divergence (Ackerly 2003; Grime 2006; McGill *et al.* 2006; Wilson 2007). In this sense, our results indicate that light availability as well as biotic interactions and/or disturbance mechanisms such as those linked to grazing intensity were important for the assembly of the sapling communities. It is important to say, the method we used here works on a metacommunity scale (Pillar *et al.*

2009), although the mechanisms responsible for the patterns scaled-up to the metacommunity act in a community, microhabitat scale. Considering this, trait convergence within communities may be observed in one part of the gradient whereas limiting similarity may act in another part of the gradient, resulting in both TCAP and TDAP at the metacommunity level (Pillar & Duarte 2010).

By averaging trait data per community, we were able to explore convergence along the gradient (Pillar *et al.* 2009). Looking at our community-level resulting patterns, we may say that low SLA, i.e. small LA in relation to a high leaf dry mass, enables plants to establish in forest patches with open canopies. On the other hand, high SLA, i.e. large LA in relation to low leaf dry mass, enables plants to establish under closed canopies, such as of the interior of our large patch, where the low light levels are likely to limit plant growth and survival (Clark & Clark 1992). But how saplings with low SLA also managed to establish under low light conditions? We discuss this later. Leaf toothed margins (TM) are considered an adaptation to very low temperatures (Table 1), as this trait increases transpiration and photosynthate production early in the growing season (BakerBrosh & Peet 1997; Royer & Wilf 2006). Our system indeed presents two marked seasons, one hotter and another colder. However, why was TM relative abundance higher under more closed canopies is not clear for us yet. The first inference regarding SLA, LA and TM patterns would be that environmental filtering related to canopy openness is probably determining convergence of sapling traits in parts or at least in one part of the gradient.

We assessed how divergence behaved along the gradient through regressions of functional diversity taking into account different trait sets maximising TDAP on canopy openness. Overall, the tendency of divergence taking all the traits may indicate limiting

similarity occurring more strongly in communities under more closed canopies, as suggested in Fig. 4a. Nonetheless, it is not easy to interpret how limiting similarity is acting to generate niche partitioning when we evaluate a set composed by six traits having different influences on plant performance. In this sense, the patterns arising in Fig. 4b and c are much clearer. Divergence of SLA and SP may be related to grazing intensity correlated with canopy openness, while divergence of SLA and LA may be an outcome of biotic interactions such as competition for the light resource correlated with canopy openness. We discuss these topics more deeply later.

CONVERGENCE OF TREE SAPLING TRAITS RELATED TO CANOPY OPENNESS

Higher values of community-level averaged LA were related to intermediate proportions of canopy openness. Overall, survival of plants with high LA is likely to be limited in open areas, since we may expect that large leaves dehydrate in hot and dry conditions. Indeed, only plants having low SLA managed to colonise open forest patches (Fig. 5), especially those where canopy is ca. 18 % or more opened. Such pattern probably results from a strong environmental filtering. Variables we found to be correlated with canopy openness such as air maximum temperature and air relative minimum moisture probably influence the pattern of SLA convergence in more opened canopies. Hotter and dryer microhabitats, under open canopies of small forest patches, may limit survival of plants having high SLA, as they possibly dehydrate under such conditions, whereas milder and moister microhabitats, under closed canopy of large patch interiors, seem not to limit survival of saplings up to 1 m tall irrespective of their SLA.

Canopy openness is usually taken as an indirect measure of light availability (Nicotra, Chazdon & Iriarte 1999). Light availability is widely acknowledged as a main factor

explaining tree sapling community assembly in forest understorey (Clark & Clark 1992; Nicotra, Chazdon & Iriarte 1999; Lusk, Chazdon & Hofmann 2006). Assuming that light availability and ultimately photosynthetically active radiation (PAR) are positively correlated with canopy openness, we can attribute to their variation along plots the patterns we have found, mainly those related to SLA and LA. Accordingly, the convergence of low SLA values observed in sapling communities under more opened canopies might be explained by the high light reaching such microhabitats. Generally, plants with lower SLA have thicker laminas (Wilson, Thompson & Hodgson 1999; Westoby *et al.* 2002). Under high light, those plants do not need to invest in larger LA (i.e. photosynthetic surface area), which enables investment in thicker leaves (Westoby *et al.* 2002). Moreover, plants with thicker leaves have usually higher leaf lifespan (Westoby *et al.* 2002; Santiago & Wright 2007). Such characteristics probably constitute advantages of plants with low SLA over plants with high SLA in colonising open areas.

Despite the explanations for TCAP related to canopy openness made previously, a question remains: where does the convergence of traits occur along the gradient? A possibility of answer for this question is plotting the whole individual-based trait information against the concerning gradient, as we did for SLA in Fig. 5. By doing so, we confirmed that only plants with low SLA managed to colonise more opened plots and also that values of SLA higher than ca. 350 $cm^2.g^{-1}$ only occurred in more shaded conditions. Nonetheless, communities under more closed canopies also presented low SLA, though there was not TDAP regarding this trait alone. TDAP of SLA data in Fig. 5 is only apparent; though communities under closed canopies tended to present both low and high SLA, each of these communities when taken apart had low variation of SLA. Taking into account that in Fig. 5 there are many points overlapped due to the many communities with similar canopy openness

proportions, the interpretation of TCAP is complicated in this part of the gradient. Such varying convergence pattern under shade could be otherwise explained by an environmental filtering related to non-measured environmental variables acting over communities under more closed canopies.

DIVERGENCE OF TREE SAPLING TRAITS RELATED TO CANOPY OPENNESS

How does the divergence of traits behave along the canopy openness gradient? Results of the regressions of functional diversity regarding different trait sets maximising TDAP on canopy openness showed that there is a tendency of increasing divergence towards more closed canopies. Divergence regarding all traits may indicate that limiting similarity (MacArthur & Levins 1967; Pacala & Tilman 1994) is acting along the canopy openness gradient. However, it is difficult to interpret how limiting similarity would be occurring when we consider all the six traits together. An alternative explanation for divergence of the set including the six traits is that trait synergic effects could be occurring in the exploration of the environment. In this sense, separate evaluation of smaller trait sets may enable inferences of such synergic effects.

Indeed, when we explore Fig. 4b and c the emerging patterns suggest a better explanation of TDAP. Considering the divergence tendency of SLA and LA related to canopy openness, for instance, we propose that heterogeneity in light availability in the intra-plot scale is causing divergence of such traits when taken together in increasing shade conditions (Fig. 4c). Assuming that light availability in the forest understorey is highly patchy in a sapling neighbourhood scale (Lieberman, Lieberman & Peralta 1989; Nicotra, Chazdon & Iriarte 1999), neighbour sapling individuals should receive different light and ultimately PAR intensities. Saplings with high SLA would be better in exploring the low light reaching their leaves, as a higher relative photosynthetic surface area enables higher light absorption

(Westoby 1998). On the other hand, saplings with low SLA would be better in exploring the points of the plot where more light passes the canopy and reaches the understorey. Survival of such saplings in the forest interior may depend on their encountering of increasing light levels as they grow taller (Lusk *et al.* 2008a). Therefore, we conclude that niche partitioning mediated by limiting similarity and competition exclusion is probably occurring among sapling individuals experiencing heterogeneous light availability conditions in the large forest patch interior. This finding is similar to what Pacala & Tilman (1994) have predicted through their mechanistic and spatial models of plant competition in heterogeneous environments.

Another pattern that emerged from the evaluation of functional diversity was the divergence of SLA and SP, which we propose is related to grazing intensity correlated to canopy openness. Besides of the mechanisms mediated by environmental-structured biotic interactions, disturbance heterogeneity may also create trait divergence (Grime 2006). According to the results emerging from the functional analyses, grazing intensity seemed not to influence sapling assembly. However, grazing intensity was positively correlated with canopy openness (Table 2, Fig. 1), varying spatially throughout the landscape. The fact of we have not found significance of TCAP or TDAP regarding the grazing gradient may be explained by the type of variable used to characterise habitat use by cattle. We observed, for instance, that cattle used more intensively the small patches scattered in the grassland slope than the large patch understorey in the forest slope, where the cattle use of habitat is seasonal and not so intense. Previous to this study, we performed the functional analyses over only the 20 plots of small patches in the grassland slope and found that grazing intensity was related to the convergence of spiny plants in small patches (Carlucci et al., unpublished data). Assuming that our grazing proxy variable (evidence of habitat use by cattle) was weak in representing actual grazing intensity acting along the tree sapling metacommunity, i.e. throughout the 40

plots, and considering that cattle used more frequently and intensively the small patches in the grassland slope, we may discuss grazing intensity in the context of canopy openness. Variation in grazing intensity related to canopy openness may therefore explain the divergence of SLA and presence of spines (SP) along the metacommunity. Lower SLA, as we discussed before, is often correlated to thicker laminas and longer leaf longevity, which by their turns enable that plants invest in more protected tissues. For instance, plants with long leaf lifespan may allocate more tannins, phenols, or other defensive compounds (Coley 1983). Because of these correlations, leaves with lower SLA are better in deterring herbivory (Westoby *et al.* 2002). Indeed, there was convergence to low SLA where the canopy is more opened and grazing intensity is higher (Fig. 3a, Fig. 5) and, more interestingly, there was also a tendency of divergence (higher variation) of SLA and SP with decreasing canopy openness and decreasing grazing intensity.

IMPLICATIONS FOR TREE ADULT COMMUNITY STRUCTURE

Besides the exposed above, we may stress that we studied a homogeneous ontogeny class, i.e. saplings between 15 and 100 cm tall. Implications of the observed assembly patterns for adult community structure will depend on whether there is or not differential mortality (Clark & Clark 1992) related to distinct values of SLA. One possibility is that plants with lower SLA depend on the opening of gaps in forest canopy created by tree falls to grow up an adult. Since they have higher leaf longevity (Westoby *et al.* 2002), these plants may also accumulate denser foliages, which results in a higher total leaf area (Lusk *et al.* 2008a). By having longer leaf longevity and higher total photosynthetic surface area, such plants may tolerate low light until reaching better light conditions (Lusk *et al.* 2008a) through slow growing or creation of new canopy gaps.

WHAT WE HAVE ACTUALLY FOUND VS. WHAT WE HAVE HYPOTHESISED

Contrary to what we have hypothesised, we found no evidence of convergence of leaf pubescence related to canopy openness and microclimate gradients. We hypothesised also that shaded environments would filter only high SLA, expecting that only shade-tolerant plants would survive under such conditions, but we found that the whole range of SLA values occurred in the large patch forest interior. Nonetheless, we were correct when we hypothesised that sapling communities under more opened canopies tend to converge to lower SLA values. We were somewhat correct when we hypothesised that the presence of spines would be related to grazing, although we found no direct evidence of convergence related to grazing intensity by considering both slopes. Besides this, lower SLA may represent a proxy for defence against herbivores. Beyond which we have hypothesised, our results revealed trait-convergence and trait-divergence patterns that indicate mechanisms essential for tree sapling community assembly in forest patches.

FINAL REMARKS

The entirely functional approach we used here, i.e. without considering species or phylogenetic information, was very useful to infer likely niche mechanisms involved in tree sapling assembly in forest patches. By adopting an individual-based trait approach we assumed that both intra-specific and intra-population trait variability were relevant for revealing the assembly patterns. Nonetheless, further studies should examine whether the inclusion of species and phylogenetic information would improve or blur our understanding of sapling community assembly. Among several options, we can assess to which extent our findings can be extrapolated to other scales; e.g. we can evaluate in future studies what is the

role of phenotypic plasticity (Lusk *et al.* 2008b) in enabling sapling establishment in a large variety of abiotic and biotic scenarios. It is also important to say that this is a rare example of study evaluating both convergence and divergence trait patterns combined in a metacommunity framework where mechanisms of assembly are inferred in their environment context. Thereby, environment in our case was explicitly considered (McGill *et al.* 2006) and did not represent "a nuisance, obscuring or mimicking the assembly rules" (Wilson 1999). Finally, we argue that, besides the great value for interpreting trait-convergence, the use of individual-based trait data in a metacommunity framework is the best way to directly explore how trait-divergence actually behaves along a gradient and to localise exactly in which part or parts of the gradient higher variation of such trait is occurring.

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Table 1. Synthesis of plant vegetative measured traits, their possible effect on plant fitness and their

relation to environmental and biotic factors as revealed by previous studies

Functional trait	Related environmental gradient	Trait response mechanism to the ecological filter(s)	Trait effect on plant performance	References
Specific leaf area	Light availability	Variable with light gradients depending on if deciduous or evergreen plant	Trade-off between light absorption and cost of building more protected tissues	Westoby 1998; Lusk *et al.* 2008b
Mean leaf area	Light availability, air temperature and moisture	Higher in warmer, moister and shaded environments	Higher LA enables more light absorption per leaf	Cornelissen *et al.* 2003
Trichome	Air moisture	Avoid dehydration by diminishing leaf temperature and transpiration rate	Enables survival in arid environments	Ehleringer & Werk 1986
Compound leaf	Air moisture	Correlation with seasonally-dry environments	Not yet well understood	Malhado *et al.* 2010; Warman, Moles & Edwards 2010
Toothed leaf margin	Air temperature	Increase transpiration and photosynthesis in decreasing temperatures	Enables survival and growing in low temperature	BakerBrosh & Peet 1997; Royer & Wilf 2006
Spine	Grazing intensity by large mammals	Avoid herbivory by large grazers	Enables survival under grazing	Howe & Westley 1988

Table 2. Synthesis of the hypotheses of the study regarding tree sapling functional traits responses to ecological gradients measured along 40 plots (mean area = 4.5 ± 0.1 m^2) located in forest patches, southern Brazil. * Gradients assumed to be correlated with proxy variables (the other gradients presented significant correlations; see Fig. 1 and main text). Signals indicate if correlation of microhabitat variables is positive (+) or negative (-)

Proxy variables	Correlated microhabitat variables	Hypothesised trait response	Consequence on sapling metacommunities as environmental filter(s)	Why are the relations expected?
Canopy openness	Light availability* (+), grazing intensity (+), air microclimatic maximum temperature (+) and minimum moisture (-)	Higher SLA and LA and abundance of non-pubescent plants in more closed canopies	Convergence of SLA and LA: higher SLA and LA under shade and lower SLA and LA under open canopies	Under shaded and moister microhabitats, larger non-pubescent leaves are able to capture low light[1,2], while plants with low SLA develop without dehydrate under open canopies[2]
Evidence of habitat use by cattle	Grazing intensity* (+), canopy openness (+)	Higher abundance of spiny plants in plots under higher grazing intensity	Dominance by spiny species	Spiny plants are avoided by large herbivores[3]

[1] Ehleringer & Werk (1986); [2] Cornelissen *et al.* (2003); [3] Howe & Westley (1988).

Table 3. Traits chosen for description of tree sapling individuals sampled in forest patches in southern Brazil

Traits	Label	Unit	Trait type	Trait states
Specific leaf area	SLA	$cm^2.g^{-1}$	quantitative	-
Mean leaf area	LA	cm^2	quantitative	-
Trichome	TR	-	binary	1: pubescent leaves, 0: non-pubescent leaves
Compound leaf	CL	-	binary	1: compound leaves, 0: single leaves
Toothed leaf margin	TM	-	binary	1: toothed leaf margins, 0: untoothed leaf margins
Spine	SP	-	binary	1: spiny individual, 0: non-spiny individual

Table 4. Trait subsets maximising, at the community level, the expression of convergence and divergence patterns of tree sapling functional traits related to canopy openness and grazing intensity gradients in forest patches, southern Brazil. Values stressed in bold indicate significant results: * $P \leq$ 0.05; ** $P \leq 0.01$. For trait labels, see Table 3

	TCAP		TDAP	
	Traits	ρ	Traits	ρ
Canopy openness	SLA, LA, TM	**0.4673****	SLA, LA, TR, CL, TM, SP	**0.3713***
Grazing intensity	SLA, LA	0.2247	SLA, SP	0.1639
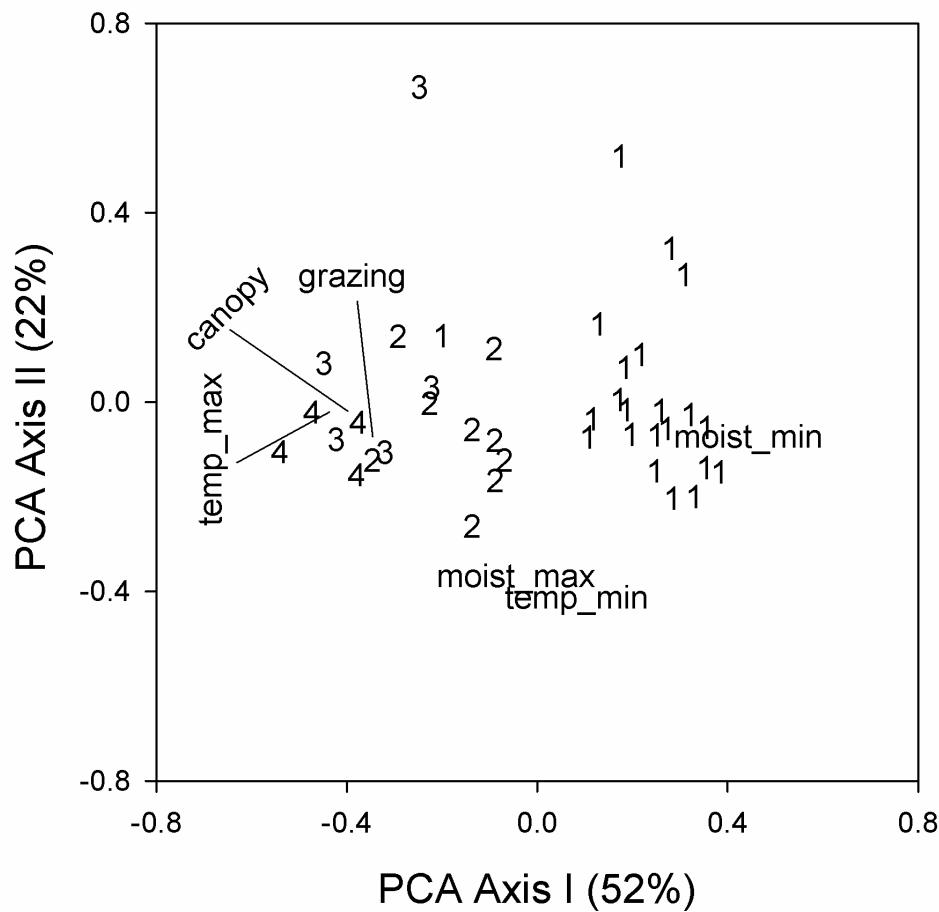
Fig. 1. Environmental gradients acting in tree sapling microhabitat scale along 40 plots located in forest patches, southern Brazil. The diagram was generated by PCA based on the correlations of environmental variables. Bootstrap resampling showed that PCA Axis I was stable ($P = 0.03$). Labels for environmental variables: canopy openness, canopy; grazing intensity, grazing; maximum air temperature, temp_max; minimum air temperature, temp_min; maximum air relative moisture, moist_max; minimum air relative moisture, moist_min. Communities are represented by classes of canopy openness — class 1, 0% to 15%; class 2, 15.1% to 30%; class 3, 30.1% to 50%; class 4, higher than 50%. For detailed information on the correlations between environmental variables, see the main text.
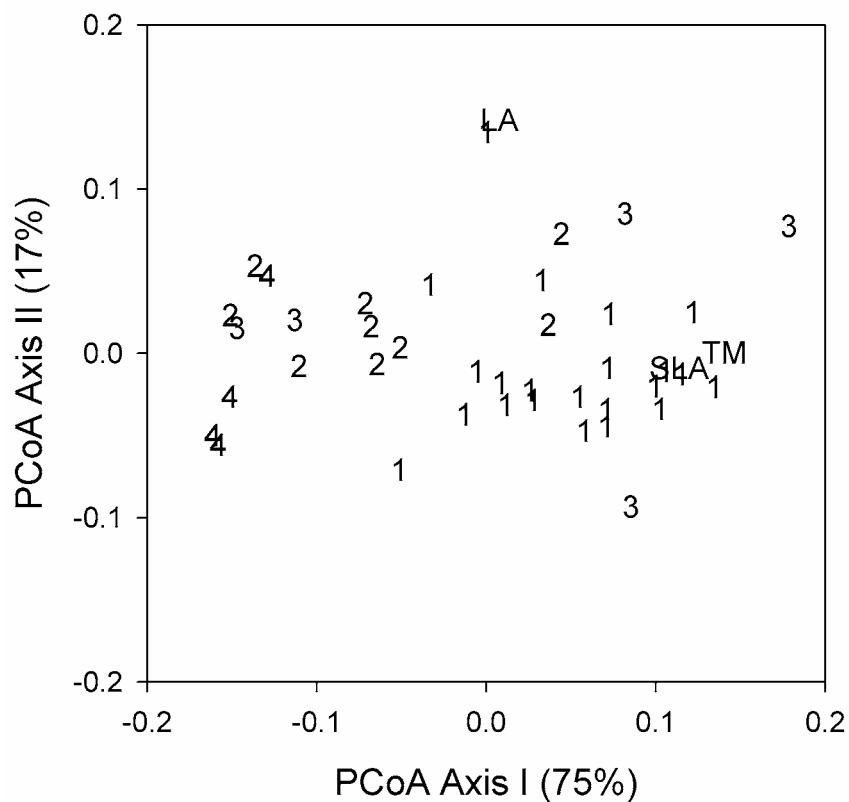
Fig. 2. Convergence assembly patterns of specific leaf area (SLA), leaf area (LA) and toothed leaf margin relative abundance (TM) of sapling individuals related to canopy openness gradient in forest patches, southern Brazil. The diagram was generated by PCoA of communities based on Euclidean distances computed on the normalised mean traits that maximised trait-convergence pattern. Communities are represented by classes of canopy openness — class 1, 0% to 15%; class 2, 15.1% to 30%; class 3, 30.1% to 50%; class 4, higher than 50%.
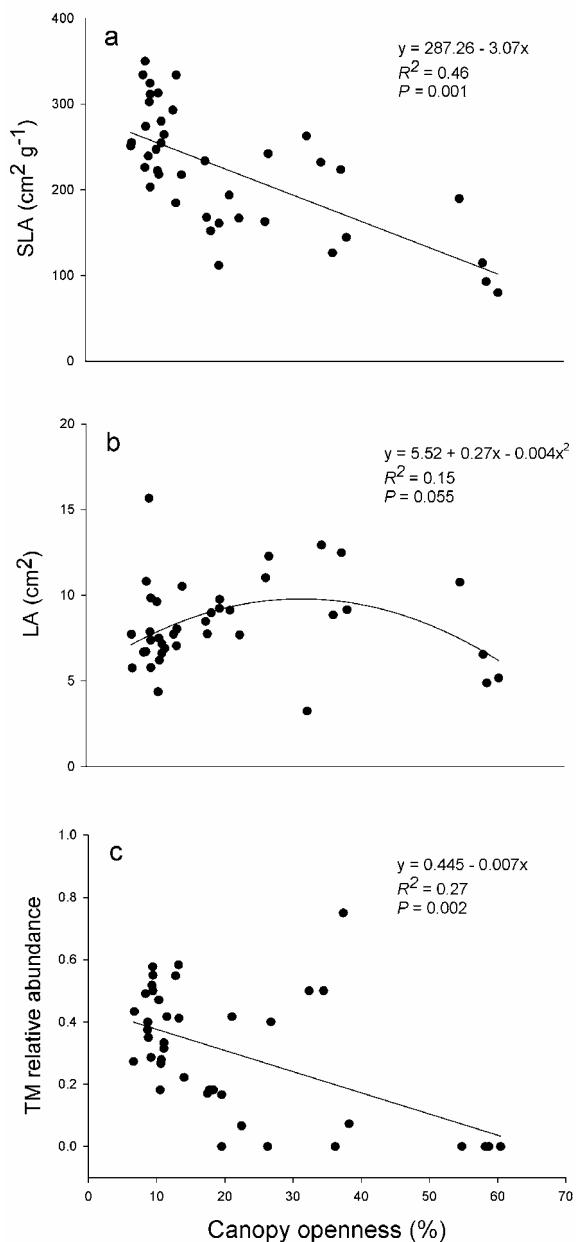
Fig. 3. Convergence patterns of community-level averaged SLA (a), LA (b) and toothed leaf margin (TM) relative abundance (c) of sapling individuals related to canopy openness gradient in forest patches, southern Brazil. Each point is a community (n = 40). *P*-values were obtained using randomisation of the response variable (Manly 2007). TCAP Mantel correlation using data of all individuals for each trait in functional analysis: SLA, $\rho(\mathbf{TE})$ = 0.42 (*P* = 0.006); LA, $\rho(\mathbf{TE})$ = 0.14 (*P* = 0.24); TM relative abundance, $\rho(\mathbf{TE})$ = 0.40 (*P* = 0.009).
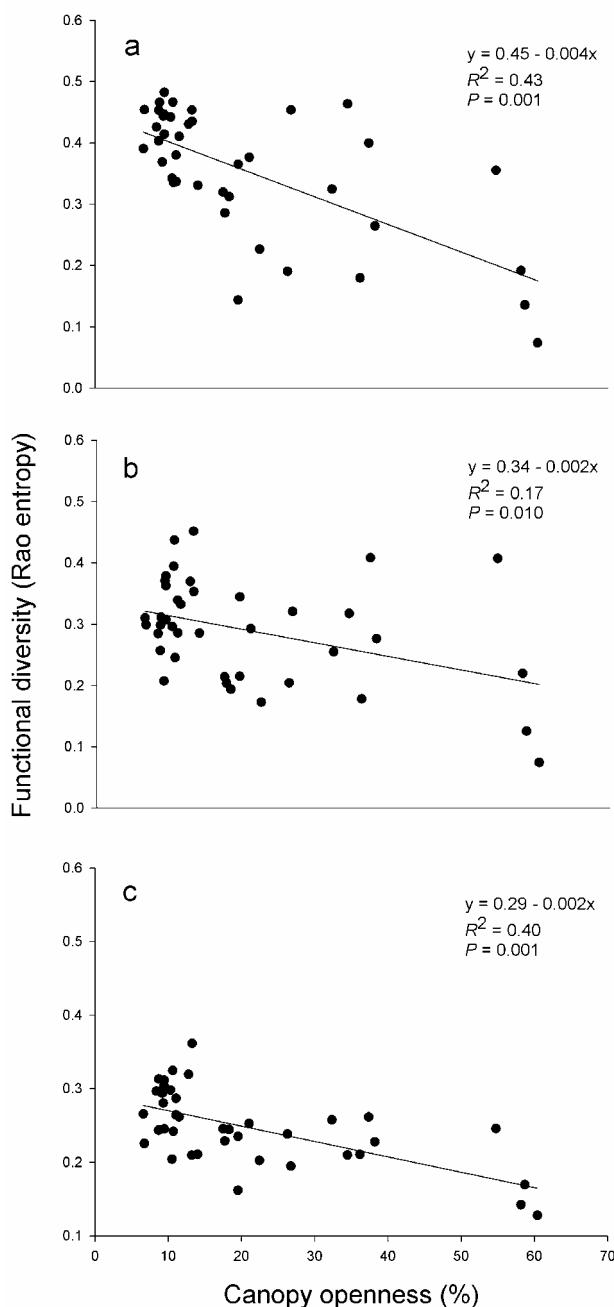
Fig. 4. Divergence patterns of tree sapling functional traits related to canopy openness gradient in forest patches, southern Brazil. Rao quadratic entropy was calculated for each community (n = 40) as a measure of functional diversity, regarding the trait sets that maximised TDAP: (a) SLA, LA, TR, CL, TM and SP; (b) SLA and SP; (c) SLA and LA. Mantel correlation using data of all individuals for each trait set in functional analysis: a, $\rho(\mathbf{XE.T})$ = 0.37 (P = 0.012); b, $\rho(\mathbf{XE.T})$ = 0.36 (P = 0.014); c, $\rho(\mathbf{XE.T})$ = 0.23 (P = 0.058).
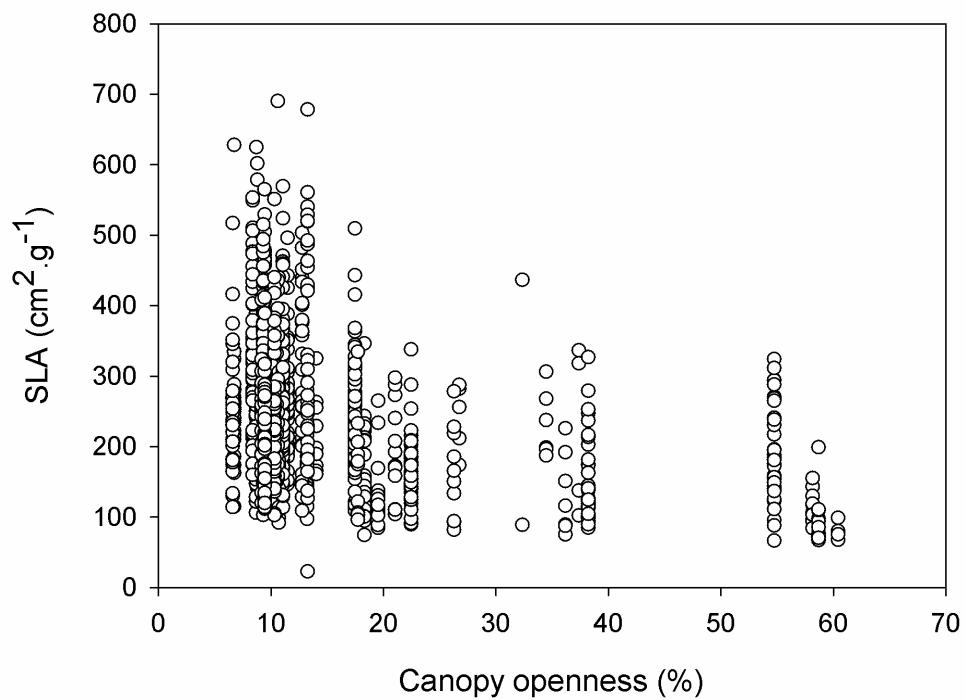
Fig. 5. Scatter plot of mean individual SLA of tree saplings as related to canopy openness in forest patches, southern Brazil. Each point represents a sapling individual (n = 1132).

Appendix 1. Statistical values of matrix correlation (ρ) using trait sets that maximised trait-convergence assembly pattern (TCAP) and trait sets that maximised trait-divergence assembly pattern (TDAP) of tree saplings related to canopy openness in forest patches, southern Brazil. Sets in bold are those that were used in the functional analyses.

TCAP		TDAP	
ρ(**TE**)	Trait set	ρ(**XE.T**)	Trait set
0.4673	**SLA, LA, TM**	0.3714	**SLA, LA, TR, CL, TM, SP**
0.4462	SLA, TM	0.3705	SLA, TR, CL, TM
0.4236	LA, TM	0.3634	**SLA, SP**
0.4198	SLA	0.3612	SLA, LA, TR, TM
0.4106	SLA, LA	0.3394	LA, TR, CL, TM
0.4017	TM	0.3375	SLA, LA, TM, SP
0.3909	SLA, LA, CL, TM	0.3353	SLA, LA, TR, TM
0.3775	SLA, CL, TM	0.3332	SLA, TM, SP
0.3555	LA, CL, TM	0.3328	SLA, TR, TM, SP
0.3373	CL, TM	0.3299	SLA, LA, SP
0.3060	SLA, LA, CL	0.3279	SLA, CL, TM, SP
0.2933	SLA, CL	0.3260	SLA, LA, CL, TM
0.2771	SLA, LA, TR, CL, TM	0.3214	SLA, TR, TM
0.2744	SLA, LA, CL, TM, SP	0.3207	SLA, LA, TR, CL
0.2690	SLA, TR, CL, TM	0.3170	TR, CL, TM, SP
0.2647	SLA, CL, TM, SP	0.3142	SLA, TR, CL, TM
0.2556	SLA, LA, TR, TM	0.3133	LA, CL, TM, SP
0.2543	SLA, LA, TM, SP	0.3034	CL, TM, SP
0.2446	SLA, TR, TM	0.2913	LA, TR, CL, TM
0.2444	LA, TR, CL, TM	0.2831	LA, TM, SP
0.2425	SLA, TM, SP	0.2681	LA, TR, TM, SP
0.2407	LA, CL, TM, SP	0.2655	LA, TR, TM
0.2344	TR, CL, TM	0.2643	TR, CL, TM
0.2308	LA, CL	0.2320	**SLA, LA**
0.2283	CL, TM, SP	0.2203	SLA, LA, TR, CL
0.2123	LA, TR, TM	0.2126	SLA, LA, CL, SP
0.2118	SLA, LA, TR, CL, TM, SP	0.2103	SLA, CL, SP
0.2095	CL	0.2102	SLA, TR, CL, SP
0.2090	LA, TM, SP		
0.2052	SLA, TR, CL, TM, SP		
0.2000	TR, TM		

CONSIDERAÇÕES FINAIS

Medida de atributos baseados no indivíduo

Neste trabalho, foram utilizados dados de atributos funcionais medidos para cada indivíduo arbóreo juvenil registrado. Até certo ponto, teve-se que adaptar uma série de etapas de medida dos atributos para a realidade de falta de equipamentos específicos para tal. Por exemplo, para medir SLA precisa-se da medida da área das folhas frescas e da massa das folhas secas. Como não havia na época das coletas de dados um medidor de área foliar que pudesse ser levado ao campo e como os juvenis muitas vezes eram pequenos demais para se mantê-los hidratados, adaptou-se um método no qual se desenharam folhas de todos os juvenis para posterior recorte do papel com a marca das folhas e medida das áreas foliares com base em imagens dos recortes em computador (ver detalhes do método no Cáp. 1). O método foi eficaz para a medida das áreas foliares, mas foi deveras trabalhoso. Sugere-se que em próximos trabalhos com espécies arbóreas seja adotado o método amplamente utilizado por ecofisiólogos, no qual se obtém da planta de interesse um pequeno disco da lâmina foliar de área conhecida e após mede-se no disco de lâmina foliar os demais atributos de interesse, como espessura e massa seca (Rosado & de Mattos 2010). Caso seja importante se saber não só uma área relativa da lâmina foliar, mas também a área foliar em si, uma alternativa que provavelmente seria simples e eficaz é a de coletar as folhas a campo e logo armazená-las entre papel úmido em sacolas plásticas vedadas de modo a evitar a desidratação das folhas até a medida da área foliar.

Avanços teóricos representados por este trabalho

Os resultados encontrados revelaram padrões tanto de convergência quanto de divergência de atributos que indicaram mecanismos para a organização de comunidades de plantas arbóreas juvenis em manchas florestais. A abordagem inteiramente funcional utilizada neste trabalho, isto é sem considerar informação filogenética ou de espécies, foi muito útil para a inferência de prováveis mecanismos de nicho envolvidos na organização das comunidades estudadas. Entretanto, avaliar se a inclusão da informação filogenética ou de espécies aumentará a compreensão da organização das comunidades de juvenis arbóreos será muito interessante. Entre diversas opções, poderá ser avaliado em futuros estudos até que ponto os resultados aqui encontrados podem ser extrapolados para outras escalas; por exemplo, poderá ser avaliado o papel da plasticidade fenotípica (Lusk *et al.* 2008) em permitir que juvenis da mesma espécie se estabeleçam em uma grande variedade de cenários abióticos e bióticos. Assim, nossos resultados foram valiosos como uma primeira tentativa de elencar os principais fatores estruturadores das comunidades de juvenis arbóreos em manchas florestais se desenvolvendo sobre campo nativo no extremo sul do Brasil. É importante ressaltar também que este é um exemplo raro de estudo avaliando padrões tanto de convergência como de divergência de atributos conjugados em um contexto de metacomunidades em que os mecanismos de organização são inferidos à luz de gradientes ambientais. Portanto, neste trabalho o ambiente foi explicitamente considerado (McGill *et al.* 2006) e não representou "um incômodo, obscurecendo ou simulando 'regras de montagem'" (Wilson 1999). Finalmente, nós defendemos que o uso de dados de atributos baseados em indivíduos (e não em médias por espécies) em um contexto de metacomunidades é a melhor maneira de explorar diretamente como a convergência e a divergência de atributos realmente

se comporta ao longo de um dado gradiente, pois contempla a variação intra-específica e intra-populacional dos atributos.

As manchas florestais estudadas e a ocorrência de Araucaria angustifolia *e de* Podocarpus lambertii *além da latitude 29.5º S*

Apesar de não ter sido incluída a informação sobre as espécies dos juvenis arbóreos nesta dissertação, pretende-se fazê-lo em trabalhos futuros. Além disso, um levantamento de atributos foliares de árvores adultas deverá ser feito na mesma área em breve. O Apêndice 1 fornece a lista de espécies arbóreas que registramos como juvenis em 40 parcelas dispostas nas manchas florestais estudadas. Para mais detalhes sobre o desenho amostral, ver Cáp. 1. De maneira geral, não foram encontradas espécies típicas do Planalto, além de *Araucaria angustifolia* (Bertol.) Kuntze e *Podocarpus lambertii* Klotzsch ex Endl. No entanto, foram encontradas duas espécies de *Ilex* L., gênero característico da Floresta com Araucária do Planalto Sul-Brasileiro.

A única característica que une a Floresta com Araucária, como o próprio nome diz, é a presença de *Araucaria angustifolia* (e talvez de *P. lambertii*), já que ao longo do gradiente latitudinal dessa formação florestal sua composição florística e de elementos migratórios varia consideravelmente (Duarte, Carlucci & Pillar 2009). Segundo Hueck (1972) a área de distribuição da araucária compreende as grandes altitudes do sul do Brasil, incluindo altitudes médias de 600 a 800 m no Planalto Sul-Brasileiro, com algumas poucas áreas atingindo mais de 1000 m. Conforme o mesmo autor, as araucárias são encontradas nos Estados do Rio Grande do Sul (a partir do planalto ao norte do rio Jacuí, cerca de 30º de latitude S), Santa

Catarina, Paraná e São Paulo, onde estão as áreas mais contínuas; e nos do Rio de Janeiro, Minas Gerais e na província de *Misiones*, na Argentina, onde há manchas menores e isoladas. Apesar de o autor considerar que a formação florestal em questão tem seu limite sul no Planalto, ao norte do rio Jacuí, ele admite a ocorrência isolada de *A. angustifolia* ao sul desse rio (cerca de 31º de latitude S). Já os outros limites geográficos estariam, ao norte, no rio Doce, em Minas Gerais (cerca de 18º de latitude S), à leste, no limite das escarpas e divisores de água do Planalto Sul-Brasileiro e da Serra do Mar, e à oeste, em *Misiones*, na Argentina (Hueck 1972).

O limite austral da Floresta com Araucária é um assunto que está em debate científico há bastante tempo, pelo menos desde 1909, quando foi publicado o livro de Lindman, posteriormente republicado (Lindman & Ferri 1974). Nessa discussão, de um lado, Reitz, Klein & Reis (1983) citam a ocorrência de *A. angustifolia* ao sul do rio Jacuí, na Serra do Sudeste, formando "agrupamentos nativos" nos municípios de Santana da Boa Vista, Dom Feliciano, São Lourenço do Sul e Canguçu. No Município de Canguçu, os autores afirmam ter havido "o maior núcleo de pinhal do Escudo Rio-Grandense", o qual teria dezenas de quilômetros quadrados. Uma área ao sul do município, que avaliando relatos de moradores locais se adéqua ao grande núcleo citado por Reitz, Klein & Reis (1983), foi visitada por nós em 2009 e hoje encontra-se praticamente totalmente desmatada. Portanto, Reitz, Klein & Reis (1983) consideram que o limite sul da formação Floresta com Araucária está na Serra do Sudeste (especificamente em Canguçu), a cerca de 31º de latitude Sul, contrariando o que dizem muitos trabalhos sobre o tema. Backes (1988, 1999) bem como Dutra & Stranz (2003) entram em consonância com Reitz, Klein & Reis (1983), indicando que os núcleos de Floresta com Araucária ocorrentes na Serra do Sudeste são pequenos mas fitogeograficamente importantes. De outro lado, obras importantes como o "Inventário Florestal do Pinheiro no

Sul do Brasil" (IBDF 1978) e "A Vegetação no Rio Grande do Sul" (Lindman & Ferri 1974) excluem tais áreas do mapa de ocorrência de *Araucaria angustifolia*, considerando a existência de uma introdução antropogênica pretérita da espécie na Serra do Sudeste. Rambo (1956) não menciona a existência de tais áreas. Em uma posição intermediária, estão as obras que citam o limite sul da escarpa do planalto no Rio Grande do Sul como fronteira austral da distribuição da espécie, contrariando a figura de Kurt Hueck da qual fazem uso (citando Hueck 1953) mas que destaca quatro núcleos de ocorrência de *A. angustifolia* ao sul do Jacuí, na Serra do Sudeste (Klein 1960; Reitz & Klein 1966).

A grande questão sobre o limite sul da distribuição de *Araucaria angustifolia* é que, caso as áreas da Serra do Sudeste sejam consideradas nativas, haveria uma ocorrência disjunta da espécie e, talvez, do tipo vegetacional Floresta com Araucária. Em outras palavras, a espécie e a formação ocorreriam do norte, desde os núcleos pequenos e esparsos da Serra do Mar, no sudeste brasileiro e na província de *Misiones*, na Argentina, passando pelas áreas maiores e mais contínuas do Paraná, Santa Catarina e Rio Grande do Sul, até a borda meridional do Planalto Sul-Brasileiro no último Estado (ocorrência amplamente aceita pela comunidade científica), e, separados do restante da área de ocorrência pela Depressão Central gaúcha (bacia do rio Jacuí), os núcleos da Serra do Sudeste, no sudeste do Rio Grande do Sul como seu verdadeiro limite sul. Esse tema é especialmente importante no que concerne a uma possível migração da espécie *Araucaria angustifolia* ou mesmo da flora típica da formação Floresta com Araucária rumo ao sul, ou alternativamente a uma possível evidência remanescente de que a espécie tenha ocorrido continuamente até essas latitudes, talvez há centenas de milhares de anos atrás. A resolução desse mistério, entretanto, provavelmente só seja alcançada através de estudos paleopolínicos e genéticos. De qualquer forma, tais áreas

devem ser protegidas, já que seu desconhecimento até mesmo por grande parte da comunidade científica facilita a negligência de sua conservação.

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APÊNDICES

Apêndice 1. Ocorrência de espécies de plantas arbóreas juvenis em parcelas dispostas em manchas florestais pequenas ou no interior de mancha grande com presença de *Araucaria angustifolia* (Bertol.) Kuntze e *Podocarpus lambertii* Klotzsch ex Endl. se desenvolvendo sobre campo nativo na Serra do Sudeste do Rio Grande do Sul.

Espécies	Manchas pequenas	Mancha grande
ANACARDIACEAE		
Lithraea brasiliensis Marchand	X	X
ANNONACEAE		
Annona cf. *salicifolia* (Schltdl.) Ekman & R.E.Fr.		X
AQUIFOLIACEAE		
Ilex cf. *brevicuspis* Reissek		X
ARAUCARIACEAE		
Araucaria angustifolia (Bertol.) Kuntze	X	X
ARECACEAE		
Syagrus romanzoffiana (Cham.) Glassman		X
ASTERACEAE		
Dasyphyllum spinescens (Less.) Cabrera	X	X
BORAGINACEAE		
Cordia americana (L.) Gottschling & J.S.Mill.		X
CANNABACEAE		
Celtis iguanaea (Jacq.) Sarg.		X
CARDIOPTERIDACEAE		
Citronella paniculata (Mart.) R.A.Howard		X
CELASTRACEAE		
Maytenus muelleri Schwacke		X
EBENACEAE		
Diospyros inconstans Jacq.		X
ERYTHROXYLACEAE		
Erythroxylum myrsinites Mart.	X	X
EUPHORBIACEAE		
Sebastiania brasiliensis Spreng.		X
Sebastiania commersoniana (Baill.) L.B.Sm. & Downs		X
FABACEAE		
Calliandra cf. *tweediei* Benth.		X
LAURACEAE		
Cinnamomum cf. *amoenum* (Nees) Kosterm.		X
Nectandra megapotamica (Spreng.) Mez		X
Ocotea puberula (Rich.) Nees		X
Ocotea pulchella (Nees) Mez	X	X
MALVACEAE		
Luehea divaricata Mart. & Zucc.		X
MELASTOMATACEAE		

Miconia hiemalis A.St.-Hil. & Naudin ex Naudin		X
MELIACEAE		
Cedrela fissilis Vell.		X
Trichilia claussenii C.DC.		X
Trichilia elegans A.Juss.		X
MORACEAE		
Sorocea bonplandii (Baill.) W.C.Burger , Lanjouw & Boer		X
MYRTACEAE		
Blepharocalyx salicifolius (Kunth) O.Berg	X	X
Eugenia uniflora L.	X	X
Eugenia uruguayensis Cambess.	X	X
Myrcia palustris DC.		X
Myrcianthes pungens (O.Berg) D.Legrand		X
Myrrhinium atropurpureum Schott	X	X
PODOCARPACEAE		
Podocarpus lambertii Klotzsch ex Endl.	X	X
PRIMULACEAE		
Myrsine coriacea (Sw.) R.Br.	X	X
Myrsine lorentziana (Mez) Arechav.		X
RUBIACEAE		
Guettarda uruguensis Cham. & Schltdl.		X
RUTACEAE		
Zanthoxylum fagara (L.) Sarg.	X	X
SALICACEAE		
Casearia decandra Jacq.	X	X
Casearia silvestris Sw.	X	X
Xylosma pseudosalzmanii Sleumer		X
Xylosma schroederi Sleumer ex Herter	X	X
Xylosma tweediana (Clos) Eichler	X	X
SAPINDACEAE		
Allophylus edulis (A.St.-Hil., Cambess. & A.Juss.) Radlk.	X	X
Cupania vernalis Cambess.		X
Matayba elaeagnoides Radlk.	X	X
SAPOTACEAE		
Chrysophyllum marginatum (Hook. & Arn.) Radlk.	X	X
SOLANACEAE		
Cestrum strigilatum Ruiz & Pav.	X	X
STYRACACEAE		
Styrax leprosus Hook. & Arn.	X	X
SYMPLOCACEAE		
Symplocos uniflora (Pohl) Benth.		X
THYMELAEACEAE		
Daphnopsis racemosa Griseb.	X	X
VERBENACEAE		
Citharexylum montevidense (Spreng.) Moldenke	X	X