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ANITA STIVAL DOS SANTOS

Efeitos de filtros ambientais nos padrões de diversidade de árvores na Floresta Atlântica do Sul do Brasil sob uma perspectiva de metacomunidades

Porto Alegre
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Velhas Árvores

Olha estas velhas árvores, mais belas
Do que as árvores novas, mais amigas:
Tanto mais belas quanto mais antigas,
Vencedoras da idade e das procelas...

O homem, a fera, e o inseto, à sombra delas
Vivem, livres de fomes e fadigas;
E em seus galhos abrigam-se as cantigas
E os amores das aves tagarelas.

Não choremos, amigo, a mocidade!
Envelheçamos rindo! envelheçamos
Como as árvores fortes envelhecem:

Na glória da alegria e da bondade,
Agasalhando os pássaros nos ramos,
Dando sombra e consolo aos que padecem!

Olavo Bilac

À minha abençoada e linda família, com todo amor e gratidão, nas pessoas de Pedro, Ivanir, Erivelto, Ecléia, Cláudia, Larissa, Luiza e Maria Júlia

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Sumário

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Resumo

Entender padrões de diversidade e composição de espécies ao longo de múltiplas escalas espaciais constitui um dos principais objetivos em ecologia e biogeografia. A relativa importância dos mecanismos responsáveis por estruturar as comunidades de plantas e como eles interagem para influenciar estes padrões têm sido foco de intensos debates. No presente estudo, foram utilizados dados do Inventário Florístico Florestal de Santa Catarina a fim de investigar os padrões de diversidade de espécies de árvores e suas relações com a heterogeneidade ambiental sob uma das perspectivas oriundas da teoria de metacomunidades, conhecida como "sorteio de espécies". A predição chave deste ponto de vista é a de que a composição de espécies varia em resposta a diferenças nas condições ambientais entre manchas de hábitat. O presente estudo é focado nessa predição e objetivou entender como processos relacionados a filtros ambientais interagem direta e indiretamente sobre os padrões de diversidade em uma área de 95000 km 2 (dados de 432 unidades amostrais). Foi utilizada modelagem de equações estruturais (PLS Path Modeling), a fim de investigar os efeitos interativos da topografia, clima, balanço de água e energia e geometria das manchas de floresta sobre os padrões de alfa (α) e beta (β) diversidade de uma metacomunidade de floresta atlântica no sul do Brasil. Fatores relacionados a filtros ambientais mostraram substanciais efeitos sobre a diversidade alfa e beta. A quantidade total da variação na beta diversidade explicada pela filtragem de hábitat foi alta (64%), corroborando a predição testada no nível de metacomunidades. Os fatores mais importantes para explicar a diversidade beta foram: extremos climáticos, balanço de água e energia e alfa diversidade, enquanto tamanho da mancha e balanço de água e energia foram os fatores chaves para a alfa diversidade. O teste de Mantel parcial mostrou que os efeitos ambientais ocorrem amplamente independente de efeitos espaciais, reforçando a predição testada. O estudo provê forte suporte empírico para a predição de que a beta diversidade reflete primariamente processos determinísticos associados com o nicho das espécies e suas respostas às condições ambientais na escala espacial considerada.

Palavras-chave: diversidade alfa, Floresta Atlântica subtropical, diversidade beta, modelagem de equações estruturais, sorteio de espécies, variação climática.

Abstract

Understanding patterns of species diversity and composition across multiple scales is one of the main purpose in ecology and biogeography. The relative importance of the mechanisms that structure plant communities and how they interact to influence these patterns remains a topic of hot debate. In the present study, we use data from the Forest Inventory of Santa Catarina to investigate the patterns of species diversity of subtropical Atlantic forests and its relationships with environmental heterogeneity on a metacommunity perspective (species-sorting). The key prediction of this viewpoint is that community composition varies in response to differences in environmental conditions among habitat patches. Our study focused on this perspective, aiming to understand how environmental filtering processes interact directly and indirectly on diversity patterns in an area of 95000 km 2 (data from 432 forest plots). We employed structural equation modeling (PLS Path Modeling) to disentangle the interactive effects of topography, climate, water-energy balance, and geometry of forest patches upon the alpha and beta diversity of a subtropical forest metacommunity in southern Brazil. Factors related to environmental filtering showed substantial effects upon tree alpha and beta diversity. The total amount of variation in beta diversity explained by environmental filtering was high (64%) and was even more when together with alpha diversity (73%), corroborating the prediction of species-sorting model at the metacommunity level. Climatic extremes, water-energy balance and alpha diversity were the key determinants of beta diversity and patch size and water- energy balance the key determinants of alpha diversity in the South Brazilian Atlantic forests. Partial mantel test showed that environmental effects occurred largely independent of spatial effects, reinforcing the tested prediction. Our study provides strong empirical support for the prediction that beta diversity primarily reflects deterministic factors associated with species niches and their responses to environmental conditions in the studied spatial scale.

Keywords: alpha diversity, subtropical Atlantic forest, beta diversity, structural equation modeling, species sorting, climatic variation

Apresentação

A presente dissertação consiste em um artigo científico, pautado na investigação do papel relativo dos filtros ambientais para os padrões de diversidade alfa (α) e beta (β) em comunidades de árvores da Floresta Atlântica no Sul do Brasil, sob uma perspectiva da teoria de metacomunidades. O objetivo principal foi testar a predição de que a β-diversidade reflete, principalmente, processos determinísticos associados ao nicho das espécies e suas relações com condições ambientais.

Na introdução geral são descritos alguns resultados prévios, com a finalidade de contextualizar a Floresta Atlântica no Estado de Santa Catarina. Além disso, são discutidos assuntos relacionados aos processos que determinam os padrões de diversidade de espécies ao longo de múltiplas escalas espaciais.

O manuscrito que consiste o capítulo principal da dissertação encontra-se formatado de acordo com as normas do periódico “Perspectives in Plant Ecology, Evolution and Systematics”, ao qual será submetido, com exceção de tabelas e figuras que foram incluídas ao longo do texto para facilitar a compreensão dos resultados apresentados.

Finalmente, no item considerações finais, são discutidos alguns aspectos acerca do conhecimento gerado, suas contribuições, perspectivas e sugestões para a área de pesquisa.

General Introduction

Subtropical Atlantic Forest

Brazilian subtropics hosts an important and singular portion of the Atlantic Forest, one of the world's biodiversity hotspots (Mittermeier et al. 2004). In this region, species composition differs considerably from the Atlantic forest at lower latitudes, where tropical species find the end of their distribution range (Oliveira-Filho et al. 2013). The subtropical portion of the Atlantic Forest biome is known by the outstanding heterogeneity of its vegetation, which is commonly classified into three main forest types: Seasonal Forests (SF, encompassing semideciduous and deciduous forest), Mixed *Araucaria* Forest (MAF) and Rain Forests (RF), as well as associated ecosystems such as mangroves, coastal forests and grasslands (Veloso et al. 1991, Oliveira-Filho et al. 2013).

Only more recently the subtropical Atlantic Forest has been the target of in-depth studies, which provided important advances for the understanding of compositional differences among forest types and the mechanisms that act in structuring the tree community (Jarenkow and Budke 2009, Bergamin et al. 2012; Gonçalves and Souza 2013, Oliveira-Filho et al. 2013). In Santa Catarina state, part of the region covered by subtropical Atlantic Forest, the recent achievement of the Forest Inventory (Inventário Florístico Florestal de Santa Catarina, IFFSC, (http://www.iff.sc.gov.br) contributes with detailed data (Vibrans et al. 2010) of the main three forest types that occur in this area (as showed in Figure 1). Land use change and habitat fragmentation have gradually reduced the quality and extent of these forests. Currently, only 29% of original forest cover remains in SC. RF originally covered about 29.282 km^2 of the surface of the state, MAF 42.851 km^2 and SF 7.670 km^2 (Klein 1978). Today, their cover were reduced to 40%, 24% and 16% of original forest cover, respectively

(Vibrans et al. 2013).

Analyses conducted with IFFSC data (own unpublished results; see Appendix A for methods) confirm that the composition among the main three forest types (rain, seasonal and *Araucaria* forest) differs strongly (NPMancova, F= 42,28, R^2= 0.16, p=0.0009). Along the first ordination axis in the NMDS, a clear difference in floristic composition between RF, with plots concentrated at the left, and the other forest formations, concentrated at the right, can be observed, with SF plots situated at upper extreme along the second axis (Fig. 2). Some indicator species that best characterize the different forest types are: (1) for RF: *Alchornea triplinervia* (Spreng.) Müll. Arg.*, Matayba intermedia* Radlk.*, Nectandra oppositifolia* Nees & Mart.*, Psychotria vellosiana* Benth.*, Euterpe edulis* Mart.*, Guapira opposita* (Vell.) Reitz*, Cecropia glaziovii* Snethl.*, Hieronyma alchorneoides* Allemão *and Guatteria australis* A. St.-Hil.*;* (2) for SF: *Luehea divaricata* Mart.*, Nectandra megapotamica* (Spreng.) Mez*, Machaerium stipitatum* (DC.) Vogel*, Balfourodendron riedelianum* (Engl.) Engl.*, Nectandra lanceolata* Nees & Mart.*, Chrysophyllum gonocarpum* (Mart. & Eichler ex Miq.) Engl. and *Myrocarpus frondosus* Allemão and (3) for MAF: *Araucaria angustifolia* (Bertol.) Kuntze*, Dicksonia sellowiana* Hook.*, Ilex paraguariensis* A. St.-Hil.*, Cinnamomum amoenum* (Nees) Kosterm. and *Ocotea pulchella* (Nees & Mart.) Mez (see Appendix B for a complete list of the indicator species).

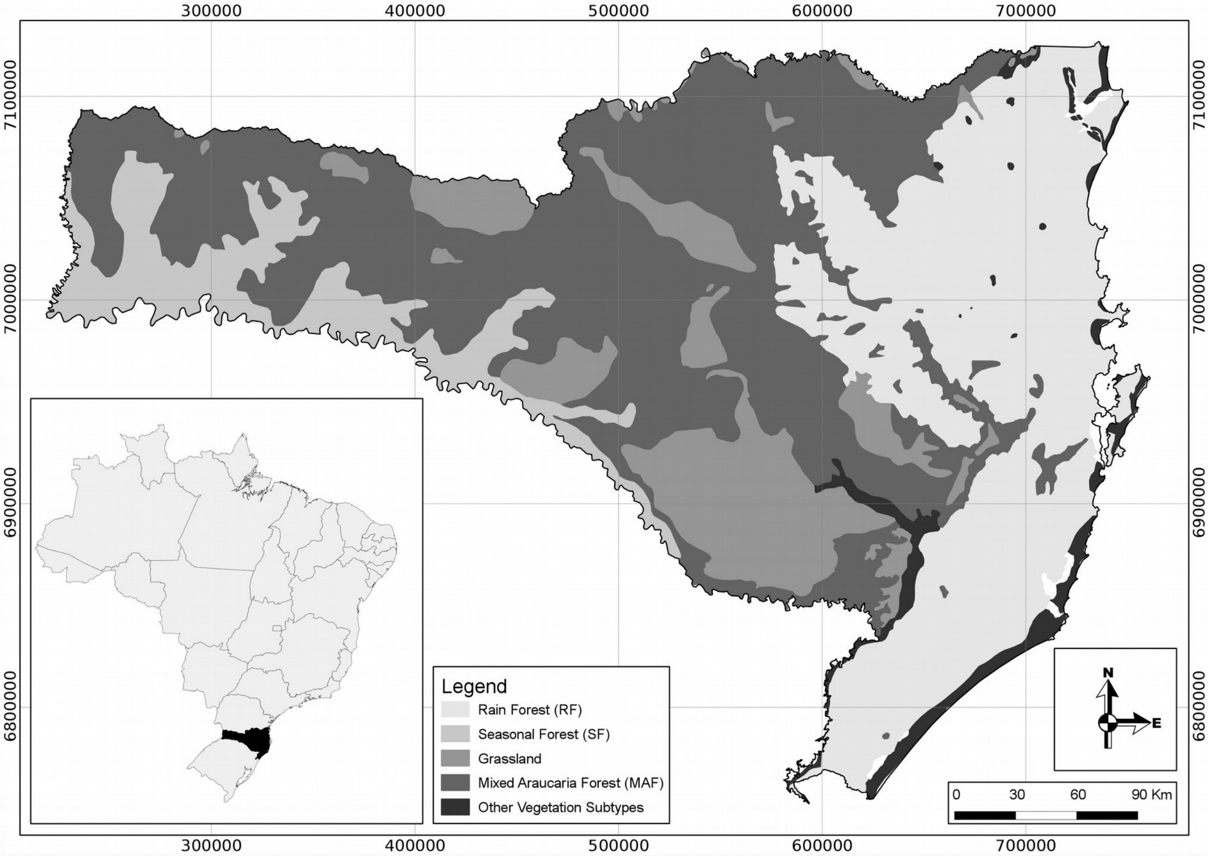

Figure 1: Geographical location of the study area in southern Brazil and spatial distribution of the different forest types as delimited by Klein (1978).

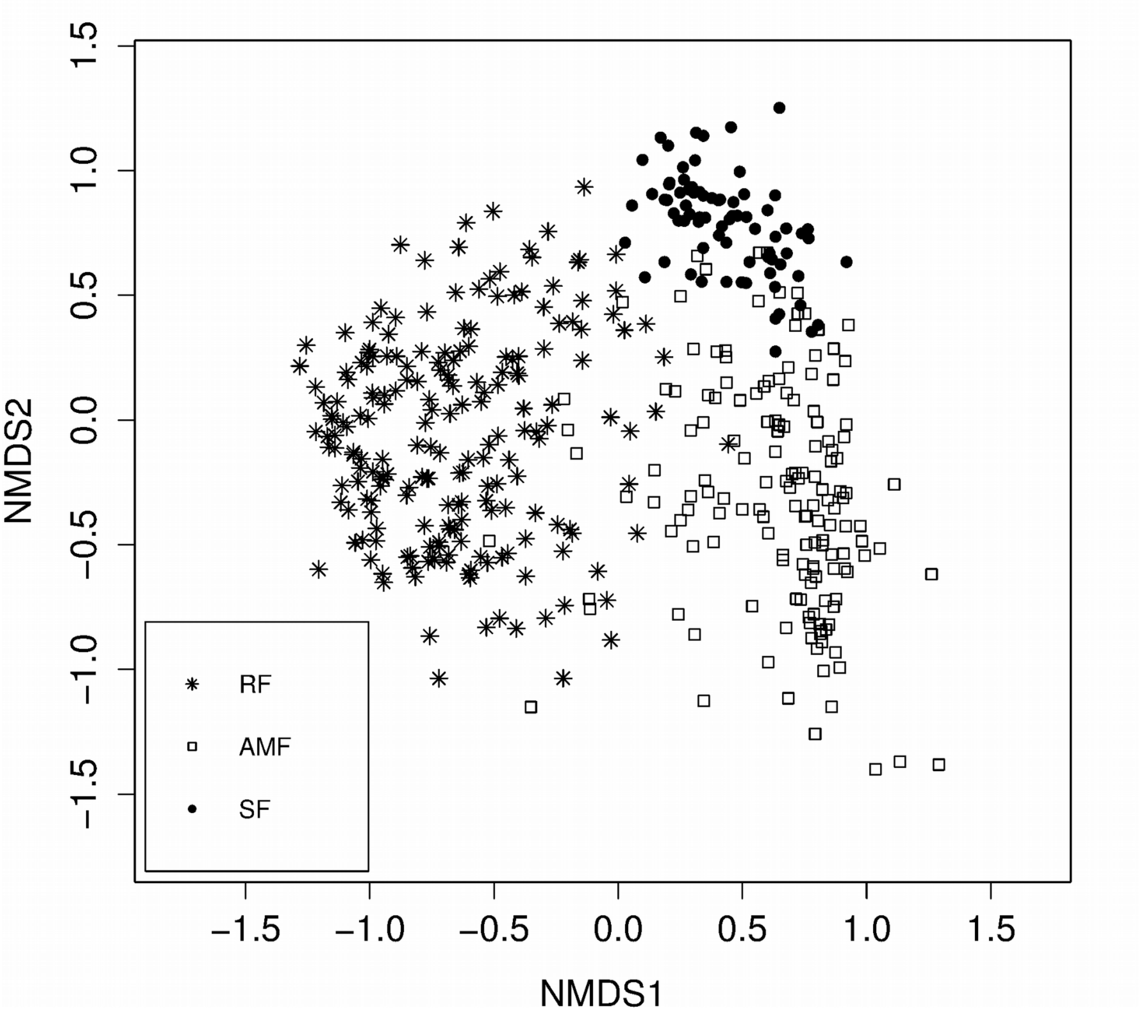

Figure 2: Non-metric multidimensional scaling ordination (NMDS) of the plots of subtropical Atlantic Forest in Santa Catarina state, southern Brazil. RF, Rainforest; SF, Seasonal Forest; MAF, Mixed Araucaria Forest.

Determinants of tree species diversity

Understanding patterns of species diversity and composition across multiple scales has long been recognized as one of the main purpose in ecology and biogeography (Scheiner and Willig 2005). The relative importance of the mechanisms that structuring plant communities and how they interact to influence these patterns remains a topic of hot debate. Three major classes of community assembly mechanisms have been suggested: (1) niche-based processes such as habitat filtering (Diamond 1975, Weiher and Keddy 1992; (2) stochastic processes (neutral) (Hubbell 2001) and (3) regional-historical processes such as speciation, dispersal, evolutionary adaptation, and habitat specialization (Ricklefs 1987, Ricklefs and Schluter 1993).

One way to investigate the role of these mechanisms, specially of niche-based and neutral processes, for determining patterns of species diversity is to examine them across multiple scales with a particular focus on β-diversity (variation in species composition among sites in a given geographic area) (Whittaker 1972, Anderson et al. 2011), which links local (α) and regional (γ) diversity. A useful and stimulating framework to organize approaches on multiple scales in ecology is the metacommunity concept: a set of local communities that are potentially linked by dispersal of one or more interacting species (Holyoak and Mata 2008). Although still in its infancy, metacommunity thinking provides several different sets of testable propositions that evoke different mechanisms of community assembly to explain the patterns of diversity across multiple scales (Leibold et al. 2004, Leibold 2011).

Even though some studies have emphasized the importance of stochastic process for the determination of species diversity patterns (Hubbell 1999, Chase 2010, Chase and Myers 2011), evidences giving support to the stronger role of deterministic processes related to environmental heterogeneity continues to grow (e.g. Gilbert and Lechowicz 2004, Cottenie 2005, Myers et al. 2013, Brown et al. 2013). Nevertheless, ecologists seem to agree that both stochastic (neutral) and deterministic (niche-based) processes may operate simultaneously to shape diversity patterns (Ricklefs and Schluter 1993, Vellend 2010, Chase and Myers 2011) and that they are, at the same time, strongly affected by the choice of sampling scale and location (Garzon-Lopez 2014).

Environmental heterogeneity can affect species diversity throughout different mechanisms that are hierarchically interconnected and operate at different scales, in consequence of variation of parameters such as topography, soil, climate, water-energy dynamics and disturbances (Whittaker et al. 2001, Willig et al. 2003, Siefert 2012). These factors and mechanisms act as filters and determine which species from the regional species pool can establish in the local community (Keddy 1992)

In the Brazilian Atlantic Forest, a number of studies recently contributed to the analysis of the mechanisms that are structuring forces for compositional patterns of the tree community, particularly in the southern part of the region (Oliveira-Filho and Fontes 2000, Bergamin et al. 2012, Gonçalves and Souza 2013, Oliveira-Filho et al. 2013). Altogether, these studies demonstrated the primary importance of climate as driver to variation in the species composition. Despite these recent efforts, little is known about how different environmental processes interact, directly and indirectly as well as simultaneously, to affect community dynamics across spatial scales.

In the present study, we use data from the IFFSC to investigate the patterns of species diversity of subtropical Atlantic forests and its relationships with environmental heterogeneity. A metacommunity perspective (Leibold 2011) and Structural Equation Modeling (SEM; Bollen 1989, Kaplan 2000) were used to disentangle the relative importance of different processes and parameters associated to environmental filtering, such as topography, climate and metrics that related to landscape heterogeneity, for tree species diversity, considering both α- and β-diversity. SEM constitutes a scientific method which is highly indicated for the analysis of ecological systems, e.g. in studying networks of relationships among observed and latent variables, as it presents strong and explicit connections between empirical data and theoretical ideas (Grace et al. 2010). We used the partial least squares (PLS) approach to structural equation modeling , known as PLS Path Modeling (PLS-PM, Tenenhaus et al. 2005, Esposito Vinzi et al. 2010a). PLS-PM can be understood as a component-based estimation method, which has been applied as a more flexible alternative to covariance-based SEM (CB-SEM). Unlike the CB- SEM, PLS-PM does not aim at reproducing the sample covariance matrix under the statistical assumptions of multivariate normal distribution and independent observations (Esposito Vinzi et al., 2010a). Thus, PLS-PM is a variance-based model strongly oriented towards prediction .

The results are presented in the following chapter, formatted in the form of a paper to be submitted to “Perspectives in Plant Ecology, Evolution and Systematics”. We expect that these results contribute to a better understanding how environmental filtering processes interact to affect tree community assembly at multiple spatial scales in South Brazilian Atlantic Forest.

ARTICLE: Interactive effects of environmental filtering predict beta-diversity patterns in a subtropical forest metacommunity

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Abstract

The metacommunity framework offers a possibility to better understand how ecological processes influence patterns of species diversity along environmental gradients. The species-sorting perspective predicts that community composition varies in response to differences in environmental conditions among habitat patches. Our study focused on this perspective, aiming to understand how environmental filtering processes interact directly and indirectly on diversity patterns in an area of 95000 km^2 (data from 432 forest plots). We employed structural equation modeling (PLS Path Modeling) to disentangle the interactive effects of topography, climate, water-energy balance, and geometry of forest patches upon the alpha and beta diversity of a subtropical forest metacommunity in southern Brazil. Factors related to environmental filtering showed substantial effects upon tree alpha and beta diversity. The total amount of variation in beta diversity explained by environmental filtering was high (64%) and was even more when together with alpha diversity (73%), corroborating the prediction of species-sorting model at the metacommunity level. Climatic extremes, water-energy balance and alpha diversity were the key determinants of beta diversity and patch size and water-energy balance the key determinants of alpha diversity in the South Brazilian Atlantic forests. Partial mantel test showed that environmental effects occurred largely independent of spatial effects, reinforcing the tested prediction. Our study provides strong empirical support for the prediction that beta diversity primarily reflects deterministic factors associated with species niches and their responses to environmental conditions in the studied spatial scale.

Keywords: alpha diversity, Atlantic forest, climatic variation, species sorting, structural equation modeling.

Introduction

A metacommunity is defined, in the broadest sense, as a set of communities that are potentially linked by dispersal of multiple species (Leibold et al., 2004). Although the metacommunity framework is still in early stages of development, it gathers a set of testable propositions which differ in the relative importance given to dispersal, environmental filtering, stochastic mechanisms of colonization and extinction, and biotic interactions in community assembly (Holyoak et al., 2005; Leibold, 2009; Meynard et al., 2013). By this, the metacommunity framework expands the field of community ecology to consider the way in which these ecological processes determine patterns of species distributions, composition or diversity at multiple spatial scales, i.e., at the local (within communities) and regional (between communities) level (Chase et al., 2005; Holyoak et al., 2005; Logue et al. 2011). Thus, metacommunity dynamics are determined by the sum of both local and regional processes (Holyoak and Mata, 2008).

The metacommunity framework explicitly encompasses four perspectives, each one evoking different mechanisms of community assembly as well as specific propositions and predictions (see Leibold, 2011), especially regarding the role of dispersal and of local environmental heterogeneity in community assembly: (i) the patch dynamics (PD) model emphasizes colonization and extinction processes in patches with identical environmental conditions; (ii) the mass-effects (ME) model highlights the role of dispersal in maintaining source-sink relations in different patches; (iii) the neutral model (NM) stresses the importance of both chance demographic events and chance dispersal events; and (iv) the species-sorting (SS) model emphasizes the role of environmental heterogeneity among patches with distinct environmental conditions that affect the fitness of species. The ME and SS perspectives are the most commonly tested and supported metacommunity perspectives in the ecological literature (Cottenie, 2005; Logue et al., 2011), on the other hand, knowledge on how different ecological processes interact to affect diversity patterns at multiple spatial scales still is rather fragmentary.

Increasingly, ecologists seem to agree that both stochastic (neutral) and deterministic (niche-based) processes may operate simultaneously at different spatial scales to shape diversity patterns (Ricklefs and Schluter, 1993; Vellend, 2010; Chase and Myers, 2011). However, the evidence in favor of deterministic processes is strong. Several recent studies have supported the higher importance of environmental filtering in maintenance of tree coexistence and diversity in tropical and temperate forests (e.g. Gilbert and Lechowicz, 2004; Keppel et al., 2011; Brown et al., 2013; Myers et al., 2013; Siefert et al., 2013). Specifically, variation in environmental characteristics (i.e. environmental heterogeneity) can affect diversity through different factors that are hierarchically interconnected and operate at different scales, such as topography, edaphic conditions, climatic conditions, water-energy dynamics and disturbances (Whittaker et al., 2001; Willig et al., 2003). These factors and processes act as filters and determine which species from the regional species pool can establish in the local community (Keddy and Weiher, 1999).

Here, we focus on the SS perspective in order to improve the understanding of how environmental filtering processes interact directly and indirectly to affect patterns of alpha (α) and beta (β) diversity in a subtropical forest metacommunity. Whittaker’s components of diversity are designed to measure how diversified the species are within a site, and how diversified the sites within a region are regarding species composition (Legendre and De Cáceres, 2013). We expect that these components of diversity can provide signs of the indirect and direct effects of environmental processes operating within and between communities. We depict these processes in terms of topography (elevation, aspect and slope), forest patch geometry (area, shape and connectivity), climate (annual trends, seasonality and extreme factors), and water-energy balance (evapotranspiration). Particularly, the integration of traits of landscape variability into the metacommunity framework is essential because landscape configuration alters ecological processes that govern and distinguish metacommunity models (Biswas and Wagner, 2012). Following Leibold (2009), we define the SS perspective as the variation in community composition determined by the optimization of fitness among species across discrete areas of habitat (patches) that vary in environmental conditions. The key prediction of this viewpoint is that community composition should depend on environmental effects independent of spatial effects (e.g. dispersal), thus local community composition should strongly track local environmental conditions (Leibold, 2009, 2011). According to Leibold (2011), dispersal is important in SS only because it provides the stream of potential colonists that allows community composition to track environmental changes in time and space. Thus, dispersal is considered to be sufficiently high to allow species to fill niches within environmentally heterogeneous habitat patches because of niche diversification (Logue et al., 2011). Specifically, the SS model presents five propositions, as follows: dispersal affects colonists, interactions among species are direct and indirect, interactions in local communities depend on local environments, coexistence requires stabilizing effects in local communities, and stochastic demography is important for allowing coexistence (Leibold, 2011).

To disentangle the interactive effects of the different environmental filtering processes on tree alpha and beta diversity at metacommunity level, we built structural equation models using tree community data from 432 forest plots distributed in a total area of 95000 km^2 in subtropical southern Brazil. We started from a conceptual structural model that assumes all potential associative and predictive relationships among ecological factors and tree species diversity on the local and the metacommunity scale (Fig. 1). Specifically, our aim was to test the prediction that variation in community composition among forest plots (beta diversity) reflects strong environmental effects, so that spatial niche separation between tree species occurs along gradients of environmental conditions (i.e. species occupy patches according to their habitat requirements). We thus expect that environmental factors explain most of the total variation in community composition and that, therefore, the unexplained variation (or residual variance) that can be assigned or not to spatial effects, should be low in the model.

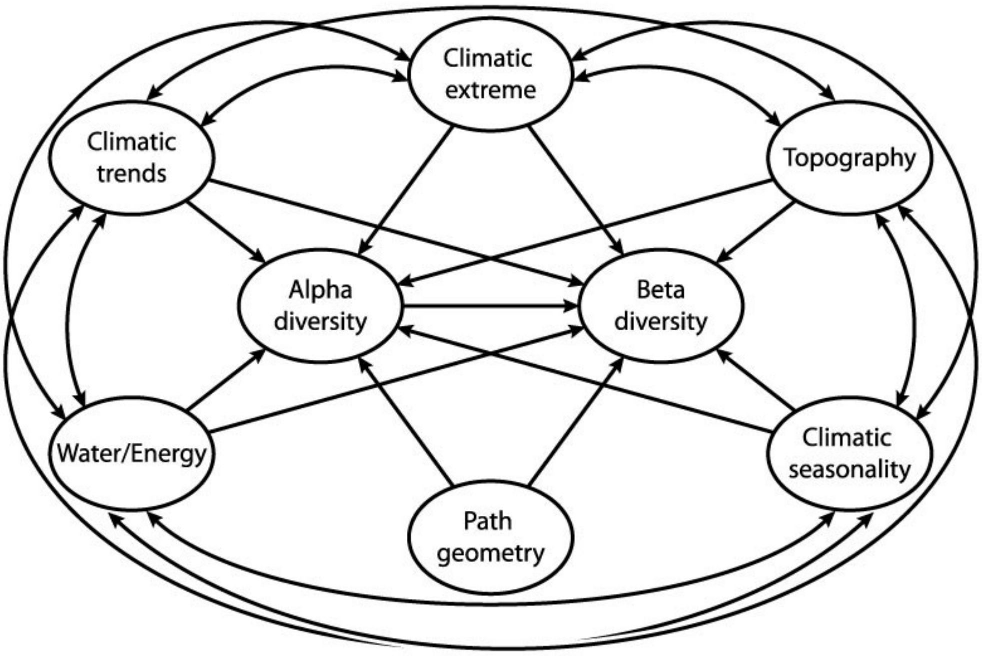

Figure 1: Conceptual structural model illustrating predictive relationships among predictor and response latent variables (straight arrows) and associative (correlational) relationships among predictor latent variables (curved arrows).

Materials and Methods

Study region

The study region comprises the state of Santa Catarina located in subtropical southern Brazil (Fig. 2), at the southern limit of the Brazilian Atlantic Forest, one of the world's biodiversity hotspots (Mittermeier et al., 2004). This region encompasses important environmental gradients in geology, topography and climate (Leite and Klein, 1990). In terms of geology, from East to West, the region is formed by: (i) Holocene sediments, which are situated along most of the coast and in the major river valleys; (ii) a strip of the crystalline basement rock, mostly Precambrian; (iii) Gondwanic sedimentary rocks; and (iv) basaltic rocks of the western highland (Scheibe, 1986). The soils are highly variable, from sandy textured to very clayey textured soils (Embrapa, 2004), with the predominance of Cambisols, Ferralsols and Nitisols (Embrapa, 2006). The Serra Geral and the Serra do Mar mountain ranges mark, respectively, the southern and northern section of the Atlantic escarpment of the highland, representing the highest elevations of the state (Klein, 1984). About 56% of the surface of Santa Catarina is covered by areas in altitudinal range of the 300-900 m, 20% by ones 900 m above sea level and 23% by ones with maximum elevation about 300 m (Nimer, 1989).

The vegetation makes part of the Atlantic Forest biome, and is commonly classified into three main forest types (Klein, 1978; IBGE, 2012): (1) Rain Forest (RF), situated in the coastal mountain range up to 200 km inwards; (2) Mixed *Araucaria* Forest (MAF) on the highland, on the edges of the sierras and in the northwestern portion of the state, spanning the cooler higher elevations. Here, forests occur in mosaics with grasslands; and (3) Seasonal

Forest (SF) in the western part of the region along the Uruguai river and its tributaries, in an altitudinal range from 150 to 800 m. Currently, only 29% of original forest cover remains in SC (Vibrans et al., 2013). RF originally covered about 29.282 km^2 of the surface of Santa Catarina, MAF 42.851 km^2 and SF 7.670 km^2 (Klein, 1978). Today, their cover has been reduced to 40%, 24% and 16% of original forest cover, respectively (Vibrans et al., 2013).

Climate in the region corresponds to Cfa (temperate humid with hot summers and temperature of the hottest month > 22 °C) and Cfb (warm summers with hottest month temperature < 22 °C) (Peel et al., 2007). Cfa predominates throughout most of the region, while Cfb occurs at higher altitudes in the highlands and in the northwestern part of the state. Mean annual temperature is 17.5 °C, and ranges (in mean) from 24 °C in summer to 13 °C in the winter, where frosts are common and snowfalls may occur in the highest areas (Nimer, 1989). Precipitation is evenly distributed throughout the year, with mean annual equal to 1660 mm, ranging from 1314 mm to 2305 mm.

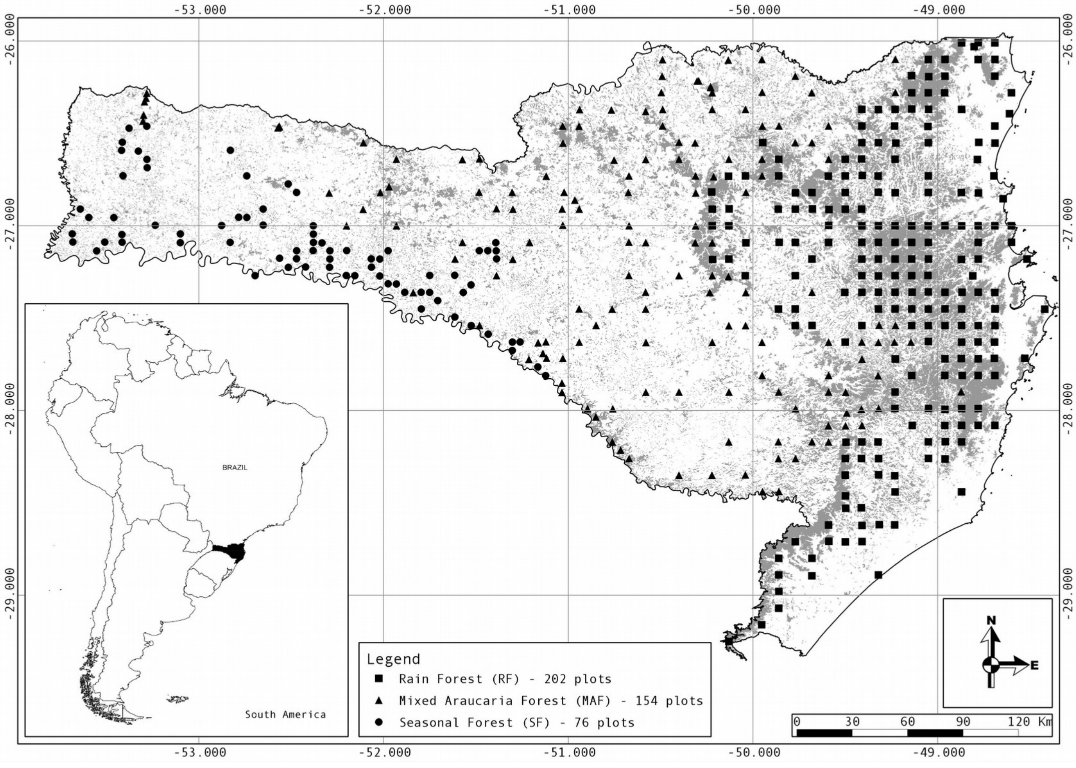

Figure 2: Geographical location of 432 forest plots embedded in Atlantic forests (Rain, Mixed Araucaria and Seasonal forests) in the state of Santa Catarina, southern Brazil. Grey areas indicate the remaining forest patches according to Fundação SOS Mata Atlântica (2013).

Tree species data

Tree species data were obtained from the Forest Inventory of Santa Catarina (Inventário Florístico Florestal de Santa Catarina, IFFSC; http://www.iff.sc.gov.br), a government database built with support from the Regional University of Blumenau (FURB), the Federal University of Santa Catarina (UFSC), the Agricultural Research and Rural Extension Company of Santa Catarina (EPAGRI) and the Brazilian Forest Service (SFB). The forest plots were systematically distributed at a 10 × 10 km grid across the entire state's territory and 5 × 5 km in the SF (the forest type most reduced in cover), overlaid to land use map based on classification of SPOT-4 images from 2005. Each forest plot is composed by a cluster of four crosswise subunits of 1.000 m^2 (20 × 50 m) allocated at four cardinal points, at 30 m away from a central point. We used a total of 432 forest plots. The number of them per forest type is proportional to its total area, with 202 forest plots for RF, 154 for MAF and 76 for SF (Fig. 2). Within each plot, all trees (including tree ferns) over > 10 cm diameter at breast height (at 1.3 m above ground) were measured and identified (see Vibrans et al., 2010 for details about sampling design and methods).

Environmental descriptors

We summarized environmental filtering processes through six blocks of variables: topography, forest patch geometry, climatic trends, seasonality, extreme climatic factors, and water-energy balance (Supplementary Material Appendix 1, Table A1). Each block of environmental predictors represents a latent variable (LV) in our structural equation modeling framework. Here we define latent variable (or construct) as an unobservable variable for which we have no direct measurements, but which is represented by a number of (measured) observed variables (Bollen, 1989). It is assumed that an observed variable, referred to herein as manifest variable (MV), contains information that reflects or indicates some aspect of their LV (Grace, 2006; Grace et al., 2010). In our case, each LV is a linear combination of the corresponding MVs, which measure different aspects (but at few dimensions) of the same latent concept (Esposito Vinzi et al., 2010a).

We used the LV topography to depict environmental conditions prevailing within each forest plot, as topographic variables can be considered as a proxy for microclimatic conditions (De Cáceres et al., 2012). To characterize the broad-scale environmental conditions in the study region, we used the LVs related to climatic heterogeneity (climatic trends, seasonality, climatic extreme) and to evapotranspiration (water-energy), an indication of energy supply, water balance and plant productivity (Fisher et al., 2011). Additionally, we used forest patch geometry to represent patch quality, which is an important aspect in the SS perspective (Leibold et al., 2004), and also to illustrate anthropogenic influences related to habitat fragmentation and disturbance. As ecological systems are spatially and temporally heterogeneous, the inclusion of features of the landscape such as area, shape and connectivity of the patches is fundamental once the landscape patterns as perceived by the organisms affect several fundamental metacommunity processes (Biswas and Wagner, 2012).

All topographic and climate variables were obtained from the WorldClim Global Climate with spatial resolution equivalent to 30 arc-seconds (~ 1 km) (Hijmans et al., 2005). The variables related to water-energy balance were gathered from the Global Aridity and PET Database (Trabucco and Zomer, 2009). Annual evapotranspiration (AET) is an index of actual water flux related to habitat productivity (Rosenzweig, 1968), potential evapotranspiration (PET) is proportional to the ability of the atmosphere to remove water through evapotranspiration, and Global Aridity Index (GAI) is expressed as a generalized function of precipitation and PET, which may be used to quantify precipitation availability over atmospheric water demand (Trabucco and Zomer, 2009). Finally, predictors related to patch geometry were obtained from the IFFSC database. These variables were measured in a circular area (buffer) of 2800 m radius (ca. 2460 ha) around the centre of each forest plot. Patch area measures the forest habitat availability inside the buffer, patch core area measures the forest portion excluding their edge, which was defined by a fixed distance of 50 m, and patch shape is an index that assesses the geometric complexity (curvilinear, compact, elongated or rounded forms) of a forest patch in comparison to a circular patch. The value of the index is equal to 1 when a patch is circular; the more it deviates from the circular pattern, the greater the value of the index will be.

Species diversity

We measure tree species diversity within and between forest plots through Whittaker's components of diversity (Whitaker, 1972). We defined alpha diversity (α-diversity) as the local diversity within plots and beta diversity (β-diversity) as the variation in community composition among plots in the study region, i.e., the compositional differentiation among the forest patches of our metacommunity. The LV α-diversity was composed by three diversity measures accounting for the effective number of species present at individual forest plots. The effective number of species or Hill numbers of order q (Hill, 1973) is the number of equally common species needed to produce the observed value of a diversity index (which is determined by q, Jost et al., 2011). The value of q determines the sensitivity of the measure to species relative abundances, thus we used $q = 0$ to consider all species equally (species richness), $q = 1$ to emphasize common species (exponential of Shannon entropy) and $q = 2$ to emphasize dominant species (inverse Simpson concentration). The LV β-diversity was represented by the first two axes of a principal coordinates analysis

(PCoA) of vegetation data based on the Hellinger distance matrix. Hellinger distance (Legendre and Gallagher, 2001) is an appropriate alternative for the β-diversity assessment, as it assigns low weights to rare species to measure the dissimilarity between each pair of sampling units (Legendre and De Cáceres, 2013). Hill numbers were calculated in the package 'vegan' using function 'renyi' (Oksanen et al., 2013), in the R environment (R Core Development Team, 2013).

Structural equation modeling

We used the partial least squares (PLS) approach to structural equation modeling (SEM, Bollen, 1989; Kaplan, 2000), known as PLS Path Modeling (PLS-PM, Tenenhaus et al., 2005; Esposito Vinzi et al., 2010a) in order to test the validity of a set of predictive relationships among LVs (Fig. 1). Overall, SEM constitutes a scientific framework highly indicated for studying networks of relationships involving MVs and LVs due to its strong and explicit connection between empirical data and theoretical ideas (Grace, 2006; Grace et al., 2010).

PLS-PM can be understood as a component-based estimation method, which has been applied as a more flexible alternative to covariance-based SEM (CB-SEM). Unlike the CB-SEM, PLS-PM does not aim at reproducing the sample covariance matrix under the statistical assumptions of multivariate normal distribution and independent observations (Esposito Vinzi et al., 2010a). Thus, PLS-PM is a variance-based model strongly oriented towards prediction (i.e. it attempts to maximize the explained variance for both the MVs and LVs), while CB-SEM is a covariance-based model strongly oriented to optimize the statistical accuracy of the estimated parameters (Chin and Newsted, 1999; Tenenhaus et al., 2005; Esposito Vinzi et al., 2010a). While CB-SEM is based on the classical parametric inferential framework, PLS-PM is based on nonparametric resampling procedures such as Bootstrap and Jackknife (Chin, 1998). PLS-PM provides the so-called ‘latent variable scores’ that have beneficial characteristics for prediction, and then the endogenous variable’s scores are regressed on the latent predictor variables scores (Esposito Vinzi et al., 2010a; Henseler and Sarstedt, 2013). The path coefficients in PLS-PM are calculated as the standardized regression coefficients of a (multiple) linear regression of each endogenous LV on the predictor LVs (Esposito Vinzi et al., 2010a). Overall, the path coefficients measure the strength and direction of direct (simple paths) and indirect (compounds paths) effects among LVs. As mentioned before, a LV is an unobservable variable (construct) that is indirectly described by a set of MVs (Tenenhaus et al., 2005). In the statistical sense, we measured the LVs as linear combinations of its own MVs. Thus, PLS-PM is referred to as a component-based method because LVs are calculated as a weighted sum of their MVs, similar to what is done in PCA (Sanchez, 2013).

The PLS-PM framework encompasses two sets of linear equations models: (i) the structural model (or inner model) relating some endogenous LVs to other LVs (according to Fig. 1), and (ii) the measurement model (or outer model) relating the MVs to their own LV (Wold, 1985; Lohmöller, 1989). Basically, there are two ways to relate MVs to their own LV: the reflective way and the formative way (Tenenhaus et al., 2005). In the reflexive mode (outwards directed), each MV ‘reflects’ (is an effect of) the same latent concept, thus any block of MVs must be homogeneous and unidimensional. In the formative mode (inwards directed), the LVs are ‘generated’ (caused) by its own MVs, where they are a linear function of its LV plus a residual term. This implies considering the block of MVs as full dimensional with the LVs being formed by as many dimensions as there are MVs in a block (Esposito Vinzi et al., 2010b). In many real applications, the LVs are neither unidimensional (reflexive) nor full dimensional (formative), which implies use an estimation capable to yield solutions somewhere between the reflexive and formative ways (Esposito Vinzi et al., 2010b). Here we used the PLScore mode, which is an intermediate form between the reflexive and formative modes, where the blocks are multidimensional but with fewer dimensions than the number of MVs (Esposito Vinzi and Russolillo, 2013; Esposito Vinzi et al., 2010b). PLScore mode is oriented to maximize correlations among LVs, using PLS regression (PLS-R, Tenenhaus, 1998) to compute the outer weights. We employed PLS-R within the outer estimation phase as a more stable and better interpretable alternative to OLS regression in the presence of multicollinearity among MVs (Esposito Vinzi et al., 2010a). PLS-R regression decomposes both predictors (X) and responses (Y) as a product of a common set of orthogonal components (X-scores), which are predictors of Y and also model X, and also a set of specific loadings (Abdi, 2003). The orthogonality of the PLS components eliminate the multicollinearity problem inside of LVs. We chose the number of PLS components for each LV through cross-validation (Wold et al., 2001). When the number of PLS components equals 1, the outer estimation is just like a reflexive mode, while when the number of PLS components equals the number of MVs in the LV, the outer estimation is just like a formative model (Esposito Vinzi et al., 2010b).

We checked the quality of the outer model (or measurement model) by means of their coefficients of loading (i.e. correlation between a LV and its own MVs) and communality, which is only the squared loading (i.e. fraction of variance of the MVs explained by their own LV) (Tenenhaus et al., 2005). In this procedure, we retained in the accepted model only MVs with loading higher than 0.7 (Esposito Vinzi et al., 2010a). As communality is simply a squared loading, a loading equal to 0.7 means that $0.7^2 \approx 50\%$ of the variance in an MV is captured by its LV (Sanchez, 2013). We assessed the quality of the inner model (or structural model) by examining the following coefficients: coefficient of determination, R^2 (i.e. the amount of variance in a endogenous LV which is explained by the predictor LVs), redundancy (i.e. the amount of variance of MVs in an endogenous LV that is predicted by the predictor LVs associated to endogenous LV), goodness-of-fit index (GoF, Tenenhaus et al., 2004) and the relative GoF (GoF_{rel}, Esposito Vinzi et al., 2010a). GoF represents the geometric mean of the average communality and the average R^2, and the GoF_{rel} contrasts the communalities of a PLS-R with the communalities of a PCA, and the R^2 values of a PLS-R with the R^2 values of a CCoA. We used these indexes to provide measures of overall prediction performance for the whole model as well as for the outer and inner models separately (see Henseler and Sarstedt, 2013, for more details). We examined the cross-loadings matrix as a criterion of discriminant validity (Chin, 1998). By this criterion, the loading of each MV is expected to be larger than all of its cross-loadings, thus if an MV has a higher correlation with another LV than with its respective LV, the appropriateness of the model should be reconsidered (Henseler et al., 2009). All raw variables were submitted to standardization: we scaled the MVs to unit variance by dividing them by their standard deviations, and centered them by subtracting their averages (Wold et al., 2001).

Model validation procedure was based on bootstrap resampling, where bootstrap confidence intervals were obtained by 1000 iterations in order to assess the precision of the PLS-PM parameter estimates, i.e., the outer weights, the loadings, the path coefficients, the R^2 values and the total effects (Tenenhaus et al., 2005; Esposito-Vinzi et al., 2010a). Bootstrap validation for direct effects (standardized path coefficients) is shown in results. The initial PLS path models were performed in the package ‘plspm’ (Sanchez et al., 2013), in the R environment (R Core Development Team, 2013), and the final PLS path model was implemented in the PLSPM module of the XLSTAT software (Addinsoft SARL, 2013), which allowed us to use advanced options not available in R.

Mantel test

Complementarily, we used partial Mantel test (Legendre and Legendre, 1998) to verify if the observed beta diversity patterns were consistent with the species-sorting model or if significant spatial patterns, that could be consistent with any of the other perspectives, existed. We tested the spatial correlation between the ecological distance (beta diversity) and the environmental distance while controlling for spatial distance (i.e., independent of spatial distance), and tested the correlation between the beta diversity and the spatial distance independent of environmental distance. To assess how much the correlations decreased by controlling the effect of spatial distance, we used simple Mantel tests. The standardized Mantel statistic r_M (analogous to a Pearson's r coefficient) was computed according to Legendre and Legendre (1998). The ecological distance was based on a Hellinger distance matrix, environmental distance on a Euclidean distance matrix of the standardized variables used in PLS-PM, and spatial distance on a Euclidean distance matrix of the geographical coordinates of the forest plots. The geographical coordinates in a spherical system (latitude/longitude) were centered prior to the computation of Euclidean distance matrix (Borcard et al., 2011). The Mantel test was performed in the package 'vegan' (Oksanen et al., 2013), in the R environment (R Core Development Team, 2013).

Results

A total of 660 tree species were recorded in the 432 IFFSC forest plots in southern Brazil. The number of species was higher in Rain Forest (572) than in the Mixed *Araucaria* Forest (370) and Seasonal Forest (205). The number of species was weakly correlated with the number of individuals sampled in the whole data set ($r = 0.35$) as well as in each forest type, as follows: Rain Forest ($r = 0.49$), Mixed *Araucaria* Forest ($r = 0.13$) and Seasonal Forest ($r = 0.28$).

The prediction performance of the PLS-PM was high for the outer, inner and global models (Table 1). In general, the coefficients presented in table 1 showed that manifest and latent variables were well predicted by the PLS-PM framework. The fit of the outer, inner and global models improved substantially when weak manifest variables (with loading < 0.7) were excluded. The following manifest variables were discarded: slope, aspect, patch shape index, patch connectivity, precipitation seasonality, mean temperature of wettest quarter, precipitation of driest month, precipitation of driest quarter, precipitation of coldest quarter and global aridity index. These variables were weakly correlated with alpha and beta diversity. The R^2 coefficient showed that endogenous latent variables were acceptably predicted by the explanatory latent variables (Table 1). The R^2 values provided an unbiased estimate of the proportion of variance explained; adjusted R^2 provided very similar values to R^2. The average communality coefficient indicated that variance of the manifest variables was well reproduced by its respective latent variable (average communality ≥ 0.50, Table 1).

Table 1: (a) Overall Prediction performance of the PLS Path Modeling measured through the goodness-of-fit index (GoF) and the relative goodness-of-fit index (GoFrel) for the global model and for the measurement (outer) and structural (inner) models. Shown are the GoF indexes obtained by 1000 bootstrap resamples (Mean boot.), the bootstrap standard error (Std. error), and the 95% bootstrap confidence interval. (b) Global fit of each regression equation relating each endogenous latent variable to their predictor latent variables is shown through R2 and adjusted R2 coefficients, global quality measure of the outer model is shown through the average communality (Av. com.), and global quality measure of the inner model by the average redundancy (Av. red.).

(a)	**Value**	**Mean boot.**	**Std. error**	**Lower (95%)**	**Upper (95%)**
Global GoF	0.690	0.692	0.017	0.660	0.727
GoF$_{rel}$	0.860	0.875	0.028	0.801	0.917
GoF outer model	0.957	0.953	0.013	0.925	0.979
GoF inner model	0.900	0.919	0.026	0.840	0.951
Mean	0.851	0.860	0.021		

(b)	**Type**	$\boldsymbol{R^2}$	**adj.** $\boldsymbol{R^2}$	**Av. com.**	**Av. red.**
Topography	Exogenous			-	
Patch size	Exogenous			0.954	
Climatic trends	Endogenous	0.947	0.947	0.500	0.470
Seasonality	Endogenous	0.503	0.502	0.596	0.300
Extreme climatic factors	Endogenous	0.981	0.981	0.588	0.577
Water-energy balance	Endogenous	0.779	0.778	0.939	0.732
Alpha diversity	Endogenous	0.350	0.342	0.790	0.276
Beta diversity	Endogenous	0.734	0.730	0.500	0.367
Mean		0.716	0.713	0.666	0.454

Factors related to environmental filtering showed substantial effects upon tree alpha and beta diversity. In relation to alpha diversity, environmental filtering explained 35% of the total variation (Table 1). Topography, patch size, seasonality and water-energy balance had a direct significant effect on alpha diversity (Table 2, Fig. 3). Alpha diversity decreased with increasing topography. Topography had an indirect path on alpha diversity mediated through climatic trends (Table 3). Alpha diversity increased with increasing patch size and water-energy balance through a direct path, while it decreased with increasing seasonality. The model showed an indirect path mediated through topography and climatic trends, but the relations between patch size, water-energy balance and alpha diversity can not be explained through any other relations in the model.

Table 2: Direct effects of the predictor latent variables upon the response latent variables (alpha and beta diversity) measured through standardized path coefficients (SPC). Shown are the standard error of the path coefficients (Std. error), the significance test of the coefficients (t) and probability (Pr > |t|), the bootstrap coefficients obtained by 1000 bootstrap resamples (Mean boot.), the bootstrap standard error (Std. error), and the 95% bootstrap confidence interval.

Alpha diversity	**SPC**	**Std. error**	**t**	**Pr > |t|**	**Mean boot.**	**Std. error boot.**	**Lower (95%)**	**Upper (95%)**
Topography	–0.748	0.205	–3.652	0.000	–0.781	0.236	–1.267	–0.322
Patch size	0.385	0.045	8.605	0.000	0.383	0.043	0.291	0.471
Climatic trends	–0.560	0.333	–1.681	0.094	–0.797	0.652	–2.438	0.116
Seasonality	–0.246	0.100	–2.451	0.015	–0.235	0.094	–0.407	–0.044
Extreme climatic factors	0.047	0.283	0.166	0.868	0.254	0.532	–0.535	1.592
Water-energy balance	0.200	0.085	2.366	0.018	0.214	0.100	0.039	0.438
Beta diversity	**SPC**	**Std. error**	**t**	**Pr > |t|**	**Mean boot.**	**Std. error boot.**	**Lower (95%)**	**Upper (95%)**
Topography	0.316	0.133	2.375	0.018	0.404	0.187	0.078	0.824
Patch size	–0.204	0.031	–6.556	0.000	–0.182	0.046	–0.272	–0.090
Climatic trends	0.204	0.214	0.950	0.343	0.603	0.677	–0.178	2.443
Seasonality	–0.090	0.065	–1.399	0.162	–0.076	0.062	–0.195	0.053
Extreme climatic factors	–0.493	0.182	–2.713	0.007	–0.812	0.549	–2.288	–0.167
Water-energy balance	0.241	0.055	4.419	0.000	0.151	0.134	–0.152	0.350
Alpha diversity	–0.384	0.031	–12.345	0.000	–0.370	0.032	–0.431	–0.305

The total amount of variation in beta diversity explained by factors related to environmental filtering together with alpha diversity was high ($R^2 = 0.73$, Table 1). However, environmental filtering alone explained a large fraction of variation in community composition among forest plots ($R^2 = 0.64$, complete model not shown). Topography, patch size, extreme climatic factors, water-energy balance and alpha diversity had a direct significant effect on beta diversity (Table 2, Fig. 3). The structural model showed both indirect and direct paths (effects) between topography, patch size, extreme factors, water-energy balance and beta diversity, and a direct path between alpha and beta diversity.

However, both extreme factors and water-energy balance had a low indirect effect on beta diversity (see Table 3). Beta diversity increased with increasing topography (elevation) inside forest plots (Fig. 4). Topography had an indirect path on beta diversity mediated through extreme climatic factors and annual climatic trends (Table 3). Beta diversity decreased with increasing patch size (Fig. 4). The model showed an indirect path for patch size mediated through alpha diversity. Beta diversity decreased with increasing extreme factors, increased with increasing water-energy balance and decreased with increasing alpha diversity (Fig. 4). These three last relations can not be explained through any other relations in the model.

Table 3: Direct, indirect and total effects of the structural relationships among latent variables for the PLS Path Modeling. Direct effects are given by the standardized path coefficients, indirect effects as the product of the path coefficients through an indirect path, and the total effects as the sum of both the direct and indirect effects.

Relationship	**Direct effect**	**Indirect effect**	**Total effect**
Topography → Climatic trends	–0.973	0.000	–0.973
Topography → Seasonality	1.970	–1.335	0.635
Topography → Extreme climatic factors	–0.078	–0.887	–0.965
Topography → Water-energy balance	0.000	–0.120	–0.120
Topography → Alpha diversity	–0.748	0.320	–0.428
Topography → Beta diversity	0.316	0.355	0.672
Patch geometry → Alpha diversity	0.385	0.000	0.385
Patch geometry → Beta diversity	–0.204	–0.148	–0.352
Climatic trends → Seasonality	1.372	0.000	1.372
Climatic trends → Extreme climatic factors	0.929	0.036	0.965
Climatic trends → Water-energy balance	0.883	1.229	2.183
Climatic trends → Alpha diversity	–0.560	0.145	–0.415
Climatic trends → Beta diversity	0.204	0.086	0.290
Seasonality → Extreme climatic factors	0.026	0.0000	–0.1592
Seasonality → Water-energy balance	1.016	–0.003	1.013
Seasonality → Alpha diversity	–0.246	0.204	–0.042
Seasonality → Beta diversity	–0.090	0.247	0.157
Extreme climatic factors → Water-energy balance	–0.098	0.0000	–0.098
Extreme climatic factors → Alpha diversity	0.047	–0.020	0.027

Extreme climatic factors → Beta diversity	–0.493	–0.034	–0.527
Water-energy balance → Alpha diversity	0.200	0.0000	0.200
Water-energy balance → Beta diversity	0.241	–0.077	0.164
Alpha diversity → Beta diversity	–0.384	0.0000	–0.384

We found a significant correlation between beta diversity and environmental distance independent of the spatial proximity of the forest plots (partial Mantel $r_M = 0.45$, $P = 0.001$). The correlation in question was little reduced by partialling out the effect of spatial distance. The Mantel correlation (r_M) between beta diversity and environmental distance was 0.55 ($P = 0.001$), indicating that environmental effects occurred largely independent of spatial effects, corroborating with the species-sorting model. On the other hand, we found a weak correlation between beta diversity and spatial proximity independent of the environmental distance (partial $r_M = 0.07$, $P > 0.05$), where partialling out the effect of the environment resulted in a quite reduced correlation, indicating that environmental variables were spatially structured. The Mantel correlation between beta diversity and spatial proximity was 0.37 ($P = 0.001$).

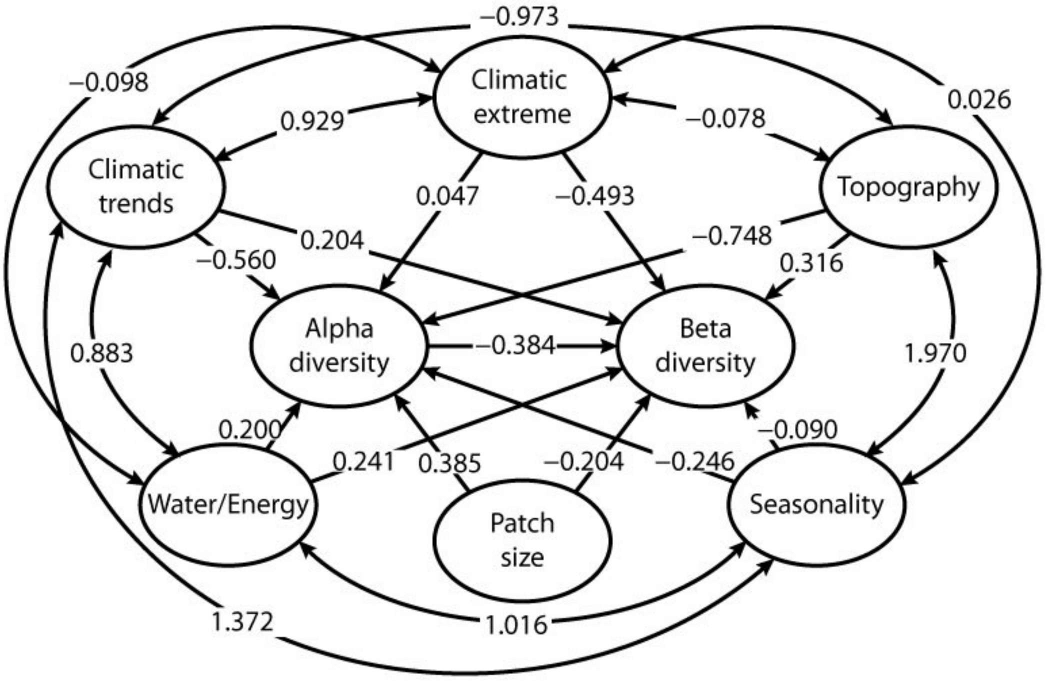

Figure 3: PLS Path Modeling showing the strength and direction of the postulated relationships among latent variables. Direct effects are shown through standardized path coefficients.

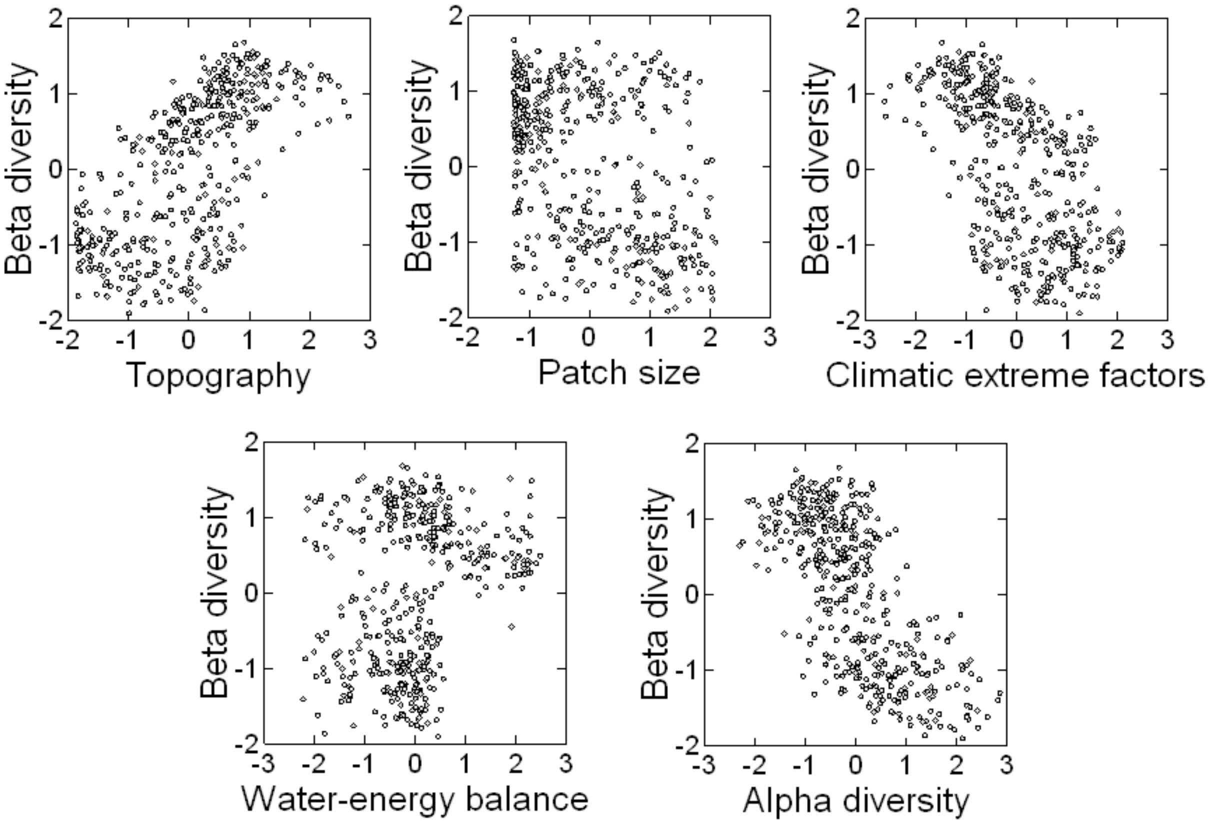

Figure 4: Significant relationships between predictor and response (beta diversity) latent variables. These relationships are shown via standardized latent variables scores obtained in PLS Path Modeling.

Discussion

Beta diversity and the species-sorting perspective of metacommunity theory

Overall, this study contributes to our understanding regarding how factors related to environmental filtering interact directly and indirectly to affect tree diversity patterns in subtropical forests. Our results support the ideas behind the species-sorting model, which apparently worked well to explain beta-diversity patterns at the metacommunity level. The species-sorting perspective predicts that community composition varies in response to differences in environmental conditions among habitat patches. This perspective has much in common with niche theory, which predicts that beta diversity varies deterministically along environmental gradients, but not along spatial gradients among communities that share the same species pool (Chase and Myers, 2011). Although both approaches predict that composition of communities should depend on environmental effects independent of spatial effects, environmental distance and spatial proximity together can, to some extent, influence beta diversity patterns at the metacommunity level as postulated by the mass-effects perspective in metacommunity theory (Leibold, 2011). When the spatial proximity affects both species and environment, we expect that habitat patches situated at short distances are more likely to be similar in terms of species composition and environmental conditions than those located further apart (Legendre, 1993). The results of the partial Mantel test suggest that environmental effects are independent of the spatial proximity of the forest plots, corroborating with the species-sorting model, and reinforce the idea that deterministic (niche-based) processes seem to play a key role in structuring tree beta diversity in the South Brazilian Atlantic forests.

It is important to point out that although spatial effects are often interpreted as dispersal limitation in the neutral and mass-effects perspectives, these effects can arise simply in consequence of the omission of important environmental variables (that are themselves spatially structured) in the model (Anderson et al., 2011; Dray et al., 2012) or due to a mismatch between the scale of analysis and the scale of species–environment relationships (De Knegt et al., 2010). Thus, the inferences on the role of niche-based vs. neutral processes in community assembly can be limited by possible confounding factors (Peres-Neto et al., 2012).

Among the four metacommunity models which have been described in literature, there is a variety of empirical evidence for species-sorting and mass-effects (Holyoak and Mata, 2008; Loeuille and Leibold, 2008; Logue et al., 2011). A compilation of 158 data sets by Cottenie (2005) found that 69 metacommunities (44%) best fit the species-sorting model, 46 (29%) a combination of species-sorting and mass-effects models, and only 13 (8%) the neutral or patch dynamics models; 19 data sets could not be uniquely associated with these three types, and 11 had no significant components. Independent of the perspective evoked, we suppose that most of the metacommunities should display some significant environmental component due to differences in fitness among species in consequence of environmental constraints. Conceptually, species sorting is the variation in community composition that is determined by the optimization of fitness among species across patches (Leibold, 2009). Unlike under the neutral perspective, here dispersal only is important to allow that compositional changes follow changes in local environmental conditions (Leibold et al., 2004). Therefore, if variation in fitness in response to environmental constraints allows for different species in different habitat patches, dispersal can maintain persistent local populations, even in patches where they are at a disadvantage regarding their fitness (Vellend, 2010).

Determinants of tree alpha and beta diversity

We found that factors related to environmental filtering explained a large fraction of the total variance of beta diversity compared to alpha diversity at the metacommunity level. These results indicate that spatial scale dictates the perception of which processes predominate. Thus, our results suggest that beta diversity was well predicted by coarse-grained environmental drivers (e.g. climate) that operate at large spatial scales (regional/continental), but alpha diversity not. The high unexplained variation we observed for alpha diversity may be attributed in part to the low representativeness of fine-grained drivers in our study. Patch area, patch core area and patch shape were the only variables closest to the fine-resolution available here. However, only area and core area (both combined in one latent variable) showed to play some role in determining local diversity. The positive relation between available patch area and local diversity we found is consistent with ecological theory (Ewers and Didham, 2006). In general, habitats with larger area and consequently high structural heterogeneity are expected to contain a large fraction of the landscape-wide species pool (Tscharntke et al., 2012). Thus, large forest patches contain the greatest local diversity as well as the greatest number of rare and shade-tolerant tree species (Hill et al., 2003).

In a recent meta-analysis from 63 published studies that analyzed vegetation–environment relationships, Siefert et al. (2012) demonstrated that the importance of climate factors relative to edaphic factors increased with increasing spatial extent and grain, suggesting that vegetation–environment relationships depend on the scale of observation. In our model, the good ability to predict variation in community composition was likely possible only due to the large spatial extent covered by the study region (95.000 km^2), which in turn favored our analysis to capture primarily climatic variation. Recently, Garzon-Lopez et al.

(2014) showed that species-specific spatial aggregation due to dispersal limitation was clearly a ‘confounding factor’ in the detection of environmental effects. They found that dispersal constraints decreased the number of significant habitat associations for tropical tree species, and that spatial scale dictated the relative importance of deterministic (niche-based) and stochastic (neutral) processes in the spatial distribution of tree species. Thus, significant habitat associations increased with the plot size (spatial grain), suggesting that species were neutrally structured at smaller scales and niche-structured at larger scales. Inspired by these findings, we highlight that further analysis is needed to quantify the influence of spatial aggregation characteristics on the species-environment relationships we found to evaluate the consistency of the observed patterns across the scales.

Although some processes, such as those related to climate, can influence both alpha and beta diversity, these components have different ecological determinants, as they reflect ecological mechanisms that operate within and among communities, respectively (Ricklefs and Schluter, 1993). It is well established that diversity within and between communities responds to several factors acting at several spatial scales, e.g., species interactions, landscape heterogeneity, the size of the regional species pool, migration/extinction dynamics, stochastic variation, and dispersal (Ricklefs, 1987; Ricklefs and Schluter, 1993). Even though we include here only drivers related to environmental heterogeneity of the region, these drivers in turn appear to be (according to the scale of our study) the key sources of variation of the tree beta diversity in the South Brazilian Atlantic forests.

Particularly, the extreme climatic factors, water-energy balance and alpha diversity were the key determinants of beta diversity, while patch size and water-energy balance were the key determinants of alpha diversity in the South Brazilian Atlantic forests. There is a growing observational evidence that climatic variation is an important broad-scale predictor of the tree species diversity (both alpha and beta) in several forest types across the world

(Davidar et al., 2007; Wang et al., 2008; Tang et al., 2012; Oliveira-Filho et al., 2013; Gonçalves and Souza, 2013). In this context, local communities are assembled from the regional pool through the interaction between the species traits and the climatic filters that regulate (together with other factors) the arrival of propagules of different species in any assemblage within a metacommunity (Keddy and Weiher, 1999; Weiher et al., 2011). As the climatic conditions vary in the study area along elevation gradients, various species occurring at lower altitudes where temperature conditions are milder are not found at higher altitudes or at sites where frequently strong selective phenomena such as killing frost, severe cold period and snowfalls occur (Oliveira-Filho et al., 2013). Thus, the harsh abiotic conditions impose a deterministic filter on community assembly, where a niche selection prevents a subset of the species pool from persisting in some localities (Chase and Myers, 2011). The fact that both alpha and beta diversity were positively related to water-energy balance (a linear combination of actual and potential evapotranspiration) stresses the role of both energy regime and water regime (an indicative of plant productivity) in the studied system. Evapotranspiration is one of the best climatic correlates of species diversity (Currie, 1991; Wright et al., 1993). Many studies have shown that diversity (as richness) correlates positively with evapotranspiration, suggesting that a positive relationship exists between richness and productivity of the habitat (Maurer, 2009). Overall, high productivity in habitats maintains larger numbers of individuals per species and thus reduces the probability of stochastic extinction, and may also increase the total variety of microhabitats and permit greater microhabitat specialization (Latham and Ricklefs, 1993).

When alpha diversity is very low relative to the gamma diversity (regional species pool), as in this study, beta diversity is expected by random chance to be very high (Chase and Mayers, 2011). As all three diversity components (α, β, γ) are interconnected, it is unclear whether a change in β is due to some assembly mechanism (deterministic or stochastic), or whether it is this mechanism that affects α, necessarily causing a concomitant change in β (Chase et al., 2011). We provided a robust way to deal with this situation using structural equation modeling. We suggest that this type of analytical framework is a powerful approach to disentangle the relative importance of various processes upon beta independent of alpha (and vice versa). A clear advantage of this framework is the ability to estimate direct and indirect effects in multiple pathways in contrast with the standard multivariate analyses, which consider only a single relationship at a time (direct effect).

It is important to note that our study was designated to test a specific prediction of ‘environmental control’ within the metacommunity framework (species-sorting perspective, Leibold, 2009, 2011). Therefore the species-environment relationships were postulated by means of simple assumptions regarding the role of environmental heterogeneity on beta diversity without considering others processes such as dispersal. Our model showed that deterministic (niche-based) factors had complex direct and indirect effects on beta diversity, explaining a large fraction of the total variance. Using structural equation modeling, we provide a strong empirical support for the tested prediction, highlighting the importance of deterministic factors associated with species niches and their responses to environmental conditions.

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References

Abdi, H., 2003. Partial Least Squares (PLS) Regression, in: Lewis-Beck, M, Bryman, A., Futing, T. (Eds.), Encyclopedia of Research Methods for the Social Sciences. Sage, Thousand Oaks, pp. 792–795.

Addinsoft. 2013. XLSTAT. Statistics Package for Excel. Available at: http://www.xlstat.com.

Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L., Sanders, N.J., Cornell, H. V, Comita, L.S., Davies, K.F., Harrison, S.P., Kraft, N.J.B., Stegen, J.C., Swenson, N.G., 2011. Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. Ecol. Lett. 14, 19–28.

Biswas, S.R., Wagner, H.H., 2012. Landscape contrast: a solution to hidden assumptions in the metacommunity concept? Landsc. Ecol. 27, 621–631.

Bollen, K.A., 1989. Structural equations with latent variables. Wiley, New York.

Borcard, D., Gillet, F., Legendre, P., 2011. Numerical Ecology with R. Springer, New York.

Brown, C., Burslem, D.F.R.P., Illian, J.B., Bao, L., Brockelman, W., Cao, M., Chang, L.W., Dattaraja, H.S., Davies, S., Gunatilleke, C.V.S., Gunatilleke, I. a U.N., Huang, J., Kassim, a R., Lafrankie, J. V, Lian, J., Lin, L., Ma, K., Mi, X., Nathalang, a, Noor, S., Ong, P., Sukumar, R., Su, S.H., Sun, I.F., Suresh, H.S., Tan, S., Thompson, J., Uriarte, M., Valencia, R., Yap, S.L., Ye, W., Law, R., 2013. Multispecies coexistence of trees in tropical forests: spatial signals of topographic niche differentiation increase with environmental heterogeneity. Proc. Biol. Sci. 280, 20130502.

Chase, J.M., Amarasekare, P., Cottenie, K., Gonzalez, A., Holt, R.D., Holyoak, M., Hoopes, M.F., Leibold, M.A., Loreau, M., Mouquet, N., Shurin, J.B., Tilman, D., 2005. Competing theories for competitive metacommunities, in: Holyoak, M., Leibold, M.A., Holt, R.D. (Eds.), Metacommunities Spatial Dynamics and Ecological Communities. The University of Chicago Press, Chicago, pp. 335–354.

Chase, J.M., Kraft, N.J.B., Smith, K.G., Vellend, M., Inouye, B.D., 2011. Using null models to disentangle variation in community dissimilarity from variation in α-diversity. Ecosphere 2, art24.

Chase, J.M., Myers, J.A., 2011. Disentangling the importance of ecological niches from stochastic processes across scales. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 366, 2351–2363.

Chin, W.W., 1998. The partial least squares approach to structural equation modeling, in: Marcoulides, G.A. (Ed.), Modern Methods for Business Research. Lawrence Erlbaum Associates, Mahwah, pp. 295–336.

Chin, W.W., Newsted, P.R., 1999. Structural equation modelling analysis with small samples using partial least squares, in: Hoyle, R.H. (Ed.), Statistical Strategies for Small Sample Research. Sage, Thousand Oaks, pp. 307–341.

Cottenie, K., 2005. Integrating environmental and spatial processes in ecological community dynamics. Ecol. Lett. 8, 1175–1182.

Currie, D.J., 1991. Energy and large-scale patterns of animal- and plant-species richness. Am. Nat. 137, 27–49.

Davidar, P., Rajagopal, B., Mohandass, D., Puyravaud, J.-P., Condit, R., Wright, S.J., Leigh, E.G., 2007. The effect of climatic gradients, topographic variation and species traits on the beta diversity of rain forest trees. Glob. Ecol. Biogeogr. 16, 510–518.

De Cáceres, M., Legendre, P., Valencia, R., Cao, M., Chang, L.-W., Chuyong, G., Condit, R., Hao, Z., Hsieh, C.-F., Hubbell, S., Kenfack, D., Ma, K., Mi, X., Supardi Noor, M.N., Kassim, A.R., Ren, H., Su, S.-H., Sun, I.-F., Thomas, D., Ye, W., He, F., 2012. The variation of tree beta diversity across a global network of forest plots. Glob. Ecol. Biogeogr. 21, 1191–1202.

De Knegt, H.J., van Langevelde, F., Coughenour, M.B., Skidmore, A.K., de Boer, W.F., Heitkönig, I.M.A., Knox, N.M., Slotow, R., van der Waal, C., Prins, H.H.T., 2010. Spatial autocorrelation and the scaling of species-environment relationships. Ecology 91, 2455–2465.

Dray, S., Pélissier, R., Couteron, P., 2012. Community ecology in the age of multivariate multiscale spatial analysis. Ecol. Monogr. 82, 257–275.

Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA). 2004. Solos do Estado de Santa Catarina. Available at:http://ainfo.cnptia.embrapa.br/digital/bitstream/item/88186/1/BPD-46-2004-Santa-Catarina-.pdf. Last accessed 16 April 2014.

Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA). 2006. Sistema brasileiro de classificação de solos. Available at:http://ainfo.cnptia.embrapa.br/digital/bitstream/item/93143/1/sistema-brasileiro-de-classificacao-dos-solos2006.pdf . Last accessed 16 April 2014.

Esposito Vinzi, V., Russolillo, G., 2013. Partial least squares algorithms and methods. Wiley Interdiscip. Rev. Comput. Stat. 5, 1–19.

Esposito-Vinzi, V., Russolillo G., Trinchera, L., 2010b. An integrated PLS regression-based approach for multidimensional blocks in PLS path modeling. 42èmes Journées Stat. la Société Française Stat., 1–6.

Esposito-Vinzi, V., Trinchera, L., Amato, S., 2010a. PLS path modeling: from foundations to recent developments and open issues for model assessment and improvement, in: Handbook of Partial Least Squares. Springer, New York, pp. 47–82.

Ewers, R.M., Didham, R.K., 2006. Confounding factors in the detection of species responses to habitat fragmentation. Biol. Rev. Camb. Philos. Soc. 81, 117–142.

Fisher, J.B., Whittaker, R.J., Malhi, Y., 2011. ET come home: potential evapotranspiration in geographical ecology. Glob. Ecol. Biogeogr. 20, 1–18.

Garzon-Lopez, C.X., Jansen, P. a., Bohlman, S. a., Ordonez, A., Olff, H., 2014. Effects of sampling scale on patterns of habitat association in tropical trees. J. Veg. Sci. 25, 349–362.

Gilbert, B., Lechowicz, M.J., 2004. Neutrality, niches, and dispersal in a temperate forest understory. Proc. Natl. Acad. Sci. U. S. A. 101, 7651–7656.

Gonçalves, E.T., Souza, A.F., 2013. Floristic variation in ecotonal areas: patterns, determinants and biogeographic origins of subtropical forests in South America. Austral Ecol. 39, 122–134.

Grace, J. B., 2006. Structural equation modeling and natural systems. Cambridge University Press, New York.

Grace, J.B., Anderson, T.M., Olff, H., Scheiner, S.M., 2010. On the specification of structural equation models for ecological systems. Ecol. Monogr. 80, 67–87.

Henseler, J., Ringle, C.M., Sinkovics, R., 2009. The use of partial least squares path modeling in international marketing. Advan Int. Mark. 20, 277–319.

Henseler, J., Sarstedt, M., 2013. Goodness-of-fit indices for partial least squares path modeling. Comput. Stat. 28, 565–580.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25, 1965–1978.

Hill, J.L., Curran, P.J., 2003. Area, shape and isolation of tropical forest fragments: effects on tree species diversity and implications for conservation. J. Biogeogr. 30, 1391–1403.

Hill, M.O., 1973. Diversity and evenness: a unifying notation and its consequences. Ecology 54, 427.

Holyoak, M., Leibold, M.A., Mouquet, N., Holt, R.D., Hoopes, M.F., 2005. Metacommunities: a framework for large-scale community ecology, in: Holyoak, M., Leibold, M.A., Holt, R.D. (Eds.), Metacommunities Spatial Dynamics and Ecological Communities. The University of Chicago Press, Chicago, pp. 1–31.

Holyoak, M., Mata,T. M., 2008. Metacommunities, in: Sven E. and Brian F. (Eds), Encyclopedia of ecology. Academic Press, Oxford, pp. 2313-2318.

Instituto Brasileiro de Geografia e Estatística (IBGE)., 2012. Manual técnico da vegetação brasileira. Available at: http://www.ibge.gov.br. Last accessed 21 January 2014.

Jost L., Chao, A., Chazdon, R., 2011. Compositional similarity and β (beta) diversity, in: Magurran, A., McGill, B. (Eds.), Biological diversity: frontiers in measurement and assessment. University Press, Oxford, pp. 66-84.

Kaplan, D., 2000. Structural equation modeling: foundations and extensions, Analysis of Ecological Communities. Sage, Thousand Oaks.

Keddy, P., Weiher, E., 1999. Introduction: the scope and goals of research on assembly rules, in: Weiher, E., Keddy, P. (Eds), Ecological Assembly Rules: Perspectives, Advances, Retreats. Cambridge University Press, New York, pp. 1–20.

Keppel, G., Tuiwawa, M. V., Naikatini, A., Rounds, I. A., 2011. Microhabitat specialization of tropical rain-forest canopy trees in the Sovi Basin, Viti Levu, Fiji Islands. J. Trop. Ecol. 27, 491–501.

Klein, R.M., 1978. Mapa fitogeográfico do estado de Santa Catarina, in: Reitz, R. (Ed.), Flora Ilustrada Catarinense. Herbário Barbosa Rodrigues, Itajaí.

Klein, R.M., 1984. Aspectos Dinâmicos da Vegetação do Sul do Brasil. Sellowia 36: 5-54.

Latham, R. E. and Ricklefs, R. E., 1993. Continental comparisons of temperate-zone tree species diversity, in: Ricklefs, R. E., Schluter, D. (Eds), Species Diversity in Ecological Communities. University of Chicago Press, Chicago, pp. 294–314.

Legendre, P., 1993. Spatial autocorrelation: trouble or new paradigm? Ecology 74, 1659–1673.

Legendre, P., De Cáceres, M., 2013. Beta diversity as the variance of community data: dissimilarity coefficients and partitioning. Ecol. Lett. 16, 951–963.

Legendre, P., Gallagher, E., 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129, 271–280.

Legendre, P., Legendre, L., 1998. Numerical ecology. 2nd English edition., Developments in environmental modelling. Elsevier, Amsterdam.

Leibold, M. 2011. The metacommunity concept and its theoretical underpinnings, in: Scheiner, S. M., Willig, M. (Eds), The theory of Ecology. University of Chicago Press, Chicago, pp. 163–184.

Leibold, M. A., 2009. Spatial and metacommunity dynamics in biodiversity, in: Levin S.A.

(Ed.), The Princeton Guide to Ecology. Princeton Univ. Press, Princeton, pp. 312–319.

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M., Gonzalez, A., 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecol. Lett. 7, 601–613.

Leite, P.F., Klein, R.M., 1990. Geografia do Brasil: região sul. Instituto Brasileiro de Geografia e Estatística, Rio de Janeiro.

Loeuille, N., Leibold, M. A., 2008. Evolution in metacommunities: on the relative importance of species sorting and monopolization in structuring communities. Am. Nat. 171, 788–99.

Logue, J.B., Mouquet, N., Peter, H., Hillebrand, H., 2011. Empirical approaches to metacommunities: a review and comparison with theory. Trends Ecol. Evol. 26, 482–491.

Lohmöller, J.B., 1989. Latent variable path modeling with partial least squares. Physica, Heidelberg.

Maurer, B.A. 2009. Spatial patterns of species diversity in terrestrial environments, in: Levin, S.A (Ed.), Princeton Guide to Ecology. Princeton University Press, Princeton, pp. 464-473.

Meynard, C.N., Lavergne, S., Boulangeat, I., Garraud, L., Van Es, J., Mouquet, N., Thuiller, W., 2013. Disentangling the drivers of metacommunity structure across spatial scales. J. Biogeogr. 40, 1560–1571.

Mittermeier, R.A., Gil, P.R., Hoffman, M., Pilgrim, J., Brooks, T., Mittermeier, C.G., Lamoreux, J., Da Fonseca, G.A.B., 2004. Hotspots Revisited. CEMEX, Mexico City.

Myers, J. a, Chase, J.M., Jiménez, I., Jørgensen, P.M., Araujo-Murakami, A., Paniagua-

Zambrana, N., Seidel, R., 2013. Beta-diversity in temperate and tropical forests reflects dissimilar mechanisms of community assembly. Ecol. Lett. 16, 151–7.

Nimer, E., 1989. Climatologia do Brasil. Instituto Brasileiro de Geografia e Estatística, Rio de Janeiro.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Wagner, H., 2013. vegan: community ecology package. R package version 2.0-10. Available at: http://CRAN.R-project.org/package=vegan. Last accessed 21 January 2014.

Oliveira-Filho, a. T., Budke, J.C., Jarenkow, J. a., Eisenlohr, P. V., Neves, D.R.M., 2013. Delving into the variations in tree species composition and richness across South American subtropical Atlantic and Pampean forests. J. Plant Ecol. 1–23.

Peel, M., Finlayson, B.L., McMahon, T.A., 2007. Updated world map of the Köppen-Geiger climate classification. Hydrol. Earth Syst. Sci. 11, 1633–1644.

Peres-Neto, P.R., Leibold, M.A., Dray, S., 2012. Assessing the effects of spatial contingency and environmental filtering on metacommunity phylogenetics. Ecology 93, S14–S30.

R Core Development Team, 2013. R: A language and environment for statistical computing. - R Foundation for Statistical Computing. Available at: http://www.R-project.org. Last accessed 21 January 2014.

Ricklefs, R.E., 1987. Community diversity: relative roles of local and regional processes. Science 235, 167–171.

Ricklefs, R.E., Schluter, D., 1993. Species diversity: regional and historical influences, in: Ricklefs, R.E., Schluter, D. (Eds.), Species Diversity in Ecological Communities: Historical and Geographical Perspectives. University of Chicago Press, Chicago, pp. 350-

363.

Rosenzweig, M.L., 1968. Net primary productivity of terrestrial communities: prediction from climatological data. Am. Nat. 102, 67–74.

Sanchez, G., 2013. PLS path modeling with R. Available at: http://www.gastonsanchez.com/PLS_Path_Modeling_with_R.pdf. Last accessed 21 January 2014.

Sanchez, G., Trinchera, L., Russolillo, G., 2013. Plspm: tools for partial least squares path modeling (PLS-PM). http://cran.r-project.org/web/packages/plspm/index.html. Last accessed 21 January 2014.

Scheibe, L.F., 1986. A geologia de Santa Catarina. Geosul 1: 7–38.

Siefert, A., Ravenscroft, C., Althoff, D., Alvarez-Yépiz, J.C., Carter, B.E., Glennon, K.L., Heberling, J.M., Jo, I.S., Pontes, A., Sauer, A., Willis, A., Fridley, J.D., 2012. Scale dependence of vegetation-environment relationships: a meta-analysis of multivariate data. J. Veg. Sci. 23, 942–951.

Siefert, A., Ravenscroft, C., Weiser, M.D., Swenson, N.G., 2013. Functional beta-diversity patterns reveal deterministic community assembly processes in eastern North American trees. Glob. Ecol. Biogeogr. 22, 682–691.

Tang, Z., Fang, J., Chi, X., Feng, J., Liu, Y., Shen, Z., Wang, X., Wang, Z., Wu, X., Zheng, C., Gaston, K.J., 2012. Patterns of plant beta-diversity along elevational and latitudinal gradients in mountain forests of China. Ecography 35, 1083–1091.

Tenenhaus M. 1998. La Régression PLS. Théorie et Pratique. Editions Technip, Paris.

Tenenhaus, M., Amato, S., Vinzi, E.V., 2004. A global goodness-of-fit index for PLS structural equation modelling, in: The XLII SIS Scientific Meeting. pp. 739–742.

Tenenhaus, M., Vinzi, V.E., Chatelin, Y.M., Lauro, C., 2005. PLS path modeling. Comput. Stat. Data Anal. 48, 159–205.

Trabucco, A., Zomer, R.J., 2009. Global aridity index (global-aridity) and global potential evapo-transpiration (global-PET) geospatial database. Consortium for Spatial Information. Available at : http://www.csi.cgiar.org/. Last accessed 18 November 2011.

Tscharntke, T., Tylianakis, J.M., Rand, T. a, Didham, R.K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T.O., Dormann, C.F., Ewers, R.M., Fründ, J., Holt, R.D., Holzschuh, A., Klein, A.M., Kleijn, D., Kremen, C., Landis, D. a, Laurance, W., Lindenmayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., van der Putten, W.H., Westphal, C., 2012. Landscape moderation of biodiversity patterns and processes - eight hypotheses. Biol. Rev. Camb. Philos. Soc. 87, 661–85.

Vellend, M., 2010. Conceptual synthesis in community ecology. Q. Rev. Biol. 85, 183–206.

Vibrans, A.C., McRoberts, R.E., Moser, P., Nicoletti, A.L., 2013. Using satellite image-based maps and ground inventory data to estimate the area of the remaining Atlantic forest in the Brazilian state of Santa Catarina. Remote Sens. Environ. 130, 87–95.

Vibrans, A.C., Sevegnani, L., Lingner, D.V., Gasper, A.L. de, Sabbagh, S., 2010. Inventário florístico florestal de Santa Catarina (IFFSC): aspectos metodológicos e operacionais. Pesqui. Florest. Bras. 30, 291–302.

Wang, X., Fang, J., Sanders, N.J., White, P.S., Tang, Z., 2008. Relative importance of climate vs local factors in shaping the regional patterns of forest plant richness across northeast China. Ecography 32, 133–142.

Weiher, E., Freund, D., Bunton, T., Stefanski, A., Lee, T., Bentivenga, S., 2011. Advances, challenges and a developing synthesis of ecological community assembly theory. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 366, 2403–2413.

Whittaker, R.H., 1972. Evolution and measurement of species diversity. Taxon 21, 213–251.

Whittaker, R.J., Willis, K.J., Field, R., 2001. Scale and species richness: towards a general, hierarchical theory of species diversity. J. Biogeogr. 28, 453–470.

Willig, M.R., Kaufman, D.M., Stevens, R.D., 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. Annu. Rev. Ecol. Evol. Syst. 34, 273–309.

Wold, H., 1985. Systems analysis by partial least squares, in: Nijkamp P. et al. (Eds.), Measuring the Unmeasurable. Marinus Nijhoff, Boston, pp. 221-252.

Wold, S., Sjöström, M., Eriksson, L., 2001. PLS-regression: A basic tool of chemometrics. Chemom. Intell. Lab. Syst. 58, 109–130.

Wright, D. H., Currie, D.J., Maurer, B.A., 1993. Energy supply and patterns of species richness on local and regional scales, in: Ricklefs R. E., Schluter, D. (Eds), Species Diversity in Ecological Communities: Historical and Geographical Perspectives. University of Chicago Press, Chicago, pp. 66–74.

Supplementary material

Supplementary material Appendix 1, Table A1: Mean values and range of 29 indicator variables for the 432 studied forest plots across Atlantic Forest fragments (Rain Forest, RF; Mixed Araucaria Forest, MAF; and Seasonal Forest, SF) in southern Brazil.

Latent and indicators variables	Code	Mean (Range)		
		RF	MAF	SF
Topography				
Elevation (m)	ELEV	410.8 (1164.0)	954.9 (1037.0)	582.9 (648.0)
Slope (%)	SLOP	7.5 (36.0)	4.8 (19.0)	6.1 (15.0)
Aspect (°)	ASP	206.9 (356.0)	183.3 (355.0)	183.7 (351.0)
Patch geometry				
Patch area (ha)	PA	1444.9 (2448.3)	969.6 (2311.3)	334.9 (1236.3)
Patch core area (ha)	PCA	1045.7 (2374.2)	634.3 (2146)	87.0 (863.2)
Patch shape index	PSI	4.2 (8.4)	4.6 (9.4)	4.9 (10.2)
Patch connectivity (m)	PC	49.0 (262.9)	59.0 (499.8)	55.3 (227.5)
Climatic trends				
Annual mean precipitation (mm)	AP	1577.4 (551.0)	1663.5 (991.0)	1892.7 (563.0)
Annual mean temp (°C*10)	AMT	183.9 (64.0)	159.7 (56.0)	184.3 (37.0)
Seasonality				
Mean diurnal range	MDR	93.5 (49.0)	112.4 (54.0)	119.4 (27.0)
Isothermality	I	50.9 (13.0)	55.3 (10.0)	56.6 (6.0)
Temperature seasonality	TS	2943.6 (511.0)	3024.7 (825.0)	3125.2 (474.0)
Temperature annual range	TAR	181.2 (59.0)	201.1 (64.0)	208.7 (34.0)
Precipitation seasonality	PS	25.1 (30.0)	15.7 (16.0)	12.5 (13.0)
Extreme climatic factors				
Max. temp. of warmest	MTW	274.8 (67.0)	259.5 (70.0)	289.4 (48.0)

month	M			
Min. temp. of coldest month	MTCM	93.6 (85.0)	58.4 (52.0)	80.5 (41.0)
Mean temp. of wettest quarter	MTWQ	220.6 (66.0)	177.1 (89.0)	187.9 (81.0)
Mean temp. of driest quarter	MTDQ	148.1 (65.0)	138.1 (89.0)	166.5 (59.0)
Mean temp. of warmest quarter	MTWQ.1	220.6 (66.0)	196.8 (64.0)	221.3 (35.0)
Mean temp. of coldest quarter	MTCQ	146.3 (65.0)	120.8 (48.0)	143.4 (34.0)
Prec. of wettest month	PWM	197.0 (130.0)	178.0 (90.0)	197.8 (55.0)
Prec. of driest month	PDM	86.1 (37.0)	105.1 (80.0)	129.1 (51.0)
Prec. of wettest quarter	PWQ	536.2 (367.0)	485.1 (215.0)	531.0 (133.0)
Prec. of driest quarter	PDQ	283.9 (126.0)	356.2 (288.0)	432.1 (169.0)
Prec. of warmest quarter	PWQ.1	535.2 (367.0)	472.6 (174.0)	494.1 (145.0)
Prec. of coldest quarter	PCQ	299.3 (143.0)	368.5 (288.0)	443.4 (171.0)
Water-energy balance				
Actual evapotranspiration (mm)	AET	1192.4 (223.0)	1203.9 (381.0)	1335.0 (245.0)
Potential evapotranspiration (mm)	PET	1252.0 (324.0)	1291.2 (439.0)	1433.6 (256.0)
Global aridity index	GAI	12670.6 (5978.0)	12942.5 (6957.0)	13175.5 (4213.0)

Considerações Finais

O presente trabalho traz uma contribuição no sentido de desvendar quais processos são determinantes para a montagem de comunidades ao longo de múltiplas escalas espaciais, um dos temas centrais na área de ecologia atualmente. Os resultados obtidos fornecem uma forte evidência em favor da importância de processos determinísticos associados a filtros ambientais. A utilização de modelagem de equações estruturais (SEM), para testar uma predição oriunda da teoria de metacomunidades, constitui um diferencial em relação às abordagens comumente utilizadas para investigar padrões de diversidade de árvores na Floresta Atlântica do Sul do Brasil. Assim, a abordagem aqui utilizada representa um passo importante para o entendimento de como diferentes processos interagem para afetar os padrões de diversidade e coexistência de espécies nas florestas em questão. SEM constitui uma ferramenta altamente indicada para análises de sistemas ecológicos e as interações entre fatores bióticos e abióticos. Especificamente, o método PLSPM, apesar de ainda ser pouco utilizado na área de ecologia, começa a ganhar espaço no contexto de importantes trabalhos recentemente publicados (e.g. Moody & Sabo 2013, Majdi et al. 2013 e Medina et al. 2014).

Entretanto, visto que a diversidade é um conceito complexo que inclui diferentes escalas espaciais e entidades, abordagens referentes à diversidade funcional e filogenética surgem como análises complementares bastante promissoras quando se pretende analisar a relação entre a distribuição das espécies e fatores ambientais. Por resumirem a adaptação das espécies ao ambiente, atributos funcionais, por exemplo, possibilitam identificar padrões mais evidentes do que aqueles obtidos apenas mediante o uso da diversidade de espécies. Portanto, recomenda-se incorporar tais aspectos da diversidade em futuros estudos, o que pode prover importantes informações em relação aos processos que determinam os padrões de diversidade em metacomunidades.

Referências

Anderson, M. J. et al. 2011. Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. - Ecol. Lett. 14: 19–28.

Bergamin, R. S. et al. 2012. Indicator species and floristic patterns in different forest formations in southern Atlantic rainforests of Brazil. - Community Ecol. 13: 162–170.

Biswas, S. R. and Wagner, H. H. 2012. Landscape contrast: a solution to hidden assumptions in the metacommunity concept? - Landsc. Ecol. 27: 621–631.

Bollen, K. A. 1989. Structural equations with latent variables. - Wiley.

Brown, C. et al. 2013. Multispecies coexistence of trees in tropical forests: spatial signals of topographic niche differentiation increase with environmental heterogeneity. - Proc. Biol. Sci. 280: 20130502.

Chase, J. M. 2010. Stochastic community assembly causes higher biodiversity in more productive environments. - Science 328: 1388–1391.

Chase, J. M. and Myers, J. A. 2011. Disentangling the importance of ecological niches from stochastic processes across scales. - Philos. Trans. R. Soc. Lond. B. Biol. Sci. 366: 2351–63.

Cottenie, K. 2005. Integrating environmental and spatial processes in ecological community dynamics. - Ecol. Lett. 8: 1175–1182.

De Caceres, M. et al. 2010. Improving indicator species analysis by combining groups of sites. - Oikos 119: 1674–1684.

De Caceres, M. et al. 2010. Improving indicator species analysis by combining groups of sites. - Oikos 119: 1674–1684.

Diamond, J. M. 1975. Assembly of species communities. - In: Cody, M. L. and Diamond, J. M. (eds), Ecology and evolution of communities. Harvard Press, pp. 342–444.

Esposito-Vinzi et al. 2010a. PLS path modeling: from foundations to recent developments and open issues for model assessment and improvement. - In: Handbook of Partial Least Squares. Springer, New York, pp. 47–82.

Garzon-Lopez, C. X. et al. 2014. Effects of sampling scale on patterns of habitat association in tropical trees. - J. Veg. Sci. 25: 349–362.

Gilbert, B. and Lechowicz, M. J. 2004. Neutrality, niches, and dispersal in a temperate forest understory. - Proc. Natl. Acad. Sci. U. S. A. 101: 7651–7656.

Gonçalves, E. T. and Souza, A. F. 2013. Floristic variation in ecotonal areas: Patterns, determinants and biogeographic origins of subtropical forests in South America. - Austral Ecol. 39: 122–134.

Grace, J. B. et al. 2010. On the specification of structural equation models for ecological systems. - Ecol. Monogr. 80: 67–87.

Hill, J. L. and Curran, P. J. 2003. Area, shape and isolation of tropical forest fragments: effects on tree species diversity and implications for conservation. - J. Biogeogr. 30: 1391–1403.

Holyoak, M. and T. M. Mata. 2008. Metacommunities. - In: Sven E. and Brian F. (eds), Encyclopedia of ecology. Academic Press, pp. 2313-2318.

Hubbell, S. P. 1999. Light-Gap Disturbances, recruitment limitation, and tree Diversity in a Neotropical forest. - Science 283: 554–557.

Hubbell, S. P. 2001. The Unified neutral theory of biodiversity and biography (Levin, S.A. and Horn, H.S.(eds.). - Princeton University Press.

Kaplan, D. 2000. Structural equation modeling: foundations and extensions. - Sage.

Keddy, P. A. 1992. Assembly and response rules: two goals for predictive community ecology. - J. Veg. Sci. 3: 157–164.

Jarenkow, J.A and Budke, J.C. 2009. Padrões florísticos e análise estrutural de remanescentes de Florestas com Araucária no Brasil.- In: Fonseca, C.R.; Souza, A.F.; Leal-

Zanchet, A.M.; Dutra, T.; Backes, A. and Ganade, G. (eds.), Floresta com araucária: ecologia, conservação e desenvolvimento sustentável. Holos, pp. 113-126.

Legendre, P. and Gallagher, E. 2001. Ecologically meaningful transformations for ordination of species data. - Oecologia 129: 271–280.

Leibold, M. a. et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. - Ecol. Lett. 7: 601–613.

Majdi, N. et al. 2013. Predator effects on a detritus-based food web are primarily mediated by non-trophic interactions. - J. Anim. Ecol. in press.

McCune, B. and Grace, J. B. 2002. Analysis of ecological communities (GB MjM Software Oregon Usa Www Pcord Com, Ed.). - MjM Software Design.

Medina, N. G. et al. 2014. Species richness of epiphytic bryophytes: drivers across scales on the edge of the Mediterranean. - Ecography (Cop.). 37: 80–93.

Medina, N. G. et al. 2014. Species richness of epiphytic bryophytes: drivers across scales on the edge of the Mediterranean. - Ecography 37: 80–93.

Moody, E. K. and Sabo, J. L. 2013. Crayfish impact desert river ecosystem function and litter-dwelling invertebrate communities through association with novel detrital resources. - PLoS One 8: e63274.

Myers, J. a et al. 2013. Beta-diversity in temperate and tropical forests reflects dissimilar mechanisms of community assembly. - Ecol. Lett. 16: 151–7.

Oliveira-Filho, a. T. et al. 2013. Delving into the variations in tree species composition and richness across South American subtropical Atlantic and Pampean forests. - J. Plant Ecol.: 1–23.

Oliveira-Filho, A. and Fontes, M. 2000. Patterns of floristic differentiation among Atlantic Forests in Southeastern Brazil and the influence of climate. - Biotropica 32: 793–810.

R Core Development Team. 2013. R: A language and environment for statistical computing. -

R Foundation for Statistical Computing. Available at: http://www.R-project.org. Last accessed 21 January 2014..

Ricklefs, R. E. 1987. Community Diversity: Relative roles of local and regional Processes. - Science 235: 167–171.

Ricklefs, R. E. and Schluter, D. 1993. Species diversity in ecological communities: historical and geographical perspectives. - University of Chicago Press.

Scheiner, S. M. and Willig, M. R. 2005. Developing unified theories in ecology as exemplified with diversity gradients. - Am. Nat. 166: 458–69.

Siefert, A. et al. 2012. Scale dependence of vegetation-environment relationships: a meta-analysis of multivariate data. - J. Veg. Sci. 23: 942–951.

Tenenhaus, M. et al. 2005. PLS path modeling. - Comput. Stat. Data Anal. 48: 159–205.

Vellend, M. 2010. Conceptual synthesis in community ecology. - Q. Rev. Biol. 85: 183–206.

Vibrans, A. C. et al. 2010. Inventário florístico florestal de Santa Catarina (IFFSC): aspectos metodológicos e operacionais. - Pesqui. Florest. Bras. 30: 291–302.

Vibrans, A. C. et al. 2013. Using satellite image-based maps and ground inventory data to estimate the area of the remaining Atlantic forest in the Brazilian state of Santa Catarina. - Remote Sens. Environ. 130: 87–95.

Weiher, E. and Keddy, P. 1999. Assembly rules as general constraints on community composition. - In: Ecological assembly rules. Perspectives, advances, retreats. Cambridge University Press, pp. 1–20.

Whittaker, R. H. 1972. Evolution and measurement of species diversity. - Taxon 21: 213–251.

Whittaker, R. J. et al. 2001. Scale and species richness: towards a general, hierarchical theory of species diversity. - J. Biogeogr. 28: 453–470.

Willig, M. R. et al. 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. - Annu. Rev. Ecol. Evol. Syst. 34: 273–309.

Appendices

Appendix A: Description of the methods for data analysis used for the general introduction.

All analyses were performed using Vegan package in the R environment for statistical computing (R Core Development Team 2012), except for the analysis of indicator species, as explained below.

Non-parametric Multivariate Analysis of Covariance (NPMANCOVA)

The NPMANCOVA was performed with community composition data (432 forest plots *x* 750 species), using Bray-Curtis (Steinhaus index) dissimilarities (NPMANCOVA, Anderson 2001) to test for differences in floristic composition among the forest types. The species pool was defined as the total number of species observed across all forest plots within a type forest. The significance of the model was assessed using pseudo *F*-tests based on 9999 sequential sums of squares from permutations of the raw data

Non-metric Multidimensional Scaling (NMDS)

The NMDS was performed to illustrate pairwise dissimilarities among forest types, which iteratively finds the solution, or axes of variation that best capture the patterns in the dissimilarity matrix. We chose the number of dimensions (axes) equal to 4 to minimize the stress (i.e., maximizing the rank correlations between the calculated distances and the plotted distances). The Bray-Curtis dissimilarity demonstrated the high rank-order relation distance along environmental gradient, so we opted to run all statistical analyses based on distance matrices.

Indicator species analysis with combination of site groups

Indicator species analysis with combination of site groups (De Cáceres et al. 2010) was used as a complimentary method to NPMANCOVA to contrast the performance of individual species across three forest types (McCune and Grace 2002). The method is an extension of the original indicator value (IndVal) analysis (Dufrêne and Legendre 1997), which considers all possible combinations of sites and selects the combination for which the species may be better used as an indicator. The analysis produces the lists of indicator species significantly associated to each site groups or combinations of them (De Cáceres et al. 2010). Among these, we considered as strong indicators those with IndVal greater than 0.5, i.e. the most abundant and specific species. We performed the analysis with the species composition matrix previously submitted to Hellinger transformation (Legendre and Gallagher 2001), using the '*multipatt*' function of the R package 'indicspecies' and association index IndVal.g, which incorporates a correction for unequal group sizes. Statistical significance was tested by 999 Monte Carlo permutations.

Appendix B: Complete lists of the indicator species that characterize individual forest types (table 1) and (table 2) those that reflecting the affinities or relationships between them.

Table 1: Indicators species with value of the correlation (rpb ≥ 0.5) with significant association (p ≤ 0.05) to one forest type. For each species are indicated the group combination that obtained the highest correlation (GC) and the value of the correlation (rpb). RF, Rainforest; SF, Seasonal Forest; MAF, Mixed Araucaria Forest.

Indicator species	GC	r_{pb}
Alchornea triplinervia	RF	0.834
Matayba intermedia	RF	0.747
Nectandra oppositifolia	RF	0.747
Psychotria vellosiana	RF	0.737
Euterpe edulis	RF	0.735
Guapira opposita	RF	0.719
Cecropia glaziovii	RF	0.711
Hieronyma alchorneoides	RF	0.707
Guatteria australis	RF	0.703
Ocotea elegans	RF	0.692
Alsophila setosa	RF	0.686
Myrcia pubipetala	RF	0.686
Cyathea phalerata	RF	0.682
Annona neosericea	RF	0.649
Bathysa australis	RF	0.641
Pera glabrata	RF	0.639
Posoqueria latifolia	RF	0.634
Byrsonima ligustrifolia	RF	0.627
Aniba firmula	RF	0.617
Miconia cabucu	RF	0.617
Cryptocarya mandioccana	RF	0.613
Heisteria silvianii	RF	0.601
Sloanea guianensis	RF	0.600
Hirtella hebeclada	RF	0.597
Ocotea catharinensis	RF	0.596
Piptocarpha axillaris	RF	0.593
Virola bicuhyba	RF	0.593
Miconia cinnamomifolia	RF	0.589
Inga sessilis	RF	0.587
Protium kleinii	RF	0.576
Maytenus robusta	RF	0.572
Ocotea nectandrifolia	RF	0.548
Cyathea delgadii	RF	0.530
Myrcia brasiliensis	RF	0.519

Xylopia brasiliensis	RF	0.512
Garcinia gardneriana	RF	0.502
Magnolia ovata	RF	0.502
Luehea divaricata	SF	0.818
Nectandra megapotamica	SF	0.796
Machaerium stipitatum	SF	0.767
Balfourodendron riedelianum	SF	0.764
Nectandra lanceolata	SF	0.722
Chrysophyllum gonocarpum	SF	0.720
Myrocarpus frondosus	SF	0.716
Machaerium paraguariense	SF	0.698
Chrysophyllum marginatum	SF	0.697
Cordia americana	SF	0.691
Syagrus romanzoffiana	SF	0.686
Trichilia clausseni	SF	0.684
Lonchocarpus campestris	SF	0.667
Parapiptadenia rigida	SF	0.663
Annona sylvatica	SF	0.642
Cordia trichotoma	SF	0.631
Apuleia leiocarpa	SF	0.630
Diatenopteryx sorbifolia	SF	0.625
Phytolacca dioica	SF	0.616
Pilocarpus pennatifolius	SF	0.597
Albizia edwallii	SF	0.580
Hovenia dulcis	SF	0.576
Urera baccifera	SF	0.548
Picrasma crenata	SF	0.540
Inga vera subsp affinis	SF	0.519
Strychnos brasiliensis	SF	0.511
Araucaria angustifolia	MAF	0.798
Dicksonia sellowiana	MAF	0.753
Ilex paraguariensis	MAF	0.673
Cinnamomum amoenum	MAF	0.643
Ocotea pulchella	MAF	0.622
Mimosa scabrella	MAF	0.562
Lithrea brasiliensis	MAF	0.553
Cinnamodendron dinisii	MAF	0.545
Drimys brasiliensis	MAF	0.527
Ocotea porosa	MAF	0.525

Table 2: Indicators species with value of the correlation (rpb ≥ 0.5) with significant association ($p \leq 0.05$) to two forest types. For each species, are indicate the group combination that obtained the highest correlation (GC) and the value of the correlation (rpb). RF, Rainforest; SF, Seasonal Forest; MAF, Mixed Araucaria Forest.

Indicator species	GC	r_{pb}
Casearia sylvestris	RF + SF	0.796
Cabralea canjerana	RF + SF	0.768
Aspidosperma australe	RF + SF	0.644
Sorocea bonplandii	RF + SF	0.518
Inga marginata	RF + SF	0.502
Clethra scabra	RF + MAF	0.689
Vernonanthura discolor	RF + MAF	0.684
Ilex theezans	RF + MAF	0.662
Lamanonia ternata	RF + MAF	0.575
Myrcia splendens	RF + MAF	0.566
Piptocarpha angustifolia	RF + MAF	0.550
Ilex dumosa	RF + MAF	0.543
Casearia obliqua	RF + MAF	0.535
Prunus myrtifolia	SF + MAF	0.785
Ocotea puberula	SF + MAF	0.776
Matayba elaeagnoides	SF + MAF	0.751
Sapium glandulosum	SF + MAF	0.656
Allophylus edulis	SF + MAF	0.640
Casearia decandra	SF + MAF	0.635
Sebastiania commersoniana	SF + MAF	0.624
Styrax leprosus	SF + MAF	0.624
Campomanesia xanthocarpa	SF + MAF	0.599