UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL

INSTITUTO DE BIOCIÊNCIAS

DEPARTAMENTO DE BOTÂNICA

PROGRAMA DE PÓS-GRADUAÇÃO EM BOTÂNICA

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Determinantes ecológicos da diversidade beta de árvores em florestas Atlânticas no sul do Brasil

Porto Alegre

2017

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Tese de Doutorado apresentada ao Programa de Pós-Graduação em Botânica da Universidade Federal do Rio Grande do Sul, como parte dos requisitos para obtenção do título de Doutor em Ciências: Botânica.

Área de concentração: Ecologia Vegetal

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Porto Alegre

2017

*"*O homem vem quebrando a cara há milhares de anos pela simples razão de ele querer conquistar a natureza. Alguém chegou a escrever um livro chamado *A conquista da natureza*. A natureza não pode ser conquistada. Veja a insensatez da ideia. Você é parte da natureza, uma parte pequena, minúscula, de uma natureza tão infinita. E a parte está tentando conquistar o todo – como se seu dedo mindinho estivesse tentando conquistar você.

Como você pode conquistar a natureza?

A natureza é sua própria alma.

Quem vai conquistar quem?

Onde está a separação?

Osho

(A jornada do ser humano, 2012)

Agradecimentos

Agradeço e dedico esta tese à minha família e amigos, pelo apoio e atenção constantes, e pelo interesse no meu progresso profissional. Aloha! Aos meus pais, José Alberto e Maria Norma, pelo apoio, carinho e amor incondicionais. À minha irmã e segunda mãe Bethânia, pelo zelo e amor constantes. Aos meus afilhados Alice, Pedro, Lucas, Matheus e Gabriel, pela ALEGRIA que me proporcionam. À minha namorada, amiga, conselheira e parceira, Débora, pelo amor, companheirismo, amizade, dedicação, alegria e vibração positiva.

Ao CNPq, pela bolsa concedida, sem a qual, certamente, esta tese não teria sido possível.

Agradeço enormemente a Alexandre Christian Vibrans e Lúcia Sevegnani (*in memoriam*), pela autorização para utilizar os dados do Inventário Florístico Florestal (IFSSC) de Santa Catarina.

Sou muito grato ao meu orientador, Prof. Jarenkow, pelo apoio, amparo, orientação, cordialidade, e pela agradável convivência durante o Doutorado.

Sou muito grato também ao Prof. Gerhard, pela colaboração constante, pelas valiosas sugestões e revisões, e pela cordialidade.

Agradeço a todos os colegas e professores do laboratório Fitoeco (egressos e ingressos), que tive o prazer de conhecer durante o *doc*, pelo acolhimento, respeito, pelas trocas de experiência, *insights*, *brainstorms*, prosas e risadas. À colega e amiga Anita, pelas inúmeras colaborações na análise de dados, pelos *insights* frutíferos, e pelos conhecimentos botânicos sobre a flora da região estudada.

Sou muito grato também a Eduardo Giehl, pelo constante suporte no ambiente R, pelas diversas ajudas na análise de dados, e pelos *insights* frutíferos. Agradeço enormemente também aos colegas Luíz Esser e Daniel Grasel, pela compilação de dados e elaboração dos bancos de dados do Fitoeco.

Aos professores, colegas e funcionários do PPG Botânica, pela agradável convivência durante o Doutorado.

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Resumo

Abordagens integrativas considerando diferentes dimensões da diversidade (p.ex., taxonômica, funcional, ou filogenética) cada vez mais estão sendo utilizadas para (1) avançar o nosso conhecimento sobre os mecanismos que criam e mantém a biodiversidade, e (2) elucidar a distribuição da biodiversidade tanto em áreas geográficas de interesse como dentro de áreas protegidas. De fato, entender como a biodiversidade se distribui no espaço e como ela é mantida ao longo do tempo é fundamental para embasar o planejamento de áreas protegidas e corredores ecológicos, assim como auxiliar no manejo de espécies invasoras, restauração de habitats degradados e manejo de ecossistemas. Nessa perspectiva, os objetivos centrais desta tese foram: (1) avaliar os mecanismos ecológicos e evolutivos, que potencialmente influenciam a diversidade beta taxonômica e filogenética de árvores nas florestas Atlânticas do sul do Brasil, e (2) avaliar como os componentes taxonômicos e filogenéticos se distribuem ao longo destas florestas, e como eles são representados dentro da rede regional de áreas protegidas. Para tal, utilizei modelagem de equações estruturais (capítulo 1) para testar a validade de uma rede de hipóteses ligando dados e teoria. No capítulo 1, avaliei a relação entre a diversidade beta taxonômica e filogenética, e como elas se relacionam com a riqueza de espécies, filtragem ambiental, espaço geográfico e estrutura filogenética (agrupamento filogenético). Nesse capítulo, concluí que a diversidade beta taxonômica é influenciada principalmente pelos gradientes altitudinais e climáticos, enquanto que a diversidade beta filogenética é determinada também pelo grau de agrupamento filogenético, em nível local, que provavelmente reflete o conservadorismo de nicho dentro das linhagens e distúrbio humano, que historicamente tem conduzido as florestas estudadas a um processo de homogeneização biótica. Em relação ao segundo objetivo, utilizei uma abordagem integrativa para predizer e mapear os componentes taxonômicos e filogenéticos da diversidade de árvores e, em seguida, avaliar a efetividade da rede de áreas protegidas

em representar tais componentes nas florestas Atlânticas do sul Brasil. Nesse capítulo, concluí que as áreas protegidas são insuficientes para preservar adequadamente a biodiversidade de árvores nestas florestas. Sugeri que a expansão da rede em direção as áreas de alta singularidade taxonômica e filogenética, como definidas aqui, poderia aumentar, ao mesmo tempo, a representação da riqueza de espécies, da diversidade beta e da história evolutiva das espécies estudadas. Sugeri também que a inclusão de áreas de alta insubstituibilidade, em termos de história evolutiva, poderia ajudar a aumentar a proteção da diversidade de características e do potencial evolutivo das espécies.

Palavras-chave: Áreas protegidas, árvores, biodiversidade, conservação florestal, diversidade de espécies, diversidade filogenética, estrutura filogenética, filtragem ambiental.

Abstract

Integrative approaches considering different dimensions of biodiversity are increasingly being used in ecology and conservation to (1) advance our knowledge about the mechanisms underlying current patterns of biological diversity, and (2) elucidate the distribution of biodiversity in geographical areas of interest, and within the protected areas. Indeed, understanding how biodiversity is distributed in space and how it is maintained over time is critical to support the planning of protected areas and ecological corridors as well as assist the management of invasive species, the restoration of degraded areas and ecosystem management. In this perspective, the central goals of this thesis were: (1) to evaluate the ecological and evolutionary mechanisms that potentially influence the tree taxonomic and phylogenetic beta diversity in Atlantic forests located in southern Brazil, and (2) to evaluate how the taxonomic and phylogenetic diversity components are distributed across these forests, and how they are represented within the regional network of protected areas. For this, I used structural equation modeling (chapter 1) to test the validity of a network of hypotheses linking data and theory. In the chapter 1, I evaluate the relationship between taxonomic and phylogenetic beta diversity, and how they are related to species richness, environmental filtering, geographical space and phylogenetic structure (phylogenetic clustering). In this chapter, I conclude that taxonomic beta diversity (at the study scale) is mainly driven by the altitudinal and climatic gradients, while phylogenetic beta diversity is also determined by the degree of phylogenetic clustering at local level, more likely reflecting niche conservatism within lineages and human disturbance that has historically conducted the studied forests to a process of biotic homogenization. In relation to the second goal, I used an integrative approach to predict and map the taxonomic and phylogenetic components of tree diversity, and to assess the effectiveness of the protected areas network in representing these components in the Atlantic forests. In this chapter, I conclude that protected areas are insufficient to adequately preserve the tree biodiversity

in these forests. I suggest that expanding the network towards the areas of taxonomic and phylogenetic uniqueness, as defined here, could increase the representation of species richness, beta diversity and evolutionary history of angiosperm trees at the same time. Furthermore, the inclusion of areas of high irreplaceability in terms of evolutionary history could help to improve the protection of feature diversity and evolutionary potential of species.

Keywords: Biodiversity, environmental filtering, forest conservation, phylogenetic diversity, phylogenetic structure, protected areas, trees, species diversity.

General introduction

Species diversity is characterized by three main levels or focal scales (Whittaker, 1960, 1972): the alpha diversity that measures how diversified the species are within a site, the beta diversity that measures how diversified the sites are in species composition within a geographic area and the gamma diversity that measures overall diversity within a region, i.e., the species richness of a large number of sites from the region (Whittaker, 1960, 1972). Beta diversity which is defined in its broadest sense as variation in species composition among sites (Legendre et al., 2005; Anderson et al., 2011) unifies local-regional diversity relationships (Ricklefs, 1987) and thus captures a fundamental facet of the spatial pattern of species assemblages (De Cáceres et al., 2012). It is well established that these diversity levels are shaped by multiple mechanisms that operate within communities such as interspecific interactions and environmental filtering and those mechanisms that operate mainly at the regional level (between communities) such as speciation, extinction and geographic dispersal (Willig et al., 2003).

Beta diversity reflects two different phenomena: the replacement of some species by others among sites (i.e., spatial turnover) and the species loss linked to variation in richness among sites (i.e., nestedness; Baselga, 2010). Nestedness occurs when the species composition of small (or poor) assemblages is a subset of large (or richer) assemblages (Ulrich et al., 2009). Although the richest assemblage has unique species not present in the poorest assemblage, no species is replaced by other (Baselga, 2010). In a conservation context, these patterns require different strategies. Turnover involves devote efforts to a large number of different sites, while nestedness involves devote efforts just to a small number of the richest sites (Baselga, 2010). To effectively protect biodiversity in regions of rapid turnover, it is necessary to increased attention to the

placement and size of conservation areas (McKnight et al., 2007). Because distinct migration histories may cause sites to be dissimilar in community composition, conservation efforts dedicated to multiple sites are fundamental even when they are environmentally identical (Nekola and White, 2002). Indeed, protecting sites with high beta diversity can enhance the persistence of endemic species and different evolutionary lineages (Van Dyke, 2008). Furthermore, it may contribute to maintain the requirements of species with high habitat specificity and poor dispersal ability.

Studies focusing on beta diversity patterns can provide critical information for selecting protected areas, for creating habitat corridors along ecological gradients, and for designing of wildlife-friendly landscapes (Socolar et al., 2016). According Barton et al. (2013) any credible plan for biodiversity conservation must maintain beta diversity and the processes that shape it across the full range of taxa and spatial scales. For effectively conserve regional biodiversity is necessary to know how biological diversity is distributed within the region (Jost, 2010). Partitioning of region-level species diversity into additive ($\gamma = \alpha + \beta$) or multiplicative ($\gamma = \alpha \times \beta$) components has been applied as a key tool to disentangle scale-dependent patterns of diversity in order to determine strategies for biodiversity conservation (Crist et al., 2003; Gering et al., 2003).

Most of the biodiversity studies have focused on species diversity that is silent on evolutionary and functional differences among species because treats all species as 'taxonomically equivalent' (Devictor et al., 2010). However, there is a growing number of studies focusing on functional and phylogenetic diversity. In particular, the growing interest in including these components in biodiversity studies has two main reasons: (1) to explicitly incorporate differences among species based on their evolutionary histories

and functional traits, and to provide insights on the structure of communities (Vellend et al. 2010).

Overall, phylogenetic diversity can benefit the conservation practice by including evolutionary information and potentially feature diversity and evolutionary potential (Winter et al., 2013). In conservation, phylogenetic diversity metrics have been used to identify areas with high phylogenetic uniqueness, or with evolutionarily very young or old clades, as well as areas with phylogenetically clustered or overdispersed communities (Winter et al., 2013). In addition, it has been used to identify sets of species that maximize feature diversity and thus the option values, i.e., the biodiversity values that provide benefits and uses for future generations (Forest et al., 2007; Faith and Pollock, 2014). Clearly, adopt an integrated approach in conservation is crucial to protect the multifaceted nature of biodiversity, once areas of equal taxonomic diversity may contain species with either highly similar or distinct phylogenetic histories and functional traits (Devictor et al., 2010). This is especially important, as conservation biologists increasingly focus on the protection of multiple species (and ecological processes) across protected area networks, as opposed to protection of individual species (Wilcove, 2009). Given the urgency to address the contemporary biodiversity crisis, integrative approaches have been used to maximize the protection of different aspects of diversity under the constraints of limited resources and incomplete data (e.g., Devictor et al., 2010; Strecker et al., 2011; Daru et al., 2015; Zupan et al., 2014). Recently, Devictor et al. (2010) proposed an integrative approach based on a large-scale mapping of taxonomic, functional and phylogenetic diversity in order to disentangle areas of mismatch (divergent sites) and congruence (convergence sites) between these complementary components. Spatial mismatch between components carries a wealth of ecological information about the processes that generate and maintain biodiversity, and is of paramount importance to identify geographical areas where conservation efforts will be more effective to maximize its overall representation (Devictor et al., 2010; Safi et al., 2011; Daru et al., 2015; Sobral et al., 2014).

The protection of a significant fraction of biodiversity in a given region depends on both the monitoring of existing conservation areas and the establishment of new areas in order to include not protected species. Nevertheless, this requires some knowledge of the representation of each biodiversity component in protected areas and the recognition of areas of mismatches and congruencies between components within the region. For the Atlantic forests we studied in southern Brazil, the effectiveness of the protected area network to safeguard different facets of biodiversity is unknown, which makes it difficult to establish conservation strategies in this region.

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Capítulo 1. Using structural equation modeling to disentangle the drivers of taxonomic and phylogenetic beta diversity in subtropical tree communities [1]

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[1] Artigo formatado de acordo com o periódico *Perspectives in Plant Ecology, Evolution and Systematics*

Abstract

We assessed how taxonomic (TBD) and phylogenetic (PBD) beta diversity relate to each other, and how they relate to species richness, environmental filtering, geographical space, and phylogenetic clustering (PC). Using structural equation modeling (SEM), we test the validity of some hypotheses depicting relationships among these factors from a regional-extent dataset of tree communities in subtropical Brazilian Atlantic forests. Consistent with the postulated relations, (1) PBD increases with increasing TBD between plots, (2) PBD between plots decreases with increasing PC within plots, (3) both TBD and PBD decrease with increasing species richness within plots, and (4) environmental filtering increases PC at plot level. Regarding our fifth prediction that seasonality and harshness of climate directly reduce richness while increasing both TBD and PBD, our results showed that only temperature seasonality influenced all diversity facets. Precipitation extreme influenced only TBD and PBD, while temperature extreme influenced only richness and TBD. Regarding our last prediction that TBD and PBD were correlated with geographical space (both the location and distance apart), our results showed that only TBD was influenced by the location of the plots. Additionally, altitude was found to predict lower levels of richness and higher levels of TBD and PBD, while actual evapotranspiration was found to predict higher richness and lower TBD and PBD. After controlling for statistical dependence among diversity facets, the compositional and phylogenetic dissimilarity between plots was directly determined by the replacement of taxa (both the species and lineages) across space, as a result of environmental filtering. Our study demonstrates that at the study scale, compositional dissimilarity in subtropical tree communities is mainly driven by the altitudinal and climatic gradients, while phylogenetic dissimilarity

is also determined by the degree of phylogenetic clustering at local level, more likely reflecting niche conservatism within lineages and human disturbance that has historically conducted the studied forests to a process of biotic homogenization.

Keywords*:* Atlantic forest*,* community assembly, environmental filtering, species richness, trees.

Introduction

Taxonomic and phylogenetic beta diversity complement each other and their relation provides mechanistic insight about the ecological and evolutionary mechanisms structuring communities (Graham and Fine, 2008; Jin et al., 2015). By providing understanding about the spatial distribution of biodiversity, beta diversity can directly assist conservation management and decision-making (Laity et al., 2015; Socolar et al., 2016). Taxonomic beta diversity (TBD) measures how species composition changes across geographic space (Whittaker, 1972), and plays a crucial role in linking the local (alpha diversity) and regional (gamma diversity) diversity levels (De Cáceres et al., 2012). Phylogenetic beta diversity (PBD), known also as phylobetadiversity, measures how phylogenetic relatedness among species changes across space (Graham and Fine, 2008). PBD extends the biodiversity research by explicitly integrating the spatial and temporal components of diversity (Graham and Fine, 2008), and may substantially advance our understanding of how historical biogeography of lineages, environmental gradients and geographic distance influence community assembly (Fine and Kembel, 2011). The relationship between TBD and PBD is particularly informative about the processes that shape the regional species pools (Graham and Fine, 2008). For instance, both higher TBD and PBD are expected in a species pool that contains a high proportion of small ranged species, belonging to early-diverged clades.

Several beta diversity studies have evaluated how community structure changes as a function of environmental and spatial influences, enabling a better understanding of the mechanisms that create and maintain biodiversity, and creating a sound scientific basis to effectively protect regional (gamma) diversity (Condit et al., 2002; De Cáceres et al., 2012; Hardy et al., 2012; Myers et al., 2013; Qian et al., 2013a; Jin et al., 2015).

Patterns and processes of community organization are strongly dependent on the spatial scale on which they are examined (Levin, 1992; Siefert et al., 2012; Garzon-Lopes et al., 2014). A number of studies support the idea that dispersal limitation acts primarily at local to regional scales (e.g., Hubbell et al., 1999; Condit et al., 2002; Tuomisto et al., 2003), whereas environmental filtering operates principally at broad (regional to global) scales (e.g., Davidar et al., 2007; De Cáceres et al., 2012; Hardy et al., 2012; González-Caro et al., 2014; Santos et al., 2015). The importance of different environmental filters at different spatial scales was assessed by a recent meta-analysis on the determinants of plant community composition (Siefert et al., 2012). The results provided strong evidence that the importance of coarse-grained variables (i.e., climate factors) relative to fine-grained variables (i.e., edaphic factors) increased with increasing spatial extent and grain of sampling, highlighting a transition from a primarily edaphic influence to a primarily climatic influence. While several climate and soil variables are commonly used to depict environmental heterogeneity, we focused here on how compositional and phylogenetic dissimilarity responds to 'macroclimatic constraints', in our case seasonality and harshness of temperature and precipitation. Understanding how compositional and phylogenetic dissimilarity is related to larger regions that include climatic variation is essential to optimize the implantation of protected areas and especially to aim at minimizing the effects of ongoing climate change on plant diversity (Socolar et al., 2016).

Although substantial advances have been achieved in assessing specific mechanisms influencing patterns of both TBD and PBD, the potential for development of theoretical explorations and predictive modelling is still large (Gilbert and Bennett, 2010; Weiher et al., 2011). One motive is that inferences about the relative importance of mechanisms determining diversity have been widely made from 'exploratory

statistical tools', such as variation-partitioning methods, which are largely descriptive and somewhat limited in their capacities to examine complex multivariate hypotheses, to specify theoretical content, and to address measurement error (Grace, 2006; Grace et al., 2010). Another reason is that several studies have failed to address the interdependence among diversity components (i.e., alpha, beta, and gamma diversities) when evaluating the role of different processes; hence they were not able to discern whether the changes in TBD were due to species replacement across space ("true turnover"), as a consequence of ecological processes, or due to the fact that these same processes altered the species richness ("species loss") in local communities (alpha diversity), causing concomitant changes in TBD simply for probabilistic reasons (Baselga, 2010; Chase et al., 2011; Chase and Myers, 2011; Leprieur et al., 2012). Regarding the first cause mentioned, a large number of studies using exploratory statistics have assumed that the potential driving factors have additive effects on the response variable (Y), but in fact it is well established that drivers of alpha and beta diversity interact in a non-additive way including direct and indirect pathways (Santos et al., 2015). Thus, studying the influence of multiple interactive processes on diversity facets from non-experimental data requires evaluating non-additive effects. Structural equation modeling (SEM) offers a way to do this through a framework that integrates theory and empirical evidence (Grace, 2006; Grace et al., 2010). In contrast to the null hypothesis-oriented multivariate statistics that considers a single relationship at a time (individual processes), SEM is capable of evaluating simultaneous influences and responses through the study of direct and indirect effects (Grace, 2006).

Here, we used SEM to evaluate multivariate hypotheses on the relationship between TBD and PBD, and how these two community descriptors relate to species richness, environmental filtering, geographical space, and phylogenetic clustering (i.e.,

closely related species co-occurring more often than expected by the chance). Using a regional-extent dataset of tree communities in the subtropical Brazilian Atlantic forests, we test the following relationships (Fig. 1): (H_1) PBD increases with increasing TBD between plots, as a result of a high proportion of small ranged species belonging to early-diverged clades in the regional species pool, defined here as the total number of species across all plots studied (Graham and Fine, 2008; Eiserhardt et al., 2013). (H_2) PBD decreases with increasing phylogenetic clustering (PC) within plots (local level; Graham and Fine, 2008; González-Caro et al., 2014). (H_3) Both TBD and PBD decrease with increasing species richness within plots (Chase and Myers, 2011; Santos et al., 2015). This because the likelihood of two taxa randomly chosen from the regional pool belong to the same species or lineage will increases as new taxa are added to the compared plots. (H_4) Environmental filtering increases PC at the local level by favoring the coexistence of closely related species (with similar traits) that share appropriate adaptations for the local conditions, and display evolutionary niche conservatism (Cavender-Bares et al., 2006; Ackerly, 2009; Fine and Kembel, 2011). (H_5) Environmental filters related to seasonality and harshness of climate directly reduce the species richness within plots due to species loss, while directly increase both TBD and PBD between plots due to replacement of species and lineages between plots, respectively (Chase and Leibold, 2003; Graham and Fine, 2008; Jin et al., 2015). Because these filter control (together with other factors) the establishment or persistence of taxa, it is expected that only a subset of species and lineages of species (from the regional pool) is able to persist in stressful environments (Chase and Myers, 2011). (H_6) Both TBD and PBD are correlated with geographical space (Chase and Leibold, 2003). We expect that diversity facets either increase or decrease with spatial location (longitude or latitude) because environmental conditions are spatially structured across

region, and increase with distance between plots owing to dispersal limitation (Chase and Myers, 2011).

Material and methods

Floristic dataset

We obtained data from a regional network of plots from the Forest and Floristic Inventory of Santa Catarina, southern Brazil (Portuguese acronym: IFFSC; http://www.iff.sc.gov.br). We used 432 0.4-ha forest plots, distributed across the three major Atlantic forest types in southern Brazil, i.e., the dense forest, the mixed forest and the seasonal forest (Leite and Klein 1990), in an area of about 95,000 km^2, which comprises the whole Santa Catarina state (Fig. S1). The number of plots per forest type was proportional to the total remaining area of each type, with 202 (47%) located in the dense forest, 154 (36%) in the mixed forest and 76 (17%) in the seasonal forest. The sampling design of the IFFSC is based on a 10 km × 10 km grid across the entire territory of Santa Catarina state, except for the seasonal forest where the grid was of 5 km × 5 km because this forest type is most reduced in cover area (Vibrans et al., 2010; Vibrans et al., 2012). All trees (including tree ferns and palms) greater than or equal to 10 cm in diameter at breast height (d.b.h.) were measured and identified within each plot. Abundance values from each subunit were summed up to generate tree species data at the plot level.

Phylogenetic tree

To calculate the phylogenetic diversity metrics, we first built a phylogenetic tree for 646 angiosperm species that represent the species pool considered here, i.e., the total number of species across all plots within region. We used the Phylomatic tool in Phylocom 4.2 (Webb and Donoghue, 2005; Webb et al., 2008) to generate a phylogeny, based on a backbone phylogenetic tree (megatree R20120829 for plants), derived from the Angiosperm Phylogeny Group III reconstruction (APG III, 2009). The branch length for the phylogeny was defined based on the divergence time of taxa from their most recent common ancestor using node age estimates proposed by Wikström et al. (2001). The undated nodes in Wikström et al. (2001) were estimated using the Phylocom's branch length adjustment algorithm (BLADJ), where branch lengths were set by spacing undated nodes in the tree evenly between dated nodes to minimize variance in branch lengths (Webb et al., 2008). As stated by Swenson (2011), "the age estimates are quite crude, but they provide a substantial improvement over setting all branch lengths to one".

Environmental and spatial variables

Initially, we evaluated the statistical redundancy among 24 candidate variables (shown in Supporting Information, Table S1) grouped into eight categories, i.e., topography, geographical space, annual climate, temperature seasonality, temperature extreme, precipitation extreme, aridity and water-energy balance (evapotranspiration). We considered variables statistically redundant if their correlations were > 0.80. In addition, we examined how these variables relate to species richness, species

abundance, TBD, PBD, and phylogenetic structure by analyzing their correlations. Finally, we selected a key variable for each category mentioned above: altitude, longitude, annual mean precipitation, temperature annual range, mean temperature of coldest quarter, precipitation of driest quarter, aridity, and annual actual evapotranspiration. As hypothesis assessment in SEM is oriented to avoid overfitting due to deep modifications in the initial model, we included only the aforementioned variables in our final path models.

Here, topography is a proxy for environmental conditions that prevail at local scale, whereas annual climate, temperature seasonality, temperature extreme, precipitation extreme, and aridity represent the temporal variability of the climate regarding mean trends, seasonality and harshness, respectively. The annual actual evapotranspiration (AET) is a water-balance variable that reflects the water and energy regimes, and thus provides an indication of plant productivity, while potential evapotranspiration (PET) is an energy variable that reflects the capacity for transpiration flow and primary productivity in circumstances where water is not limiting (Fisher et al., 2011). Here, aridity represents a generalized function between mean annual precipitation and mean annual PET that reflects precipitation availability over atmospheric water demand (Trabucco and Zomer, 2009). Topography and climatic variables (derived from the monthly temperature and rainfall values) were extracted from the WorldClim database (Hijmans et al., 2005) and evapotranspiration and aridity variables from the global aridity and PET database (Trabucco and Zomer, 2009), with 30 arc-seconds (~1 km) of spatial resolution. Geographical space represents two kinds of effects, the effect of sampling location (x–y coordinates of the plots), and the effect of spatial proximity among plots (i.e., positive spatial correlation). We selected the five

spatial eigenfunctions (Moran's eigenvector maps modeling positive spatial correlation) that had the higher correlations with both TBD and PBD.

Diversity metrics

In this study, we quantified the tree diversity through species richness, taxonomic beta diversity (TBD), phylogenetic beta diversity (PBD) and phylogenetic structure. Here, species richness represents simply the number of species per plot. TBD is the change in species composition between plots. We used the Hellinger distance (Legendre and Gallagher, 2001) to calculate dissimilarity between plots, which is equivalent to Euclidean distance using transformed abundance data (i.e., the square root of relative abundance data). PBD is the change in phylogenetic relatedness (among individuals) between plots. We used two abundance-weighted measures of PBD, the mean nearest phylogenetic neighbor distance (D_{nn}) between plots (Ricotta and Burrascano, 2008; Webb et al., 2008), which is sensitive to recent evolutionary divergences or fine-scale relatedness (i.e., terminal nodes in the tree), and the standardized Rao's quadratic entropy (Rao's *H*; Hardy and Senterre, 2007), which is sensitive to old evolutionary divergences (i.e., deeper nodes in the tree; Swenson, 2014). The D_{nn} metric is computed as the mean phylogenetic distance between a species in a plot and its most related species in other plot, taking into account relative abundance of species (Webb et al., 2008). Rao's *H* standardizes the mean phylogenetic distance (MPD) between individuals drawn randomly from each of two plots by the differences in species richness between these two plots (Swenson, 2014). Thus, Rao's *H* is a MPD-based measure of phylobetadiversity that is independent of richness. The distance in Rao's *H* corresponds to the distance to the most recent common ancestor (MRCA) of two species and not the complete distance between two species (Swenson, 2014).

The phylogenetic structure represents a nonrandom pattern of phylogenetic relatedness among co-occurring species, where a high species to genus ratio indicates the coexistence of closely related species (i.e., phylogenetic clustering, PC) and a low species to genus ratio indicates the coexistence of distantly related species (i.e., phylogenetic overdispersion, PO; Swenson, 2014). We used two indices of community phylogenetic structure, the Net Relatedness Index (NRI; Webb, 2000) that corresponds to a standardized effect size (SES) for the MPD, and the Nearest Taxon Index (NTI; Webb, 2000) that corresponds to a SES for the mean nearest taxon distance (MNTD). We standardized these metrics using the independent swap null model (Gotelli, 2000) that shuffles the species' occurrences among plots while maintaining, in the simulated communities ($n = 999$), the species richness per plot, and the frequency of occurrence of each species across plots. We computed SES for each metric as in the original work by Webb (2000), where the difference between the observed and mean expected values, divided by the standard deviation of expected values, is multiplied by negative one. Thus, NRI or NTI > 0 indicates PC and NRI or NTI < 0 indicates PO. The NRI metric is sensitive to deeper nodes in the phylogenetic tree, whereas the NTI metric is sensitive to terminal nodes in the tree (Swenson, 2014). To test specifically the relation between PC and PBD without taking into account species richness, we used the NRI and Rao's *H* metrics which are independent of richness ($r = –0.17$ and $r = 0.06$, respectively).

Structural equation modeling (SEM)

We used SEM (Bollen, 1989) to test the validity of the postulated relationships among the multiple interacting factors which are presented in path diagram (Fig. 1). We aim to disentangle the direct and indirect effects between these factors, to reveal the

strength of the relationships, and to explore the ecological and evolutionary mechanisms underlying observed patterns of diversity. Overall, SEM is best understood as a scientific framework, not a particular statistical tool which fits within a workflow process designed to advance our scientific understanding (Grace, 2006; Grace et al., 2010). The essential aim of SEM is to develop and evaluate models to infer cause-effect relationships within a system of variables (Shipley, 2000; Grace et al., 2015). Because causation is ambiguous or not well understood for some relationships, we considered the relationships among variables as statistical associations or dependencies which are subject to causal interpretation (Grace, 2006).

We fit path models in the lavaan package for R (Rosseel, 2012) using a robust maximum likelihood (ML) estimator, known as Satorra-Bentler scaled chi-square (χ^2) statistics (Satorra and Bentler, 1988), as our data did not meet the multivariate normality assumption. Overall, the Satorra-Bentler χ^2 estimates the level of kurtosis of the data, and uses this estimate to adjust the ML-based χ^2 statistic for non-normality (Rosseel, 2012). Here, we assessed model fit based on the significance level of the robust $\chi 2$ statistics together with the (robust) root mean square error of approximation (RMSEA), and the standardized root mean square residual (SRMR). We considered a good model fit if P-value > 0.05, robust RMSEA < 0.05, and SRMR < 0.05 (Browne and Cudeck, 1993; Schumacker and Lomax, 2010). A nonsignificant χ^2 value indicates that the model-implied (predicted) covariance matrix does not differ from the observed covariance matrix, and hence the specified theoretical model fits the data (Shipley, 2000; Schumacker and Lomax, 2010). In addition, the concordance between observed and predicted covariances suggests that the fitted model is a sufficient approximation of the true model (Grace et al., 2010). We performed a re-specification of model by removing nonsignificant paths in each round when the initial model does not fit the data

assuming that the observed and predicted covariances are identical expect for sampling error (Shipley, 2000). We evaluated the impact of removing nonsignificant paths based on the overall fit of the model. For instance, the χ^2 statistics will change little with the removal of weak pathways, i.e., the postulated relationships that did not represent characteristics of the data (Grace, 2006). We used the sample-size adjusted Bayesian information criterion (SABIC) to compare the prediction performance among tested models. Following common practice, we considered the model with the lowest SABIC value as the one that best predicts the data (Grace, 2006). We check the residuals between predicted and observed covariances for the fitted models by seeking to detect any missing path that could improve model fit. We used mediation analysis to estimate indirect effects of predictors (Xs) upon response (Ys) variables via mediators (Ms). The total effect of a variable on another (i.e., bivariate correlation) is equal the sum of its direct and indirect effects. The direct path represents an effect of X upon Y while holding other Xs constant. We used Bollen-Stine bootstrap (Bollen and Stine, 1993) to estimate the magnitude of indirect effects and its statistical significance (2000 iterations).

Results

The final path models relating significant predictors for TBD, PBD and species richness ($\chi^2 = 3.696$, df = 5, P-value = 0.594; robust RMSEA < 0.001; SRMR = 0.002), and to PC ($\chi^2 = 3.948$, df = 4, P-value = 0.413; robust RMSEA < 0.001; SRMR = 0.003) were found to have adequate fit. Additional evaluation of the residuals did not detect missing paths for these models.

We found a total of seven direct drivers accounting for 73% of the variation in PBD, seven accounting for 77% of the variation in TBD, and five accounting for 29% of the variation in species richness (Fig. 2). Three direct drivers accounted for 21% of the variation in PS (Fig. 3). Direct paths between drivers and diversity facets represent relationships that cannot be explained through any other relationships in the model. The increasing the TBD directly predicts higher levels of PBD (Table 1; Fig. 2), whereas the increasing the PC within plots directly predicts lower levels of PBD between plots (Table 2; Fig. 3). A lower level of PBD at regional level is directly predicted by increasing PC at local level (Table 2; Fig. 3).

Environmental filters related to altitude, temperature seasonality and water-energy balance directly predict TBD, PBD and species richness (Table 1; Fig. 2). The first two filters reduce species richness, whereas evapotranspiration increases richness. On the other hand, altitude and temperature seasonality increase both TBD and PBD, and evapotranspiration decreases these facets. Species richness increases from west to east in the studied region, whereas TBD decreases. Annual precipitation has a direct positive effect on PBD, and precipitation extreme has a direct negative effect on PBD and a positive effect on TBD. Environmental filters related to extremes in temperature and precipitation, and aridity directly predict higher levels of PC, whereas annual precipitation predicts lower levels of PC (Table 2; Fig. 3).

Temperature seasonality has an indirect positive effect through altitude on PBD, i.e., the correlation between PBD and temperature seasonality is partially explained by the correlation between PBD and altitude (robust ML = 0.266, SE = 0.035, z-value = 7.654, *P*-value < 0.001). Altitude has an indirect positive effect through precipitation extreme on TBD (robust ML = 0.205, SE = 0.019, z-value = 10.961, *P*-value < 0.001). Temperature seasonality has an indirect positive effect through altitude (robust ML =

0.144, SE = 0.020, z-value = 7.247, *P*-value < 0.001) and precipitation extreme (robust ML = 0.285, SE = 0.028, z-value = 10.361, *P*-value < 0.001) on TBD. Lastly, aridity has an indirect positive effect through precipitation extreme on PC (robust ML = 0.136, SE = 0.024, z-value = 5.627, *P*-value < 0.001).

Discussion

To the best of our knowledge, our study is the first that evaluated multiple interacting factors involving phylobetadiversity (PBD), taxonomic beta diversity (TBD), species richness, environmental filtering, geographical space, and phylogenetic structure. The verification that there are no missing paths that would improve model fit suggests that our SEM framework captured most covariance structure of the dataset. We found that the amount of variation in TBD and PBD explained by the interactive factors was high and similar for both. Overall, these facets in the Atlantic forests respond primarily to (1) environmental filtering through the sorting of taxa along altitudinal and climatic gradients, (2) spatial location of the plots (TBD was found to decrease with longitude), and (3) local diversity.

Our network of hypotheses (Fig. 1) that depicts the connections between these factors supports the findings of our path models. However, it is important to mention that we found that PBD strongly decreased with precipitation extreme, while both TBD and species richness weakly increased, unlike our initial expectation that harshness of climate reduces richness, while increasing both TBD and PBD. The observed decrease in PBD between plots with increasing extreme precipitation along region can be explained by the direct positive relation (but not statistically significant) between richness and precipitation of driest quarter, and a strong direct positive effect between phylogenetic clustering (PC) and precipitation of driest quarter. As PBD between plots

decreases with increasing the richness and PC within these plots, we found that plots in localities that experience higher levels of precipitation in driest quarter (autumn season) tend to exhibit higher richness and PC than those experiencing lower levels, and hence PBD is lower between them. Based on the above result, we were not able to conclude whether the (weak but statistically significant) direct positive relation between TBD and precipitation of driest quarter is scientifically meaningful, as we did not fully trust its generality, thus further evaluation is needed. Unlike factors that decrease richness and independently increase TBD and PBD (e.g., altitude and temperature seasonality), we found that annual actual evapotranspiration increased richness and decreased TBD and PBD, which highlights the complexity of the responses of species and lineages to climatic gradients.

It is well established that harsh abiotic conditions impose a deterministic filter on community assembly, where a niche selection prevents a subset of the species pool from persisting in localities experiencing these conditions (Chase and Myers, 2011). We found that temperature extreme (i.e., mean temperature of coldest quarter) directly predicted higher levels of PC, but did not directly influenced PBD, just as we expected. Our analysis, however, revealed a significant total correlation between PBD and temperature extreme (robust ML = −0.508, SE = 0.072, z-value = −7.002, P-value < 0.001) that cannot be explained by the other variables here used. The increasing PC with cold temperature is consistent with the evolutionary niche conservatism hypothesis that predicts that species in colder localities tend to be phylogenetically more related to each other than expected by chance (Qian et al., 2013b). Overall, when functional traits that allow species to overcome the selective forces of a given environment are phylogenetically conserved across lineages, it is expected that habitat specialization together with environmental filtering increase PC (Fine and Kembel, 2011). However,

previous studies have pointed out that human disturbance is another key factor that increases PC (disturbance influences TBD as well) in both tropical and subtropical tree communities (e.g., Feng et al., 2014; González-Caro et al., 2014). Recently, Feng and collaborators showed that the past tree harvesting in a Chinese subtropical forest significantly affected the phylogenetic and functional structure of tree communities, with potential consequences for the functioning and resilience of this forest system. Of course we cannot exclude that disturbance potentially increases phylogenetic relatedness among co-occurring species in study system, because most of the studied plots are located in early-to-late secondary forest patches (Leite and Klein, 1990; SOS Mata Atlântica, 2015) that have historically experienced high levels of habitat loss and fragmentation together with other human disturbances (e.g., selective logging).

Here, we measured the statistical dependence among diversity metrics, and tested the postulated relationships between the diversities and drivers, controlling for the potential confounding effects emerging from the associations among metrics. In agreement with evidences from previous studies (e.g., Graham et al., 2009; Chase et al., 2011), our results showed that TBD is directly influenced by the number of species that co-occur in local communities, whereas PBD is directly influenced by the number and identity of species (which in turn are strongly influenced by the regional species pool), as well as by the degree of phylogenetic clustering (PC) within communities. Note that the associations among metrics here correspond to direct effects instead of correlations; hence they are statistically independent of effects of the other variables. For instance, the positive relation between PBD and TBD we found is independent of species richness. It is well established that compositional differences between communities may potentially be overshadowed by the differences in species richness between them within a species pool (Jost, 2007; Anderson et al., 2011; Chase et al., 2011; Chase and Myers,

2011). This problem is due to how diversity is partitioned among diversity components, i.e., gamma = alpha × beta or gamma = alpha + beta (Jost, 2007). For this reason, a complete understanding on whether compositional dissimilarity is due to differences in species richness (i.e., species loss or gain) or whether is due to species replacement that is independent of richness (i.e., true turnover) is important for its correct interpretation (Baselga, 2010; Leprieur et al., 2012). Using causal modelling, we provide strong evidence that compositional and phylogenetic dissimilarity between plots is directly determined by the replacement of taxa (both the species and lineages) across space, as a result of environmental filtering, instead of indirectly determined because environmental filtering altered the number and identity of species, causing concomitant random changes in TBD and PBD, respectively. We suggest that SEM framework allows for a more complete and robust assessment about the relative influence of several processes structuring communities, while separates variation in TBD from variation in species richness, and the variation in PBD from variation in TBD, richness and phylogenetic structure.

Although we used the best information available for the study region, the phylogeny we built has low resolution below the family level, which can affect our phylogenetic diversity metrics. However, because polytomies (unresolved relationships) have a small effect on the ability to detect correlations between phylogenetic diversity and ecological factors (Cadotte et al., 2008), we suggest that the limited resolution of our phylogeny not prevented us from detecting strong signals of community assembly mechanisms on PBD in subtropical tree communities. We found that both the terminal (D_{nn}) and basal (Rao's H) metrics of phylobetadiversity were able to detect the replacement of taxa across space in response to environmental gradients.

Conclusions

Our study demonstrates that at the study scale, compositional dissimilarity in subtropical tree communities is mainly driven by the altitudinal and climatic gradients, while phylogenetic dissimilarity is also determined by the degree of phylogenetic clustering at local level, more likely reflecting niche conservatism within lineages and human disturbance that has historically conducted the studied forests to a process of biotic homogenization. These results have important implications for conservation actions focused on protecting regional diversity and on maintaining critical ecological processes for the long-term persistence of biodiversity.

Acknowledgements

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Table 1. Standardized direct effects of drivers on phylogenetic beta diversity (A), taxonomic beta diversity (B), and (C) species richness for the final path model (Fig. 2). Path coefficients are based on robust maximum likelihood (ML) estimator and robust standard errors (SE). PBD is the mean nearest phylogenetic neighbor distance (D_{nn}) between plots.

Model	Estimate	SE	Z-value	P(>|z|)
(A) PBD				
Species richness	–0.307	0.048	–6.417	0.000
Altitude	0.507	0.040	12.601	0.000
Annual precipitation	0.425	0.093	4.559	0.000
Temperature annual range	0.216	0.073	2.968	0.003
Precipitation of driest quarter	–0.600	0.086	–6.998	0.000
Annual actual evapotranspiration	–0.332	0.075	–4.432	0.000
Beta diversity	0.258	0.055	4.666	0.000
(B) TBD				
Species richness	–0.276	0.027	–10.330	0.000
Altitude	0.313	0.091	3.427	0.001
Longitude	–0.348	0.072	–4.840	0.000
Temperature annual range	0.329	0.069	4.765	0.000
Mean temperature of coldest quarter	0.209	0.111	1.888	0.059
Precipitation of driest quarter	0.268	0.074	3.618	0.000
Annual actual evapotranspiration	–0.397	0.083	–4.775	0.000
(C) Species richness				
Altitude	–0.640	0.159	–4024	0.000

Longitude	0.467	0.086	5.420	0.000
Temperature annual range	–0.220	0.085	–2.579	0.010
Mean temperature of coldest quarter	–0.504	0.186	–2.711	0.007
Annual actual evapotranspiration	0.451	0.102	4.437	0.000

Table 2. Standardized direct effects of drivers on phylogenetic beta diversity (A), and phylogenetic structure (B) for the final path model (Fig. 3). Path coefficients are based on robust maximum likelihood (ML) estimator and robust standard errors (SE). PBD is the standardized Rao's quadratic entropy (Rao's *H*) between plots and PS is the Net Relatedness Index (NRI) within plots.

Model	Estimate	SE	Z-value	P(>|z|)
(A) PBD				
Altitude	0.655	0.049	13.317	0.000
Annual precipitation	0.237	0.060	3.982	0.000
Precipitation of driest quarter	−0.742	0.073	−10.097	0.000
Annual actual evapotranspiration	0.101	0.051	1.984	0.047
Phylogenetic structure	−0.397	0.045	−8.841	0.000
(B) PS				
Annual precipitation	−0.463	0.209	−2.219	0.026
Mean temperature of coldest quarter	0.313	0.075	4.154	0.000
Precipitation of driest quarter	0.783	0.159	4.926	0.000
Aridity	0.295	0.101	2.919	0.004
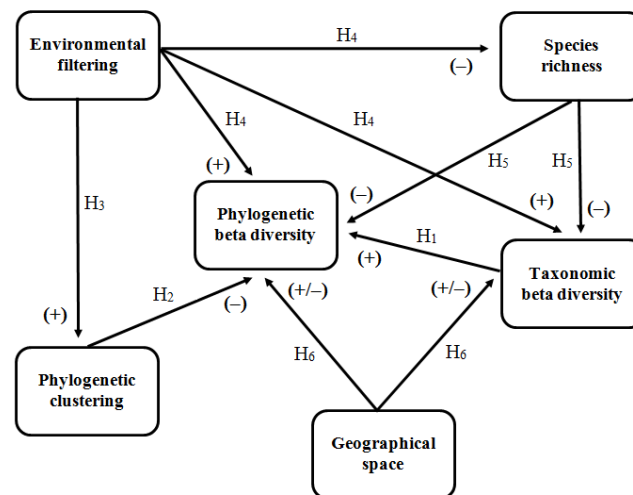
Figure 1. Path diagram summarizing multivariate hypotheses (Hn) about the role of ecological and evolutionary drivers on diversity. Are shown the nature (positive or negative) of the postulated relationships among variables. See text for theoretical background.
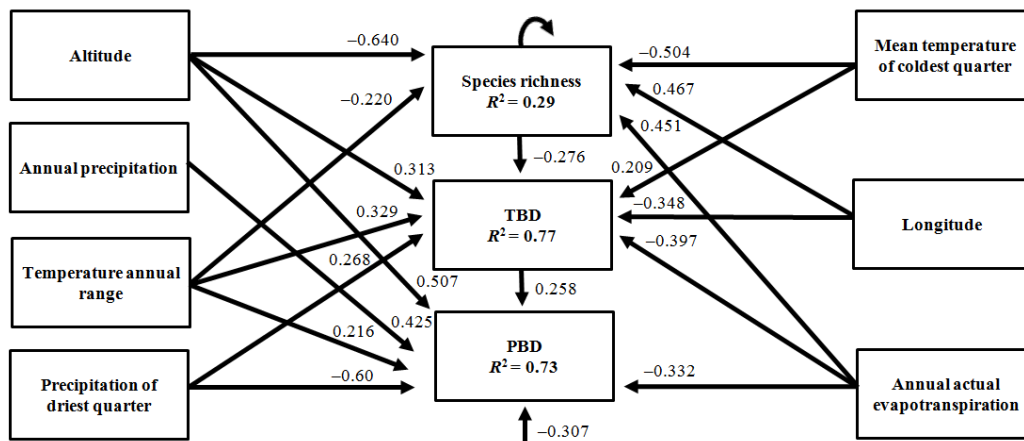
Figure 2. Final path model showing the relationships between drivers and diversity facets, i.e., the taxonomic beta diversity (TBD), phylogenetic beta diversity (PBD), and species richness, and the relationships between these facets. Here, TBD and richness simultaneously act as predictor and response variables. PBD is the mean nearest phylogenetic neighbor distance (D_{nn}) between plots. Coefficients shown are standardized path coefficients. R^2 values indicate the amount of variance in an endogenous variable that is explained by the predictors.
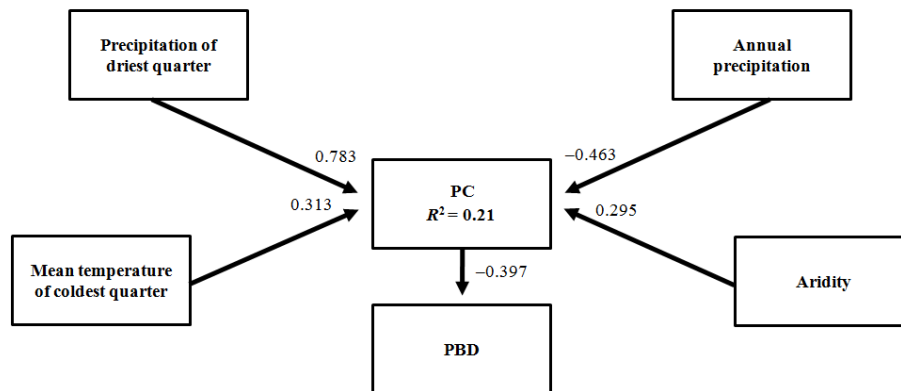
Figure 3. Final path model showing the relationships between drivers and phylogenetic structure (PS), and the relationship between PS and phylogenetic beta diversity (PBD). The relationships between environmental drivers and PBD are omitted here, but are shown in Table 2. Here, PS simultaneously acts as predictor and response variable. PBD is the standardized Rao's quadratic entropy (Rao's H) between plots and PS is the Net Relatedness Index (NRI) within plots. Coefficients shown are standardized path coefficients. R^2 values indicate the amount of variance in an endogenous variable that is explained by the predictors.

Capítulo 2: How the tree taxonomic and phylogenetic diversity is represented in protected areas in subtropical Brazilian Atlantic forests? 1

Authors

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[1] Artigo formatado de acordo com o periódico *Biodiversity and Conservation*

Abstract

Protected areas are the cornerstone of conservation efforts to maintain biodiversity. Here, we used an integrative approach to predict and map the tree taxonomic (TD) and phylogenetic (PD) diversity and to assess the effectiveness of the regional protected area network in representing these biodiversity components within the remnant Atlantic forests in southern Brazil. We first defined areas of taxonomic and phylogenetic uniqueness as those sites with higher contribution than the mean to the total beta diversity, with higher or lower PD than expected based on TD, and sites of spatial mismatch and congruence between TD and PD. We then tested whether the uniqueness areas are more or less protected than expected based on two area coverage criteria (3% and 9.7%). We found both high congruence and mismatch between TD and PD within these forests. This suggests that setting priorities on the basis of TD or PD may not adequately protect the regional biodiversity. Uniqueness areas were less protected than expected based on the 9.7% coverage criterion. The expected mean proportion of protected cells was below 5% in most of the tested categories. We suggest that expanding the network towards the areas of taxonomic and phylogenetic uniqueness could increase the representation of species richness, beta diversity and evolutionary history of angiosperm trees at the same time. Furthermore, the inclusion of areas of high irreplaceability in terms of evolutionary history could help to improve the protection of feature diversity and evolutionary potential of species, leading to better conservation outcomes.

Keywords: Biodiversity conservation, beta diversity, evolutionary history, spatial congruence, spatial mismatch, species richness.

Introduction

Biodiversity is a multifaceted concept that encompasses multiple scales in time and space and distinct components such as taxonomic, functional and phylogenetic diversity (Pavoine and Bonsall 2011). The study of biodiversity has traditionally focused on quantifying taxonomic diversity (TD), but there is a growing interest in use of phylogenetic diversity (PD) to include phylogenetic relationships (and hence evolutionary history) among species into conservation assessments (Winter et al. 2013). Extant PD comprises part of the raw material on which future evolutionary processes will operate (Rodrigues et al. 2005). In this perspective, it has been argued that protecting as much evolutionary history as possible is the best way to ensure the maintenance of feature diversity and evolutionary potential, i.e., the capacity of species to respond adaptively to environmental changes (Vane-Wright et al. 1991; Faith 1992; Vézquez and Gittleman 1998; Forest et al. 2007; Laity et al. 2015).

Because geographic areas with different sets of species can diverge greatly in the amount of evolutionary history they represent, the identification of areas with higher and lower PD than expected by chance given their species richness is important for conservation (Forest et al. 2007; Winter et al. 2013; Zupan et al. 2014; Costion et al. 2015). For example, areas with higher PD than expected are particularly interesting because they are likely to contain a high proportion of evolutionarily distinct lineages (and hence a large amount of evolutionary history). They may correspond either to zones where diversification has been slow and immigration of multiple lineages frequent (Davies and Buckley 2011), or to zones that experienced high diversification of multiple lineages together with high immigration of multiple lineages over time (Fritz and Rahbek 2012). In contrast, localities with lower PD than expected may indicate

zones where speciation has been rapid and immigration rare, i.e., zones where large radiations of few lineages occurred after few initial immigration events (Davies and Buckley 2011; Fritz and Rahbek 2012). These areas are likewise interesting for conservation because they include species that could potentially contribute to future evolutionary radiations (Collen et al. 2011; Davies and Buckley 2011; Zupan et al. 2014). Therefore, if we wish to protect as much evolutionary history as possible, one effective conservation strategy would be the protection of both ancient refugia and diversification zones. Regarding species protection, areas that contribute more than the mean to total beta diversity of a region are particularly interesting for conserving unusual species combinations (Legendre and Cáceres 2013). This implies that conservation must target a set of areas across region to represent the high species turnover along spatial or environmental gradients (Socolar et al. 2016).

Recent studies have mapped the spatial distribution of different facets of diversity and measured the levels of spatial congruence (overlap) and incongruence (mismatch) between them to identify and prioritize areas in need of protection, and to assess if one facet can effectively serve as a surrogate for others (e.g., Devictor et al. 2010; Sobral et al. 2014; Daru et al. 2015; Daru and le Roux 2016). As distinct areas may be highly diverse in both TD and PD, which results in a high spatial congruence, the mapping of spatial mismatch between them is particularly important to reveal zones where few species (low TD) represent a high amount of evolutionary history (high PD; Laity et al. 2015). Overall, spatial mismatch between diversity components may reflect differences in the biogeographical and evolutionary histories underlying the distribution of species or contrasting processes shaping the spatial distribution these components (Webb et al. 2002; Devictor et al. 2010; Stevens and Tello 2014; Daru et al. 2015). Hence, areas of

mismatch between facets may indicate unique evolutionary or ecological processes that have particular importance for conservation (Strecker et al. 2011).

The Brazilian Atlantic forest is a biodiversity hotspot that harbors high levels of diversity and endemism, and is probably one of the most highly threatened tropical forests (Mittermeier et al. 2004; Metzger 2009; Tabarelli et al. 2010). The Atlantic forest has been subject to several human disturbances, including farming, exotic tree monocultures, selective logging, urbanization, exotic species invasion, overhunting and climate change (Tabarelli et al. 2010). As a consequence of this long history of degradation, only about of 12% of their original extent remains in scattered and reduced forest patches (Ribeiro et al. 2009). The current protected areas network is clearly insufficient to protect this hotspot because it covers less than 2% of its extent. In addition, the different Atlantic forest physiognomies (i.e., the dense, mixed and seasonal forests) are unevenly protected within this network, leading to an unequal representation of taxa, evolutionary and functional processes in protected areas (Metzger 2009; Ribeiro et al. 2009; Bergamin et al. 2017). Despite the extremely worrying state of this hotspot, ecological information required to support conservation actions are still missing for the most of the regions (Lima et al. 2015).

Here, we used an integrative approach to predict and map the tree taxonomic and phylogenetic diversity and to assess the effectiveness of the regional protected area network in representing these biodiversity components in the three main Atlantic forest types in southern Brazil. Using a regional network of forest plots in an area of about 95,000 km^2, we first performed a spatial interpolation of the tree diversity components within the remnant forest extent (i.e., a mosaic of old-growth and late-secondary forests), and then tested whether the areas of taxonomic and phylogenetic uniqueness are more or less protected than expected based on two area coverage criteria: (1) the

expected mean proportion of protected cells in relation to the total surface covered by the protected areas network (3%), and (2) the expected mean proportion of 10% protected cells relative to the unprotected fraction in whole territory (97%). Here, uniqueness areas were defined as follows: (1) areas that make a higher or lower evolutionary contribution than taxonomic diversity alone (i.e., areas with higher or lower PD than expected by chance given their species richness), (2) areas with higher contribution than the mean to the total beta diversity of the region, and (3) areas of spatial mismatch and congruence between TD and PD.

Materials and methods

Study region

The study area is distributed throughout the state of Santa Catarina (SC), in a total area of 95,717 km^2 in southern Brazil (Fig. 1). This region corresponds to the southern limit of the Brazilian Atlantic forest, where three main forest types can be found (Leite and Klein 1990), as follows:

(1) Dense forest, situated in the eastern part of SC, occurring from the lowlands to steep hillslopes along the Atlantic coast and covering a large altitudinal range (approximately 0 to 1300 m.a.s.l.). High precipitation levels and low temperature variation allow for the development of a complex forest structure, evidenced by the presence of distinct tree layers and a high number of angiosperm species (Leite and Klein 1990). The dense forest occurs mainly in areas of Precambrian bedrocks and, to a lesser extent, in terrains

of Gondwanic sedimentary rocks of the Paraná Basin and in areas of Cenozoic sedimentary rocks along the coastline (Kaul 1990);

(2) Mixed forest, known also as *Araucaria* forest, distributed at altitudes ranging from 500 to 1800 m on the volcanic highland plateau (central-western portion, composed by acidic and basic rocks of the Jura-Cretaceous period) and on the sedimentary highland plateau (central-north, composed by sedimentary rocks of the Paraná Basin; Kaul 1990). The mixed forest is found in mosaics with native grasslands at higher elevations, where climate is wet and cool; here, mean annual temperature does not exceed 16°C (Nimer 1990). This forest is physiognomically characterized by the peculiar aspect of the emerging treetops of the Brazilian pine (*Araucaria angustifolia*), while its composition is marked by a unique mix of temperate and tropical species (Jarenkow and Budke 2009);

(3) Seasonal forest, distributed in the western portion of SC, on the volcanic highland plateau and along the Uruguai river basin in an altitudinal range from 150 to 800 m (Figure 1). In this forest more than 50% of the canopy tree individuals lose their leaves in response to low temperatures during the winter: two to three months show average temperature below 15°C (Leite and Klein 1990). Differences in tree beta diversity across these forests are largely determined by direct and indirect effects of environmental filtering (Santos et al. 2015).

Climate in the region is temperate humid with hot summers and temperature of the hottest month $> 22^{\circ}$C (Cfa) in the western portion at altitudes below 700 m, and along the coast in altitudes up to 500 and 600 m. At higher altitudes, i.e. in the highland region, climate is temperate humid with warm summers and temperature of the hottest month $< 22^{\circ}$C (Cfb) (Alvares et al. 2013). The annual temperature is around 18°C at altitudes between 500 m to 300 m along the coast, and at altitudes between 500 m to

450 m along the continent, while varies between $16°C$ to $14°C$ across the highest elevations of the highlands (Nimer 1990). Precipitation is evenly distributed throughout the year, with mean annual equal to 1660 mm, ranging from 1250 mm to 2250 mm (Nimer 1990).

It is important to note that Santa Catarina is among the Brazilian states with the highest deforestation rates of the Atlantic forest, although these rates have significantly decreased over the past decades (SOS Mata Atlântica 2015). Currently, the remnant forest cover in this state is estimated at 23% (SOS Mata Atlântica 2015). The most fragmented forest types in the region are the seasonal and mixed forests, which are under intense pressure (Sevegnani and Schroeder 2013), and whose remnant forest area has been reduced to 24% and 16%, respectively (Vibrans et al. 2013). The dense forest concentrates both the major remnant cover (40%) and the larger forest patches in the region (Sevegnani and Schroeder 2013).

Dataset

Tree species data were provided by the forest inventory of Santa Catarina state (Forest and Floristic Inventory of Santa Catarina, Portuguese acronym: IFFSC; http://www.iff.sc.gov.br). The IFFSC is 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 sampling design of the IFFSC is based on a 10 km × 10 km grid across the entire territory of Santa Catarina state, except for the seasonal forest where the grid was of 5 km × 5 km. This forest type is most reduced in cover and the 10 km × 10 km grid would have led to very low number of

sample points. At each intersection of the grid and where a sufficiently large forest remnant was present within a circle of 500 m, a central point was established (Vibrans et al. 2012). From each central point a cluster of four subunits of 1.000 m^2 (20 m × 50 m) composed a sampling forest plot. The four subunits were allocated crosswise towards the four cardinal points, starting at a distance of 30 m away from the central point. Out of the 437 plots available, we used 432, as we excluded three plots situated in the coastal region with very specific soil conditions and two plots for which data was not complete. The number of plots per forest type was proportional to the total remaining area of each type, with 202 (47%) located in the dense forest, 154 (36%) in the mixed forest and 76 (17%) in the seasonal forest (Fig. 1). Within each plot, all trees (including tree ferns and palms) greater than or equal to 10 cm diameter at breast height (1.3 m, d.b.h.) were measured and identified (Vibrans et al. 2010; Vibrans et al. 2012; Vibrans et al. 2013). Abundance values from each subunit were summed up to generate tree species data at the plot level.

Phylogenetic tree

To calculate the phylogenetic diversity metrics, we first built a phylogenetic tree for 646 angiosperm species that represent the species pool considered here, i.e., the total number of species across all plots within region. We used the Phylomatic tool in Phylocom 4.2 (Webb and Donoghue 2005; Webb et al. 2008) to generate a phylogeny (Fig. S2), based on a backbone phylogenetic tree (megatree R20120829 for plants), derived from the Angiosperm Phylogeny Group III reconstruction (APG III, 2009). The branch length for the phylogeny was defined based on the divergence time of taxa from their most recent common ancestor using node age estimates proposed by Wikström et

al. (2001). The undated nodes in Wikström et al. (2001) were estimated using the Phylocom's branch length adjustment algorithm (BLADJ), where branch lengths were set by spacing undated nodes in the tree evenly between dated nodes to minimize variance in branch lengths (Webb et al. 2008). As stated by Swenson (2011), "the age estimates are quite crude, but they provide a substantial improvement over setting all branch lengths to one".

Because PD metrics strongly depend on how many old lineages are included or excluded in the phylogeny (Chave et al. 2007; Vellend et al. 2010), we did not consider here a total of 11 non-angiosperm species with very long phylogenetic branches. These taxa belong to ancient clades of conifers (genera *Araucaria* and *Podocarpus*) and tree ferns (genera *Alsophila*, *Cyathea*, *Dicksonia* and *Sphaeropteris*).

Diversity metrics

We computed the (abundance-based) bias-corrected form of Chao 1 (Colwell, 2009) to estimate the minimum number of species expected in each plot using information on the rare species to adjust for the number of species present but not detected (Gotelli and Colwell 2010). The Chao1 was calculated in the R package 'vegan' (Oksanen et al. 2013).

We calculated the local contribution to beta diversity (LCBD; Legendre and Cáceres 2013) to identify plots that contribute more than the mean to total beta diversity of the region (BD_{Total}). LCBD measures the degree of distinctiveness of the plots regarding their species compositions; hence high LCBD values indicate plots that have unusual species combinations (Legendre and Cáceres 2013). We partitioned the total variance of the Hellinger dissimilarity matrix (i.e., BD_{Total}) into local contributions of

each plot in terms of community composition. An advantage of estimating BD_{Total} is that beta diversity is computed without reference to the alpha and gamma diversity components (Legendre and Cáceres 2013). We found that LCBD of the plots was negatively and weakly correlated with species richness ($r = -0.26$), indicating a weak tendency for those plots with a high LCBD to be less rich. Here, we standardized the LCBD values (z-scores) of the plots to indicate higher (+) and lower (−) contributions than average. The LCBD was calculated in the R package 'adespatial' (Dray et al. 2017).

In order to identify the plots with higher and lower PD than expected based on species richness, we used here two complementary PD metrics that differ in their sensitiveness to phylogenetic structure of communities, as follows: (1) the Faith's PD (Faith 1992) that is a phylogenetic richness metric that measures the total evolutionary history contained within a community (Tucker et al. 2016) and (2) the mean pairwise distance (MPD; Webb et al. 2008) that is a phylogenetic divergence metric that measures the average species distinctiveness within a community (Tucker et al. 2016). Here, Faith's PD index was calculated as the sum of the phylogenetic branch lengths among taxa in a plot plus the root node of the regional phylogeny (Faith 1992; Cadotte et al. 2010). Faith's PD has been one of the most widely used metrics for evaluating conservation priorities (Cadotte et al. 2010; Swenson 2014). It is classified as a terminal metric that reflects the phylogenetic structure that is dominant near the tip of the phylogenetic tree (Mazel et al. 2015). Here, MPD was computed as the average relatedness between all pairs of individuals in a plot (Webb et al. 2008). It is considered as a basal metric that is sensitive to deeper branching structure (Mazel et al. 2015). The concomitant use of richness and divergence PD metrics that are sensitive to shallow and deep branching structures, respectively, can provide a better understanding of

phylogenetic structure of communities (Mazel et al. 2015). For these PD metrics we calculated standardized effect sizes (SES) using the independent swap null model (Gotelli 2000) that shuffles species' occurrences among plots while maintaining, in the simulated communities ($n = 999$), the species richness per plot and the frequency of occurrence of each species across all plots. Thus, the SES.PD and SES.MPD metrics are expressed here as deviations from a null expectation, with values higher or lower than expected given the observed richness in the plot (Webb et al. 2008). These metrics were calculated in the R package 'picante' (Kembel et al. 2010).

Mapping diversity components

We used the Kriging interpolation method to map the spatial distribution of TD and PD for the remnant forest area in the study region (based on the forest remnants map of the SOS Mata Atlântica 2015). Kriging is known as a best linear unbiased predictor (BLUP) by minimizing the variance of the prediction error (Oliver and Webster 2015). The method has been applied to predict and map values of variables at unsampled locations, using a set of generalized linear equations based on the prior knowledge of the degree of spatial autocorrelation of the data (Webster and Oliver 2001; Fortin and Dale 2005). Kriging works as a two-step process, in which a sample variogram and a covariance function to fit this variogram are constructed to estimate the magnitude and shape of spatial autocorrelation of a target variable, and afterwards the parameters of the fitted variogram are inserted into the Kriging equations to make the predictions in the unsampled locations (Cressie 1993; Chilès and Delfiner 1999). Overall, the variogram model is a function of semi-variance (i.e., the difference squared between the values of the paired locations) versus distance (Hiemstra et al. 2009). The

procedures adopted to build the variograms, the kriging predictions and the validation of prediction models are depicted in Supplementary Information. The cross-validation statistics for each interpolated variable are shown in Table S1. These analyses were carried out in the R 'automap' package (Hiemstra 2015).

Spatial overlap between diversity components

We measured the correlation between TD (Chao1) and PD (SES.PD) from two interpolated raster maps considering only the remnant forest cover to identify areas (cells) of spatial mismatch and congruence between these components. We used a local (cell-by-cell) correlation coefficient (Spearman's rho) based on a focal neighborhood analysis of the rasterized data using the R 'raster' package (Hijmans et al. 2016). For a given raster cell, positive correlations higher than 0.20 (both high TD and PD) indicate spatial congruence and negative correlations higher than –0.20 (high TD and low PD, or vice-versa) indicate spatial mismatch. Note that Faith's PD is a metric of phylogenetic richness that is directly comparable to taxonomic richness (Chao1), while MPD is not, once it represents a phylogenetic divergence metric.

Protected areas network assessment

We overlaid the polygons of protected areas onto the interpolated raster maps, and then computed the proportion of protected cells for the areas of taxonomic and phylogenetic uniqueness (i.e., areas of higher vs. lower PD, areas of higher beta-TD, and areas of mismatch vs. congruence between TD and PD) in each conservation reserve. The proportion of protected cells was computed as the number of cells of each

uniqueness category within reserve divided by the total number of protected cells of respective category in all reserves. Of the 47 protected areas listed by the national cadastre of the Brazilian Ministry of the Environment (available online at http://www.mma.gov.br/) for the study region (Fig. S1), we assessed 27 containing at least one raster cell with remnant forest. The evaluated protected areas cover practically the same fraction of the region surface (3.07%) than the whole 47 protected areas (3.24%). Because some polygons are smaller than a single cell of the raster map, and because some cells do not cover the centre of the polygon, we used small and partly covered cells (Hijmans et al. 2016). Finally, we tested whether the whether the areas of taxonomic and phylogenetic uniqueness are more or less protected than expected based on (1) the expected mean proportion of protected cells in relation to the total proportion covered by the network (3%), and (2) the expected mean proportion of 10% protected cells relative to the unprotected fraction in whole territory (97%). Thus, we expect for each category to find, on average, at least 3% of protected cells based on the total protected extent (2,923 km^2), and 9.7% based on the unprotected coverage (92,794 km^2). Obviously, these 3% and 9.7% coverage criteria are modest given the relatively small extent of protection. We used a bootstrap one-sample *t*-test to examine these expectations from 10000 bootstrap resamples. To evaluate whether the categories of the uniqueness areas are equally represented (same median proportion of protected cells) within the network, we used a bootstrap sign test from 10000 resamples.

Results

The total proportion of areas (raster cells) with higher PD than expected based on TD was high within the remnant Atlantic forests for both the terminal-SES.PD (70%)

and basal-SES.MPD (60%) metrics. Areas with higher PD than expected are distributed mainly along the dense and mixed forests, while areas with lower PD are scattered in all Atlantic forest types (Figs. 2c,d). Areas with the highest PD values for SES.PD (Fig. 2c) are distributed in the dense forest near the Atlantic Ocean, while that for SES.MPD are located around the central-east portion of the dense forest, where a transitional zone (ecotone) between it and mixed forests can be found. For terminal metric, areas with the lowest values are distributed mainly in the interior of the dense forest. For basal metric, these areas are located mainly along the seasonal forest, and near the Atlantic Ocean. For alpha-TD (species richness), areas with the highest values are sharply concentrated in the dense forest (Fig. 2a).

For the LCBD metric, 55% of areas had higher beta diversity (beta-TD) than the mean. The highest LCBD values are scattered along the southern portion of the mixed forest in a region that comprises a mosaic of altitudinal grasslands and mixed forest patches, as well as in the extreme northeast portion of the dense forest (Fig. 2b).

Areas of spatial congruence ($r > 0.20$) and mismatch ($r > -0.20$) between TD (Chao1) and PD (SES.PD) cover the same percentage extent (40%) of the remnant Atlantic forests. Overall, both congruence and mismatch areas are distributed throughout the study region. The highest congruence values are concentrated mainly along the dense forest (near the Atlantic Ocean), which holds most of the areas of high TD and PD (Fig. 3). In contrast, the highest mismatch values are distributed in the interior of the dense forest, and to a lesser extent in the mixed forest.

Areas of congruence and mismatch were unevenly represented within the protected areas network (bootstrap sign test; $P = 0.041$), while that areas with higher and lower PD than expected did not show statistically significant difference. Areas of taxonomic and phylogenetic uniqueness (i.e., areas of higher vs. lower PD, areas of

higher beta-TD, and areas of mismatch vs. congruence between TD and PD) were on average more protected than expected based on the 3% coverage criterion (Table 1). In contrast, these areas were on average less protected than expected based on the 9.7% coverage criterion (relative 10% of the total unprotected coverage; Table 2).

Discussion

To the best of our knowledge, our study is the first that assessed the degree to which areas with higher and lower PD relative to TD, and areas of spatial congruence and mismatch between TD and PD were captured by protected areas.

Spatial distribution of tree biodiversity in a biogeographical context

We found that both the diversity components and the areas of taxonomic and phylogenetic uniqueness are unevenly distributed among the remnant Atlantic forests. Our results indicated that the dense forest holds higher TD and PD (considering only angiosperm trees) than the other forest types, while that the mixed forest displays higher TD and PD than the seasonal forest. The mixed forest presents areas with low TD (richness) but high PD and high contribution to total beta diversity. Indeed, dense forest concentrates higher remnant forest cover than the others forests, which makes difficult to compare them.

In recent studies, it has been hypothesized that (1) areas with lower PD than expected are indicative of recent evolutionary radiations, or of large radiations of few lineages in habitat patches (e.g., islands), and (2) areas with higher PD than expected are

indicative of ancient refugia, or biogeographic convergence zones that have experienced immigration of several lineages (Davies and Buckley 2011; Fritz and Rahbek 2012; Mishler et al. 2014). In our study, areas with low PD relative to TD across the Atlantic forest types do not support the hypothesis of evolutionary radiation zones, on the other hand, areas with low PD relative to TD seems to support the hypothesis of refugia. Our findings were similar to those found by Costion et al. (2015) that showed that areas with higher PD than expected in the tropical Australian rainforest were indicative of extant rainforest which was unstable during glacial cycles, and thus provided opportunities for the establishment of new lineages during periods when rainforest re-expanded from refugia, while that areas with lower PD than expected were indicative of rainforest refugia that have remained stable throughout the last glacial cycle. In the southern Brazil, the dense forest has expanded from a mountainous refugium located in the wetter slopes of the Atlantic Shield after the Last Glacial Maximum (Behling et al. 2004; Instituto Brasileiro de Geografia e Estatística, 2012). The high PD relative to TD we found in this forest suggests at least one plausible explanation: high immigration rates of several lineages together with local persistence of old lineages. Indeed, several lineages of tropical taxa from other South American source areas immigrated for the dense forest during the Holocene when climate changed for the current warmer and wet condition (Leite 2002). As a result, it has been accepted that its flora has the more recent immigration history among the studied forests (Leite and Klein 1990; Leite 2002). In this forest, early- and late-diverged (ancient Gondwana taxa) lineages of angiosperms coexist. The seasonal forest is an extension of a long-term refugium (known as the Misiones nucleus), which expanded from the early Holocene and after this period experienced only minor fluctuations until achieving its current state (Prado and Gibbs 1993; Werneck et al., 2011). The low PD relative to TD we found in this forest suggests

at least two alternative explanations: (1) phylogenetic clustering due to environmental filtering and human disturbance (Duarte et al. 2014), and (2) low immigration rates of multiple angiosperm lineages across time. The mixed forest is presumed to be a relict of an temperate wet forest that would have extended over a wider area during a cold and moist phase of the Quaternary period (Ledru 1993; Ortiz-Jaureguizar and Cladera 2006). However, this forest experienced the immigration of several tropical taxa from mountainous refugia (e.g., seaward mountain slopes) of the Atlantic Shield (Instituto Brasileiro de Geografia e Estatística 2012); thus it is characterized by a mixture of temperate and tropical floras with disparate biogeographical origins (Duarte et al. 2014). The high PD relative to TD we found in this forest seems to support this idea.

Spatial mismatch between diversity components

We found both high congruence and mismatch between TD and PD within the remnant Atlantic forests. This suggests that setting priorities on the basis of TD or PD may not adequately protect the regional biodiversity because divergence areas are scattered throughout the region. This finding highlights the need for an integrated approach to better protect both the species and the evolutionary and functional processes (Devictor et al. 2010; Strecker et al. 2011; Sobral et al. 2014; Daru et al. 2015; Daru and le Roux 2016). Indeed, it is extremely advisable to incorporate both species and evolutionary information in regional conservation initiatives because TD does not predict PD for Neotropical plants (Chave et al. 2007). In some cases, prioritizing evolutionary history in protected areas would lead at the same time to the protection of functional diversity if closely related species share similar traits that are phylogenetically conserved on the phylogeny (Zupan et al. 2014).

It is interesting to highlight that priorization of areas of mismatch between components could contribute to the protection of unique ecological or evolutionary processes, leading to better conservation outcomes (Strecker et al. 2011). Indeed, areas with higher and lower PD than expected based on TD can indicate zones of high irreplaceability in terms of evolutionary history (Voskamp et al. 2017). For instance, divergent sites containing low TD but high PD can indicate zones where few species represent a significant amount of evolutionary history (Laity et al. 2015). If the aim is to represent as much phylogenetic diversity as possible, these areas should be included in protected areas to maximize the amount of evolutionary history conserved (Vézquez and Gittleman 1998). We found that areas of spatial mismatch between diversity components are scattered across the Atlantic forest types, implying a major challenge for regional conservation strategies focused on maximizing the protection of evolutionary history.

Effectiveness of the network of protected areas

We showed that areas of taxonomic and phylogenetic uniqueness have not reached the 9.7% coverage criterion within protected areas network. Although all they have reached the minimum 3% criterion, most of the values were below 5%. Therefore, the regional network did not provide a suitable representation for all areas that exceed the minimum coverage criterion. Obviously, these findings highlight the need to expand the current network in order to improve the protection of tree biodiversity. It is important to emphasize that both the size and spatial distribution of protected areas must be considered in future conservation actions. They vary greatly in size (0.14 to 837.44 km^2), and are largely concentrated in the dense forest, and very few represented in the

other Atlantic forest types. Although the total extension of protected areas has been growing in the last decades, improvements are still needed in the planning of new conservation areas. This is mainly because climate change and land use can profoundly alter environmental conditions and require the migration of species to survive. We suggest that expanding the network towards the areas of taxonomic and phylogenetic uniqueness, as defined here, could increase the representation of species richness, beta diversity and evolutionary history of angiosperm trees at the same time.

Although most conservation actions are performed at fine spatial scales (Ferrier 2002), future initiatives may benefit from the mapping presented here to select potential sites in need of protection. Our mapping highlights areas of high conservation value that hold distinct taxonomic and phylogenetic signatures. Because we used complementary PD metrics that emphasize both deep and shallow evolutionary histories, we were able to identify areas of particular evolutionary history that in some circumstances would not be identified by using one single metric.

Further research is needed to investigate patterns of spatial mismatch along the Atlantic forests emphasizing others biodiversity components (e.g., functional diversity) and other taxonomic groups. In this perspective, understanding how PD and TD relate across different taxonomic groups will help to better comprehend and protect biodiversity as a whole (Zupan et al. 2014).

The conservation of the Brazilian Atlantic forests' biodiversity is a huge challenge because almost all of the remnant forest cover is located on private land (more than 90%), where most of the forests are less than 50 ha (more than 80%) and almost 50% of them is less than 100 m from the edge (Ribeiro et al. 2009, 2011). Besides, the Brazilian national system of protected areas covers only around 1% of its total area (Ribeiro et al. 2009, 2011), which is way below the 10% recommended by the Global Strategy for

Conservation (Secretariat of the Convention on Biological Diversity, 2002). In this scenario, it is evident that it is impossible to achieve effective conservation goals by protecting only the remnant forests on private lands. This suggests that there is a significant opportunity to establish ecological restoration actions on landscapes that would result in greater conservation benefits (Tambosi et al. 2014). Recently, Tambosi et al. (2014) showed that there are approximately 15 million hectares (10%) distributed along landscapes with high restoration effectiveness in this hotspot (*ca.* 150 million hectares), which corresponds to an area similar to its current remaining extent (*ca.* 12%).

In the face of increasing threats from land use and climate change, which may alter ecosystem functioning and induce the loss of evolutionary potential of species (Devictor et al., 2010), and in the face the lack of investments in conservation, public policies should encourage the establishment of other conservation strategies besides the creation of protected areas. Such strategies include wildlife-friendly farming methods (see Green et al. 2005). Green et al. (2005) suggest that increase yields on already-converted land could be a useful strategy to reduce the conversion of remaining habitats by the agricultural expansion.

Limitations

Although we used the best information available for the study region, our study has two main limitations that should be addressed. First, the phylogeny we used has a low resolution below the family level, which can affect our phylogenetic diversity metrics. Second, the prediction errors of our maps are unbiased but the accuracy of estimates (i.e., the correlation between the observed and predicted values in sampled

locations) is only reasonable (see Table S1 in Supplementary Information). However, the prediction accuracy we found is acceptable here given the limitations of all interpolation methods to predict and map diversity indices (Granger et al. 2015). Recently, Granger et al. (2015) showed that the mapping of the diversity indices is not a trivial issue, once these indices are not spatially additive, implying that diversity of a given region is not equal to sum of the diversities of the places present in such region.

Conclusions

Our results showed that the regional protected areas network is insufficient to preserve tree biodiversity of the Atlantic forests in southern Brazil. This finding, together with the fact that diversity components strongly diverge in space, pose a challenge for effectively protect biodiversity in these forests. We suggest that expanding the network towards the areas of taxonomic and phylogenetic uniqueness could increase the representation of species richness, beta diversity and evolutionary history of angiosperm trees at the same time. Furthermore, the inclusion of areas of high irreplaceability in terms of evolutionary history could help to improve the protection of feature diversity and evolutionary potential of species. Although the systems of protect areas are the cornerstone of conservation strategies, the long-term persistence of biodiversity depends of the integration between these systems and the long-term ecosystem management to maintain critical ecological and evolutionary processes, mitigate habitat fragmentation, and cope with climate change (Turner and Pressey 2009). The present work offers a useful approach to identify areas of particular conservation value and to evaluate the representativeness of protected areas in capturing

areas of high taxonomic and phylogenetic distinctiveness. Moreover, this integrated approach may be easily applied in other regions using various taxonomic groups.

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Table 1. Expected mean proportion of protected cells for areas of taxonomic and phylogenetic uniqueness within the protected areas network (3% coverage criterion). Are shown the bootstrapped mean values from 10000 resamples, the (95%) bootstrap confidence intervals and the *t*-statistic. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

| Diversity metrics	Mean	Lower CI	Upper CI	t_{value}
SES.PD				
Higher PD	4.388	1.423	7.353	0.960
Lower PD	3.947	0.935	6.959	0.645
SES.MPD				
Higher PD	3.508	0.846	6.170	0.392
Lower PD	4.883	1.442	8.325	1.123
LCBD				
Higher PD	3.511	1.004	6.018	0.419
Chao1 and SES.PD				
Spatial congruence	4.545	1.712	7.379	1.141
Spatial mismatch	6.277	0.272	12.282	1.142

Table 2. Expected mean proportion of protected cells for areas of taxonomic and phylogenetic uniqueness within the protected areas network (9.7% coverage criterion). Are shown the bootstrapped mean values from 10000 resamples, the (95%) bootstrap confidence intervals and the *t*-statistic. * $P < 0.05$; **$P < 0.01$; *** $P < 0.001$.

| Diversity metrics	Mean	Lower CI	Upper CI	t_{value}
SES.PD				
Higher PD	3.367	0.935	5.799	−5.343***
Lower PD	3.383	1.042	5.725	−5.535**
SES.MPD				
Higher PD	3.224	1.649	4.798	−8.440***
Lower PD	3.061	0.527	5.596	−5.374***
LCBD				
Higher PD	3.742	0.933	6.552	−4.359***
Chao1 and SES.PD				
Spatial congruence	5.260	1.993	8.527	−2.845**
Spatial mismatch	3.511	1.410	5.611	− 6.167***
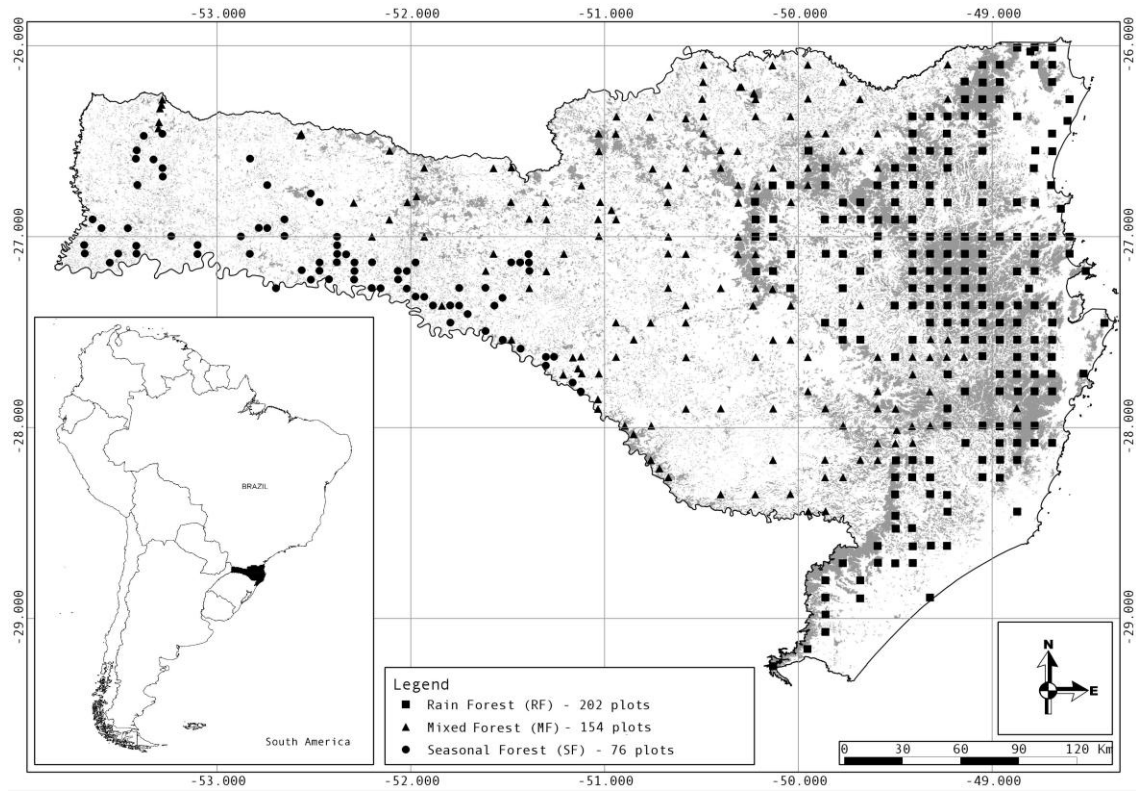
Figure 1. Location of 432 plots distributed across the three main Atlantic forest types (dense, mixed and seasonal forests) in southern Brazil. Grey areas indicate the remnant forest cover according to SOS Mata Atlântica (2015).
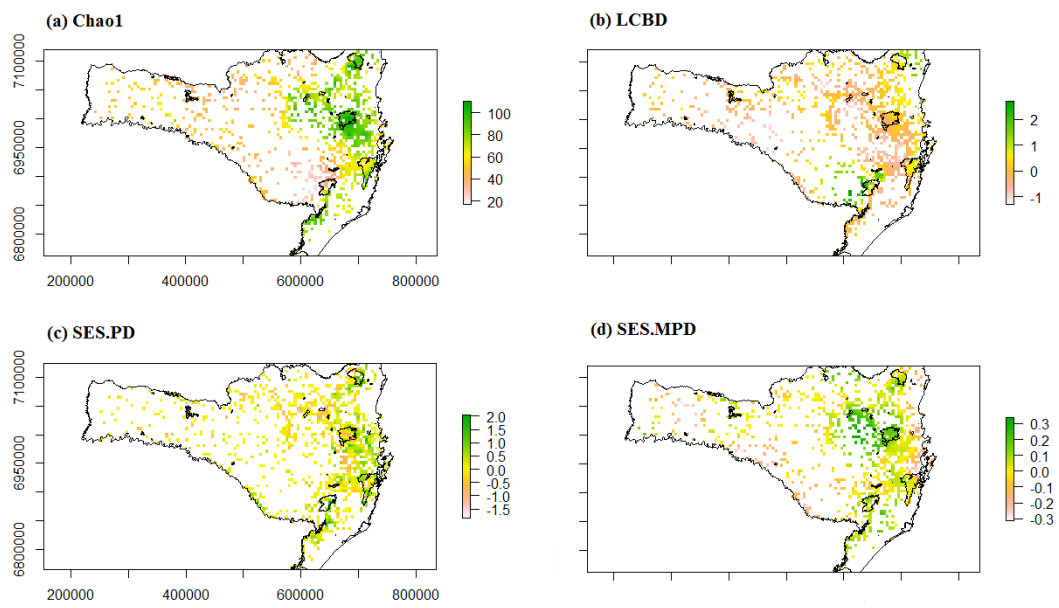
Figure 2. Spatial distribution of tree taxonomic and phylogenetic diversity in the remnant Atlantic forests in southern Brazil. Polygons indicate the delimitation of protected areas.
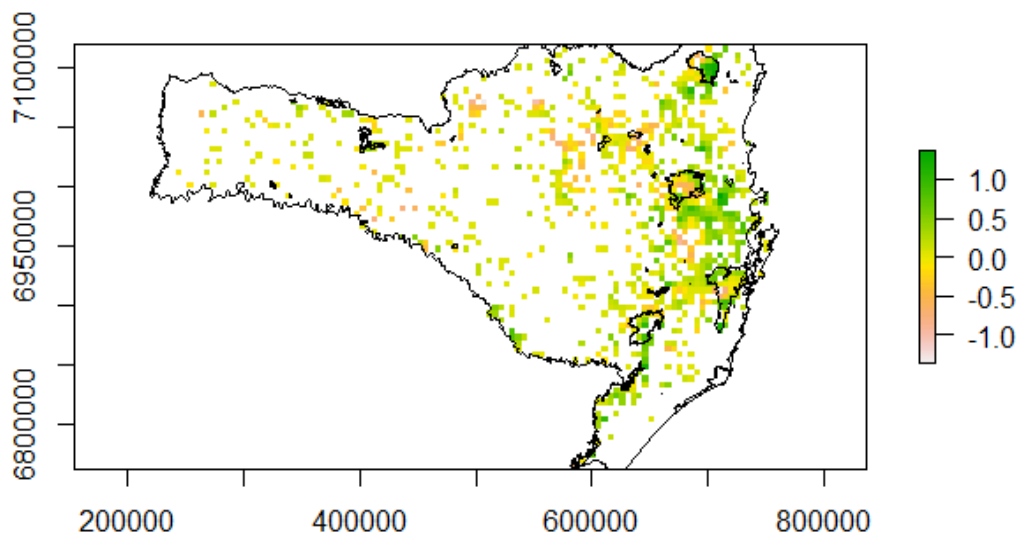
Figure 3. Spatial congruence and mismatch between TD (Chao1) and PD (SES.PD) in the remnant Atlantic forests in southern Brazil. Polygons indicate the delimitation of protected areas.

Supplementary Information

How the tree taxonomic and phylogenetic diversity is represented in protected areas in subtropical Brazilian Atlantic Forest?
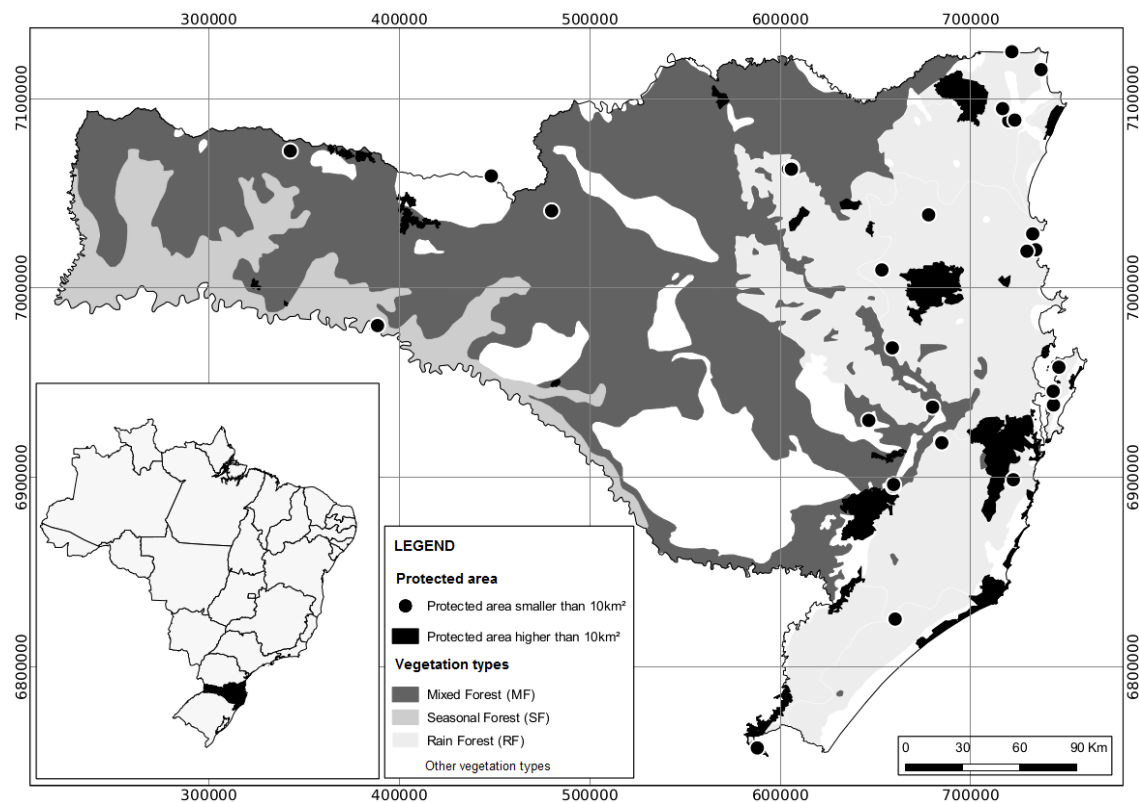
Figure S1. Location of the study region in southern Brazil, indicating the original extent of the main Atlantic Forest types and the existing protected areas in each type. Other types represent altitudinal grasslands within the mixed forest domain.

Variogram modelling

We first computed a sample variogram from residuals using Generalized Least Squares (GLS) estimation, and then fitted a variogram model to the estimated sample

variogram by iterative reweighted least squares (IRLS) estimation. We used the Matérn covariance function (Stein 1999), which is a generalization of different theoretical variogram models, as a flexible way to measure both short and long distance variation (Hengl 2009). The initial guess of the variogram parameters (nugget, range, sill) we used in the IRLS estimation are described in the documentation of the automap R package (Hiemstra 2015). The IRLS algorithm iteratively converges to the selection of the variogram model with the smallest residual sum of squares (Hiemstra et al. 2009). Three key parameters are estimated in the variogram fitting procedure, as follows: (1) the nugget that depicts a portion of variation that is not spatially autocorrelated or is spatially structured at a scale finer than can be detected by the sampling, (2) the sill that represents the semi-variance value that is reached at the range, and is equal to the variance of the data (the presence of a sill implies that the data are stationary), and (3) the range that indicates the maximal distance at which the target variable is spatially autocorrelated (beyond range, the sampling units are spatially independent; Fortin and Dale, 2005; Legendre and Legendre 2012).

We compared the fitted variograms from raw and standardized data by visual inspection and statistical fitting to select the best variogram model. Basically, the fitted models were plotted on the graph of the experimental variogram to assess whether the fit looked reasonable; when both models seemed to fit well, the one with the smallest residual sum of squares (RSS) was chosen (Oliver and Webster 2015). We assumed that residuals were stationary when variogram reached an upper bound or asymptote, i.e., the sill variance (Oliver and Webster 2015).

Kriging spatial interpolation

In order to build interpolated maps by Kriging, we assume that the value of a variable Z at a given location x is a realization of a random function $Z(x)$, which can be modeled as a sum of three components (Chilès and Delfiner 1999; Webster and Oliver 2001; Fortin and Dale 2005):

$$Z(x) = m(x) + \varepsilon(x) + \varepsilon,$$

where $m(x)$ is the deterministic structural component, i.e., the average value of the variable within the mapping unit, $\varepsilon(x)$ is the spatially correlated random component, i.e., the spatially dependent residual from $m(x)$, and ε is the spatially independent residual component that consists of essentially uncorrelated random variation. Here, we assume also that (i) the residual $\varepsilon(x)$ has constant mean and variance, and its covariance function depends only on separation in distance between sampling locations (and not on absolute location and direction in space), and that (ii) the residual ε is normally distributed with zero mean and unit variance (Cressie 1993; Chilès and Delfiner 1999; Oliver and Webster 2015). We used ordinary Kriging which is robust with respect to moderate departures from those assumptions (Oliver and Webster 2015).

In order to evaluate the predictive abilities of the Kriging maps, we used the k-fold cross-validation, where the original sample was split in 10 equal parts and then each one was used for cross-validation (Hengl 2009). We computed four cross-validation statistics (Oliver and Webster 2015): the mean prediction error (MPE; ideally 0 for unbiased kriging), the mean squared normalized error (MSNE; ideally close to 1), the correlation coefficient between the observed and predicted values in the sampled locations (ideally 1), and the correlation coefficient between the predicted and residual values (ideally 0). In Table S1, it is possible to observe that most of the cross-validation statistics indicate a good overall performance of the Kriging models, but the correlation between the observed and predicted values indicate that prediction accuracy is only

reasonable. This is because interpolation methods cannot accurately predict diversity indices, once such indices are not spatially additive, i.e., the diversity of a given region is not equal to sum of the diversities of the places present in such region (see Granger et al. 2015).

Table S1. Cross-validation criteria for the diversity metrics used here. Are shown the mean prediction error (MPE), the mean squared normalized error (MSNE), the correlation between the observed and predicted values (Obs – Pred), and the correlation between the predicted and residual values (Pred – Resid).

	MPE	MSNE	Obs – Pred	Pred – Resid
Chao1	–0.003	0.927	0.602	–0.014
LCBD	–0.001	0.946	0.625	0.052
SES.PD	0.0009	0.965	0.486	0.035
SES.MPD	–0.0004	1.023	0.498	–0.013

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Conclusões gerais

Esta tese avança o conhecimento sobre a ecologia e conservação de árvores nas florestas Atlânticas do sul do Brasil (florestas densa, mista e sazonal). Usando uma abordagem integrativa baseada nas dimensões taxonômica e filogenética, eu mostrei como a biodiversidade de árvores se distribui no espaço, como ela é influenciada por processos ecológicos e evolutivos, e como ela é protegida pela rede de áreas de conservação existente.

(1) A diversidade é distribuída de forma bastante desigual entre as florestas Atlânticas estudadas. Maior diversidade filogenética que o esperado baseado na diversidade taxonômica (riqueza de espécies), nas florestas densa e mista, sugere altas taxas de imigração de diferentes linhagens de angiospermas, juntamente com persistência local de antigas linhagens (táxons gondwânicos). Menor diversidade filogenética que o esperado com base na riqueza, na floresta sazonal, sugere agrupamento filogenético dirigido por filtragem ambiental e distúrbio humano e, possivelmente baixas taxas de imigração de várias linhagens de angiospermas ao longo do tempo (como a floresta sazonal permaneceu relativamente estável desde o último glacial máximo).

(2) A diversidade é organizada ao longo de gradientes climáticos e altitudinais. Particularmente, a sazonalidade e severidade do clima (temperatura e precipitação) reduzem diretamente a riqueza de espécies, enquanto que aumentam diretamente a diversidade beta taxonômica e filogenética devido à filtragem de espécies e linhagens ao longo do espaço. A diversidade beta filogenética entre comunidades é influenciada também pelo agrupamento filogenético dentro das comunidades, que reflete provavelmente tanto filtragem ambiental como distúrbio humano.

(3) A rede de áreas protegidas não é efetiva em conservar a biodiversidade de árvores. Diante do cenário desfavorável para a ampliação da rede existente, principalmente devido à carência de investimentos em conservação e falta de vontade política, é preciso buscar outras estratégias, como por exemplo, a implantação de práticas favoráveis à vida selvagem (*wildlife-friendly practices*), em áreas agrícolas, através de sistemas de partilha de terras (*land-sharing*) e de poupança de terras (*land-sparing*).