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Research article

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

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ABSTRACT

The metacommunity framework offers a possibility to better understand how ecological processes influence patterns of species diversity along environmental gradients. The species-sorting perspective predicts that community composition varies in response to differences in environmental conditions among habitat patches. Our study focused on this perspective, aiming to understand how environmental filtering processes interact directly and indirectly on diversity patterns in an area of 95,000 km^2 (data from 432 forest plots). We employed structural equation modeling (PLS path modeling) to disentangle the interactive effects of topography, climate, water-energy balance, and geometry of forest patches upon the alpha and beta diversity of a subtropical forest metacommunity in southern Brazil. Factors related to environmental filtering showed substantial effects upon tree alpha and beta diversity. The total amount of variation in beta diversity explained by environmental filtering was high (64%) and was even more when together with alpha diversity (73%), corroborating the prediction of species-sorting model at the metacommunity level. Climatic extremes, water-energy balance and alpha diversity were the key determinants of beta diversity and patch size and water-energy balance the key determinants of alpha diversity in the South Brazilian Atlantic forests. Partial mantel test showed that environmental effects occurred largely independent of spatial effects, reinforcing the tested prediction. Our study provides strong empirical support for the prediction that beta diversity primarily reflects deterministic factors associated with species niches and their responses to environmental conditions in the studied spatial scale.

Introduction

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

The metacommunity framework explicitly encompasses four perspectives, each one evoking different mechanisms of community assembly as well as specific propositions and predictions (see Leibold, 2011), especially regarding the role of dispersal and of local environmental heterogeneity in community assembly: (i) the patch dynamics (PD) model emphasizes colonization and extinction processes in patches with identical environmental conditions; (ii) the mass-effects (ME) model highlights the role of dispersal in

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maintaining source-sink relations in different patches; (iii) the neutral model (NM) stresses the importance of both chance demographic events and chance dispersal events; and (iv) the species-sorting (SS) model emphasizes the role of environmental heterogeneity among patches with distinct environmental conditions that affect the fitness of species. The ME and SS perspectives are the most commonly tested and supported metacommunity perspectives in the ecological literature (Cottenie, 2005; Logue et al., 2011), on the other hand, knowledge on how different ecological processes interact to affect diversity patterns at multiple spatial scales still is rather fragmentary.

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

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

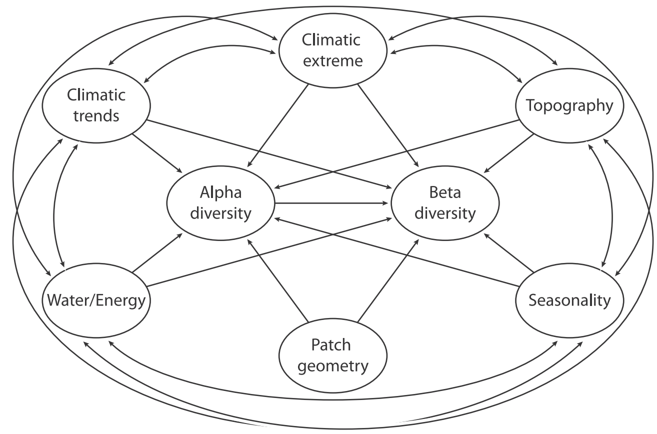

Fig. 1. Conceptual structural model illustrating predictive relationships among predictor and response latent variables (straight arrows) and associative (correlational) relationships among predictor latent variables (curved arrows).

To disentangle the interactive effects of the different environmental filtering processes on tree alpha and beta diversity at metacommunity level, we built structural equation models using tree community data from 432 forest plots distributed in a total area of 95,000 km^2 in subtropical southern Brazil. We started from a conceptual structural model that assumes all potential associative and predictive relationships among ecological factors and tree species diversity on the local and the metacommunity scale (Fig. 1). Specifically, our aim was to test the prediction that variation in community composition among forest plots (beta diversity) reflects strong environmental effects, so that spatial niche separation between tree species occurs along gradients of environmental conditions (i.e. species occupy patches according to their habitat requirements). We thus expect that environmental factors explain most of the total variation in community composition and that, therefore, the unexplained variation (or residual variance) that can be assigned or not to spatial effects, should be low in the model.

Materials and methods

Study region

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