Ecological Indicators 36 (2014) 431–440

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

Original Articles

Windborne: Can liverworts be used as indicators of altitudinal gradient in the Brazilian Atlantic Forest?

Nivea Dias dos Santos[a,*], Denise Pinheiro da Costa[b], Luiza Sumiko Kinoshita[a], George John Shepherd[a]

[a] Departamento de Biologia Vegetal, Instituto de Biologia, Universidade Estadual de Campinas – UNICAMP, 13083-970 Campinas, SP, Brazil
[b] Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, Rua Pacheco Leão 915, 22460-030 Rio de Janeiro, RJ, Brazil

ARTICLE INFO

Article history:
Received 17 June 2013
Received in revised form 27 August 2013
Accepted 28 August 2013

Keywords:
Beta diversity
Bryophytes
Indicator Species Analysis (ISA)
Niche Assembly
Mantel test
Tropical forest

ABSTRACT

Liverworts are non-vascular cryptogamic plants with wide geographic distributions due to their capacity to disperse their spores over long distances, although they have no epidermal cuticle, sensitive to external environmental conditions, found only in very specific microenvironments – and are therefore widely used as bioindicators. We evaluated the floristic composition of liverworts in localities located in different Atlantic Forest vegetation types in southeastern Brazil to address the following questions: Is the liverwort flora distributed uniformly or randomly, or does it demonstrate environmental niche restrictions at regional scales? If the distribution of liverworts is deterministic, do geoclimatic variables act as environmental filters for this flora? Can liverwort species be considered bioindicators of the different Atlantic Forest vegetation types? We undertook floristic surveys in 26 localities to evaluate the beta diversity of the liverwort flora and its correlation with environmental gradients (geoclimatic variables) using multivariate analyses and the Mantel Test. Ordination and classification methods indicated elevated beta diversity in a deterministic distribution of the liverwort flora along the Atlantic coast of southeastern Brazil. Altitude was significantly associated with the first axis of the CCA, demonstrating a floristic gradient between Lowland Forests and High Montane Forests and "Campos de Altitude". Five floristic groups were identified and 34 species could be considered bioindicators. The principal geoclimatic variables that explained the floristic groupings of liverwort species were altitude, temperature, and precipitation. The prediction that liverwort plants demonstrated environmentally determined distributions was confirmed by the Mantel Test (rM 0.557; $p < 0.0001$). Our results support the idea that the liverwort flora of the coastal Atlantic Forest in southeastern Brazil comprises part of a regional pool of species whose establishment and survival are determined by abiotic filters acting in those habitats. The low similarities between localities and the high numbers of indicator species suggest that the liverwort vegetation has a deterministic distribution at the regional level – which corroborates their use as bioindicators of vegetation types and of environmental conditions. Although species distributions are principally determined by environmental niches, geographical distances (dispersal limitation) are important in regions such as oceanic islands and coastal mountains.

1. Introduction

Understanding the patterns of floristic compositional variations between different regions (beta diversity) is one of the central aims of ecology (Chave, 2008; de Bello et al., 2010; Legendre et al., 2005). In the context of current theories, the distributions of plant species can be explained by three principal hypotheses: (1) Oligarchical Dominance, where a region is dominated by a group of superior competitors and demonstrates compositional uniformity of species over large areas (Pitman et al., 1999, 2001); (2) Neutral Assembly, where species distributions are apparently random but spatially autocorrelated due to dispersal limitations (Hubbell, 2001); or (3) Niche Assembly, with species distributions being unequal and environmentally determined (Tuomisto et al., 2003). As such, the manners in which organisms are dispersed (e.g., by wind or animal vectors – Cain et al., 2000; Nekola and White, 1999; Tuomisto et al., 2003) and environmental filters (e.g., edaphic factors – Condit et al., 2002; Honorio Coronado et al., 2009) strongly influence floristic configurations in different regions. Vegetation

Abbreviations: NP, National Park; SP, State Park.

* Corresponding author at: Departamento de Botânica, Universidade Federal de Pernambuco, Recife, PE 50670-901, Brazil. Tel.: +55 81 2126 8861; fax: +55 81 2126 8861.
E-mail addresses: nivea.dias@ufpe.br, nivea.dias@gmail.com (N.D. Santos).

1470-160X/$ – see front matter © 2013 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.ecolind.2013.08.020

scientists need to examine the floristic affinities between different regions in order to understand the processes that drive existing vegetation patterns (Condit et al., 2002; Tuomisto et al., 2003) and these studies are usually based on the hypothesis that floristic similarities can be predicted by examining environmental variables and/or the geographical distances between the regions in question (Chase and Myers, 2011; Chave, 2008).

Liverworts (Marchantiophyta) represent a phylum of terrestrial plants that, together with mosses (Bryophyta) and hornworts (Anthocerothophyta), form a paraphyletic group commonly known as "bryophytes" – the oldest lineage among the Embryophyta (Goffinet et al., 2009; Magallón and Hilu, 2009). The liverworts are represented by 5000 species throughout the world, with 1350 in the Neotropics and approximately 700 in Brazil, of which 463 occur in the Atlantic Forest (Costa, 2009; Gradstein et al., 2001; Gradstein and Costa, 2003). The spores of these plants can be dispersed over very long distances by wind, resulting in wide phytogeographical distributions as compared to angiosperms (Heinrichs et al., 2009; Schofield, 1992; van Zanten and Pócs, 1981). On the other hand, these plants do not have epidermal cuticles, are especially sensitive to adverse environmental conditions and only occur in very specific microenvironments – and are therefore frequently utilized as bioindicators of local climatic, environmental, and ecological conditions (Vanderpoorten and Goffinet, 2009).

Bryophytes can be used as bioindicators of altitudinal gradients in neotropical regions (Frahm and Gradstein, 1991; Gradstein et al., 2001) and have been identified as indicators of different vegetation types in the Atlantic Forest, with different species of mosses and liverworts being characteristic of different altitudinal belts (Costa and Lima, 2005; Santos and Costa, 2010). No studies have yet been undertaken, however, that evaluated the patterns of beta diversity of the bryophyte flora across areas with different vegetation types of Atlantic Forest at a regional scale.

Southeastern Brazil is an important region within the continuum of remnant coastal Atlantic Forest areas, and a center of diversity and endemism for many animal and plant taxa because it holds large stretches of continuous and relatively well-preserved forests (Guedes-Bruni and Lima, 1997; Laurence, 2009; Stehmann et al., 2009). The Brazilian states of Rio de Janeiro and São Paulo are known to be very species-rich and have been well studied in terms of their liverwort flora (Gradstein and Costa, 2003; Santos and Costa, 2010). Additionally, these states demonstrate wide altitudinal variations, with different Atlantic Forest vegetation types being found over relatively short distances – presenting an excellent opportunity for evaluating the importance of deterministic or stochastic processes (Niche Assembly vs Neutral Assembly) on the configuration of liverwort species distributions at a regional scale.

According to the first law of geography (Tobler, 1970), the similarities between two regions would be expected to diminish as the distance between them increased (Nekola and White, 1999); and regions that are geographically closer would also be expected to have more similar floras due to the greater possibility of their diaspores reaching those sites. Considering, however, that deterministic process, such as environmental filtering (based on ecological niches) may act more strongly on the liverwort flora than do processes related to their airborne dispersal, we hypothesize that will there will be high similarities between liverwort communities in localities with the same Atlantic Forest vegetation types, as they will provide similar environmental conditions.

We here examine the beta diversity of the liverwort floras of areas with distinct Atlantic Forest vegetation types in order to evaluate the sensitivity of the species to environmental variables related to altitude by addressing the following questions: (1) Are geoclimatic conditions good predictors of the vegetation types of the Atlantic Forest sites investigated? (2) Is the liverwort flora distributed uniformly or randomly, or does it demonstrate environmental niche-restrictions along the Atlantic coast of southeastern Brazil? If the distribution of the liverwort flora is in fact deterministic, two additional questions arise: (3) Are there liverwort species that can be considered indicators of the different vegetation types of the Atlantic Forest? (4) Do any of the geoclimatic variables analyzed act as filters to the liverwort flora?

2. Methods

2.1. Study area

The study region was located on the Atlantic coastal plain of southeastern Brazil (21°88′–23°24′S and 45°10′–41°92′W) with four altitudinal units: Baixada, Serra do Mar, Vale do Paraíba, and Serra da Mantiqueira (Domingues, 1976). The regional topography is quite irregular and is composed of mountain chains (the scarps of coastal plains) of crystalline rocks (Domingues, 1976). The highest points there are the Pico das Agulhas Negras (2791 m) located in the Planalto da Serra da Mantiqueira in the municipality of Itatiaia, Rio de Janeiro State; the Pedra dos Três Picos (2310 m) in the municipality of Nova Friburgo; and the Pedra do Sino (2263 m) in Teresópolis (the latter two being located in the Serra do Mar Range in Rio de Janeiro State) (Guedes-Bruni and Lima, 1997). The regional climate is quite variable due to altitudinal factors as well as the orientations of the mountain slopes. Proximity to the ocean results in higher regional humidity and rainfall, which tends to diminish in more inland area (Domingues, 1976). The predominant climate in Baixada and in Vale do Paraíba is hot and humid, and defines two seasons – a rainy season (in the Austral summer) and a dry season (Austral winter). The average annual temperature varies between 24 and 26 °C; the average annual precipitation is approximately 1000 mm in Baixada and 1500 mm in Vale do Paraíba. In the highest regions of the Serra do Mar and Mantiqueira ranges the climate is mesothermic super-humid, without a dry season, with average annual temperatures between 18 and 19 °C; the average annual rainfall is between 2000 and 2500 mm (Domingues, 1976; Nimer, 1989).

The concept of Atlantic Forest (*sensu lato*) adopted in the present work corresponds to that described by Oliveira-Filho and Fontes (2000) and includes both ombrophilous and semideciduous forests. The vegetation classification adopted here corresponds to that of Veloso et al. (1991), and includes the vegetation types of Lowland Forest = 5–50 m a.m.s.l., Submontane Forest = 50–500 m, Montane Forest = 500–1500 m, and High Montane Forest = > 1500 m. Three additional vegetation types were included in the study: Restinga Forest – a forest formation that occurs on sandy coastal sites at altitudes between 0 and 50 m whose genesis, composition, and structure are distinct from Dense Ombrophilous Forest (César and Monteiro, 1995; Assis et al., 2011); Mountain-Top Forest – a Cloud Forest type that occurs on the tops of tall peaks in the Serra do Mar Range on thin, rapidly draining soils (Bertoncello, 2009; Mantovani et al., 1990; Neto, 2007); and "Campos de Altitude" – open, humid formations dominated by grasses, which generally occur above 2000 m as well as on the tops of some peaks in southeastern Brazil (Martinelli and Bandeira, 1989; Safford, 1999; Vasconcelos, 2011).

2.2. Data organization

Twenty-six localities were selected (Fig. 1) in 10 separate federal, state, and private Protected Areas in the states of Rio de Janeiro and São Paulo in southeastern Brazil. We utilized data from published floristic inventories, from the databank of the bryophyte flora of Rio de Janeiro (Costa et al., 2007), and from field studies undertaken between 2009 and 2011 in ten 10 m × 10 m plots in each locality (Table 1). These plots had been established in areas with