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Original Research

Tree diversity and elevational gradient: The case of Lauraceae in the Atlantic Rainforest

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ABSTRACT

Lauraceae have an ancient evolutionary history and wide distribution, providing a great model for studies of the biogeographical distribution patterns of plant species. The effects of elevational variation on plant diversity in tropical forests have been the subject of many studies. We investigated the following question: How does the Lauraceae family contribute to the diversity of the tree community in the Atlantic Rainforest, along an elevational gradient? Data from 15 floristic surveys (plots of one ha) were analyzed, comparing the variation in the patterns of Lauraceae richness to the richness of the whole tree community. The similarity relations of the plots were analyzed based on Lauraceae species, and the distribution patterns of the family were tested through null distribution models of the species. The surveys recorded 22,895 live individual trees in total, distributed among 859 species belonging to 70 families. Lauraceae contributed 4.3% of the total abundance and presented the third highest species richness (6.4% of the total). In general, Lauraceae diversity was highest in the Montane region and their composition changed along the elevational gradient, presenting four elevational belts. The Lauraceae diversity has a strong positive relationship with abundance. We found an exponential positive correlation between elevation and the richness of the family, differing from the tree community pattern. The results showed a new pattern of species variation along elevational gradients for the tree component in the Tropical Forest. Thus, we suggest that patterns of diversity variation in tree communities should be analyzed separately among the richest families.

1. Introduction

Lauraceae are the largest family of woody magnoliids (Rohwer and Rudolph, 2005), and they are among the 10 richest families of vascular plants throughout the Neotropics (Gentry, 1988). Fifty genera are described for the Lauraceae family with approximately 2500–3000 species, with their pantropical distribution being well represented in the Americas, tropical Asia, Australia and Madagascar (Rohwer, 1993a). The ancient evolutionary history and wide distribution of Lauraceae enable studies of inferential models of distribution patterns on the biogeographical distribution of plant species (Chanderbali et al., 2001).

The history of Lauraceae indicates former separation of the major groups along geographical lines, the Gondwanan group and the Laurasian–South American group (Rohwer, 2000). Along geographical gradients in the Neotropical Forest, Lauraceae appear consistently among the richest family species (Gentry, 1988) and their species are frequently dominant elements in Montane vegetation in the forests of South America (Oliveira-Filho and Fontes, 2000; Cuello, 2002). Tropical forests are among the richest environments in terms of species richness of plant communities on Earth, presenting high levels of plant diversity and endemism (Condit et al., 1996; Myers et al., 2000; Mittermeier et al., 2011).

Latitudinal and elevational gradients settle the arrangement of the richness and distribution of vascular plant species in these forests, and two distribution patterns are usually reported for those species along elevational gradients (Gentry, 1988; Stevens, 1992; Lieberman et al., 1996; Givnish, 1999; Chown and Gaston, 2000; Lomolino, 2001; Körner, 2007). According to Stevens (1992), the

Abbreviations: MDE, mid domain effect; PBH, perimeter at breast height; PESM, Parque Estadual da Serra do Mar.

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variation pattern in the number of species along elevational gradients would be an extension of Rapoport's rule (Rapoport, 1975; Stevens, 1989), according to which there is a decrease in richness with increased elevation. This pattern is commonly explained by the same factors for latitudinal gradients, a monotonic relationship between richness and climatic factors (Rohde, 1992; Rahbek, 1995; Givnish, 1999; Grytness et al., 1999; Rahbek, 2005; McCain and Grytnes, 2010). However, several studies suggest and refer to a second pattern, wherein a higher number of species occur in regions of intermediate elevation (Rahbek, 1995; Vázquez and Givnish, 1998; Krömer et al., 2005; Homeier et al., 2010).

The geometric constraint on species ranges is a recognized factor contributing to the humped-shape relationship between species richness and elevation (Colwell and Hurtt, 1994; Lomolino, 2001; Grytness and McCain, 2007). Although these patterns have been broadly described, the relative importance of *alpha* biodiversity in the maintenance of total biodiversity differs among taxa and life forms and across different regions (Vetaas and Grytnes, 2002; Lee et al., 2013; Xu et al., 2016). Thus, in light of these differences, the distribution patterns can be analyzed through null models and through the extension of species distribution patterns along environmental gradients (Colwell and Hurtt, 1994; Gotelli, 2000; Colwell et al., 2004).

Studies performed along elevational gradients in the Atlantic Forest indicate higher tree richness at intermediate elevations, wherein Lauraceae are among the richest family species and have great importance in the structure of these communities (Scudeller et al., 2001; Joly et al., 2012; Eisenlohr et al., 2013; Sanchez et al., 2013). In this study, data from 15 floristic surveys have been analyzed, distributed along an elevational gradient (10–1093 m) in a tree community of the Atlantic Rainforest in southeastern Brazil. We performed a complete review of Lauraceae specimens from these surveys to address two main questions: (a) Is there a variation pattern of Lauraceae composition and diversity along an elevational gradient in the Atlantic Rainforest? (b) How does the Lauraceae family contribute to the species richness in a tree community of the Atlantic Rainforest?

2. Material and methods

2.1. Study area

The Atlantic Forest is an important biodiversity hotspot (Myers et al., 2000). It may be divided into two forest types: the Atlantic Rainforest, occupying the coastline of Brazil, and the Atlantic Seasonal Forest, occupying an inland region (Rizzini, 1963). It has a continuous formation, distributed over an area of approximately 1.3 million km^2 (Morellato and Haddad, 2000). However, only 11–16% of this vegetation remains (Ribeiro et al., 2009), and is mostly located in southeastern Brazil (Kronka et al., 2005).

We analyzed fifteen plots of 1 ha each, distributed along an elevational gradient (10–1093 m) in the Atlantic Rainforest of the State Park of Serra do Mar (PESM), state of São Paulo (SP), Brazil (Fig. 1). The plots were located in two of the Park's Conservation Nuclei (Picinguaba and Santa Virgínia). A letter from A to Q (plots O and L were not used, due to an incomplete survey) was assigned to each hectare. The vegetation types of each plot were determined according to the Brazilian vegetation classification (IBGE, 2012), which was adapted to the used scale. The area's climate is tropical (according to the Köppen climate classification), with higher rainfall in the summer and without significant variations along the slope (Vieira et al., 2011).

For the Picinguaba Nucleus (23°22′S, 44°48′W), located in the municipality of Ubatuba, data were acquired from 12 plots (elevation quotas). The plot locations were: one in the Coastal Plain Forest (*Restinga*, A, from 0 to 10 m above sea level – m a.s.l.); five in the Lowland Atlantic Rainforest (B, C, D, E and F, from 50 to 100 m a.s.l.); four in the Submontane Atlantic Rainforest (G, H, I and J, from 200 to 400 m a.s.l.) and two in the Montane Atlantic Rainforest (Q and P, from 600 to 800 m a.s.l.).

For Santa Virgínia Nucleus (23°17′S, 45°30′W), located in the municipalities of São Luís do Paraitinga (70%), Cunha (20%) and Ubatuba (10%), data from three plots (K, N, M), located in the Montane Atlantic Rainforest but at higher elevations (900–1100 m a.s.l.), were analyzed.

2.2. Floristic survey and data compilation

Data from 15 floristic and structural surveys were obtained directly from the researchers or from literature, compiled and revised (Alves et al., 2010; Assis et al., 2011; Campos et al., 2011; Gomes et al., 2011; Padgurschi et al., 2011; Prata et al., 2011; Ramos et al., 2011; Rochelle et al., 2011; Joly et al., 2012).

The plots have an area of 100 × 100 m^2 (one hectare) divided into 100 contiguous 10 × 10 m^2 subplots. Plots P and Q were distributed into four samples of 50 × 50 m^2, also composed of 10 × 10 m^2 subplots. The total surveyed area corresponds to 15 ha of the Atlantic Rainforest. Individual trees were marked and numbered with aluminum plates. The inclusion criterion for arborescent individuals was diameter at breast height (DBH) equal to or higher than 4.8 cm, with a perimeter at breast height (PBH) equal to or higher than 15.0 cm. Palm trees and ferns were included. The individuals were measured, mapped and identified in the field or collected for subsequent identification and inclusion in the collections of the following herbaria: UEC (State University of Campinas), IAC (Agronomic Institute of Campinas) and HRCB (Rioclarense Herbarium). The distribution of taxa per family was performed according to the Angiosperm Phylogeny Group classification (APG IV, 2016).

The herbarium was used for the identification and revision of collected Lauraceae specimens. After correct identification, the specimens were included in these collections. For individuals with identification problems, a re-evaluation was performed in the field. The identifications and/or confirmations were performed by a specialist (P.L.R. de Moraes), consulting specific literature (Kopp, 1966; Kubitzki and Renner, 1982; Rohwer, 1986, 1988, 1993a,b; Lorea-Hernández, 1996; Kurz, 2000; Flora Fanerogâmica do Estado de São Paulo, 2003; Chanderbali, 2004; Madriñán, 2004; de Moraes, 2007) and through comparison with materials from other collections. All occurrence records were revised using data bank sets from Tropicos, Specieslink, GBIF and P.L.R. de Moraes' personal data set. Each Lauraceae species identified in the present study was compared with those data sets throughout all the Atlantic Rainforest surveyed area.

2.3. Data analysis

2.3.1. General procedures

For all analysis, $\alpha \leq 0.05$ was adopted, based on 999 randomized data sets obtained from Monte Carlo permutations. The analyses were performed using EstimateS 9.0.0 software (Colwell, 2013), PC-ORD5.10 (McCune and Mefford, 2006) and R software (R Core Team, 2016), using the packages *AICcmodavg* (Mazerolle and Mazerolle, 2016), *ape* (Paradis et al., 2004), *ecodist* (Goslee and Urban, 2007), *labdsv* (Roberts 2016), and *vegan* (Oksanen et al., 2016).

A spatial correlation between species richness and floristic composition among plots was analyzed to avoid inflation in type I error rates (Diniz-Filho et al., 2003). We have performed an a priori Mantel test for two data sets (tree community and Lauraceae composition), and because spatial effects were found unlikely (Mantel