UNIVERSIDADE FEDERAL DE MINAS GERAIS
INSTITUTO DE CIÊNCIAS BIOLÓGICAS
Departamento de Botânica
Programa de Pós-Graduação em Biologia Vegetal

FELIPE ZAMBORLINI SAITER

PADRÕES FITOGEOGRÁFICOS DA REGIÃO CENTRAL DO DOMÍNIO ATLÂNTICO BRASILEIRO

Tese apresentada ao Programa de Pós-Graduação em Biologia Vegetal do Departamento de Botânica do Instituto de Ciências Biológicas da Universidade Federal de Minas Gerais, como requisito parcial à obtenção do título de Doutor em Biologia Vegetal.

Área de Concentração: Biodiversidade

BELO HORIZONTE – MG

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Área de Concentração: Biodiversidade

Orientador: Dr. Ary Teixeira de Oliveira Filho
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Em parte alguma do Brasil, nem mesmo no Pará, vi uma floresta mais exuberante do que a do Doce. As árvores todas ligadas por lianas, e reunidas a uma densa vegetação secundária de palmeiras e arbustos, curvam-se para lado das águas, e estendem seus ramos sarmentosos sobre o rio, como se desejosos de ar e de luz. A floresta forma uma densa muralha ao longo do rio, — tão densa que o olhar não penetra em sua sombra — e deve estar armado de forte facão-de-mato quem queira nela penetrar. (Relato de Charles Frederick Hartt, geólogo canadense em expedição pelo leste do Brasil em 1865-1867).

Que delicioso dia! Mas o termo delicioso ainda é por demais fraco para exprimir os sentimentos do naturalista que pela primeira vez vagueia por uma floresta brasileira. A elegância das ervas, a novidade das plantas parasitas, a beleza das flores, o verde deslumbrante da folhagem, mas sobrepujando tudo, o vigor e o esplendor da vegetação encheram-me de admiração. Estranho misto de ruídos e de silêncio reina por toda parte revestida de florestas. (Impressões do naturalista britânico Charles Darwin em seu primeiro contato com uma floresta tropical, na Bahia, em 29 de fevereiro de 1832).

Dedico esta tese à minha esposa Welida, pelo seu apoio e sacrifício durante a missão que agora encontra-se cumprida. Ela é exemplo de amor incondicional e coragem.

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À Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), pela bolsa de doutorado sanduíche.

Sumário

Resumo Geral

A região central do Domínio Atlântico brasileiro se estende do Recôncavo Baiano ao rio Paraíba do Sul (12°-22° Sul). As florestas dessa região são caracterizadas por elevados níveis de diversidade florística e endemismo. Meu objetivo principal nesta tese foi investigar o papel de variáveis ambientais e espaciais na variação florística ao longo da região central do Domínio Atlântico brasileiro. Eu usei subconjuntos distintos de um extenso banco de dados para responder perguntas específicas relacionadas a esse objetivo. O banco de dados completo foi composto por 53.237 registros de ocorrência de 3.047 espécies arbóreas em 227 localidades e 49 variáveis geoclimáticas. Para cada um dos cinco capítulos eu escolhi um escopo analítico diferente considerando algumas das seguintes técnicas: análises de ordenação, de agrupamento, de autocorrelação espacial, ANOVA, e modelos de regressão linear e de dissimilaridade ecológica. Os capítulos foram integrados sob o tema geral de conservação de florestas. Eu indiquei mudanças climáticas como causas da quebra da Floresta Atlântica em dois blocos florísticos em torno da latitude 18°-19° S. Demonstrei que variações na sazonalidade do clima e na localização geográfica são, provavelmente, as principais causas do gradiente florístico latitudinal em restingas. Notei que a variação florística no leste da Bahia está relacionada a gradientes de balanço água-energia e de temperatura, e confirmei parcialmente a consistência de uma classificação das florestas dessa região de acordo com faixas altitudinais e regime de renovação foliar. Identifiquei seis unidades florísticas na bacia do rio Doce, onde a variação florística está fortemente relacionada a mudanças sazonais na precipitação e na temperatura. Por fim, revisei a controversa classificação da Floresta de Linhares e discuti o efeito de intercâmbios florísticos sobre a sua alta diversidade.

Palavras-chave: Fitogeografia, Floresta Atlântica, macroecologia, variação florística, gradiente ambiental

Introdução Geral

O conhecimento sobre padrões biogeográficos têm sido útil para o planejamento da conservação da biodiversidade em todo o mundo (Whittaker et al. 2005). Isso se deve à capacidade de biogeógrafos em mapear regiões de acordo com suas similaridades biológicas e ecológicas, gerando suporte para decisões mais sábias em relação às estratégias de conservação (Brooks 2010, Guisan et al. 2013).

No contexto do Domínio Atlântico brasileiro, a conservação de florestas tem sido influenciada pelas contribuições de estudos sobre a distribuição geográfica de espécies de plantas arbóreas e o papel de fatores ambientais sobre a variação florística (por exemplo, Oliveira-Filho & Fontes 2000, Oliveira-Filho et al. 2005, Bertoncello et al. 2011, Nettesheim et al. 2010, Santos et al. 2011, Scudeller et al. 2001). Tais estudos, entretanto, têm estabelecido padrões fitogeográficos gerais para a Floresta Atlântica com base em listas florísticas geradas, sobretudo, em regiões que contam com um maior número de inventários florestais, tal como em parte do sudeste do Brasil.

Nas últimas duas décadas, entretanto, o número de inventários florísticos tem aumentado consideravelmente em outras regiões da costa Atlântica brasileira. Nesse contexto, destaca-se a região central do Domínio Atlântico brasileiro, compreendendo a Floresta Atlântica *sensu lato* (Oliveira-Filho & Fontes 2000) desde a bacia do Rio Paraguaçu e Recôncavo Baiano, no Estado da Bahia (aproximadamente 12° de latitude Sul) até o rio Paraíba do Sul, no norte do Estado do Rio de Janeiro (cerca de 22° de latitude Sul). Estudos ali realizados têm levado à descoberta de muitas espécies e gêneros de plantas novos para a ciência (por exemplo, Delpetre 1999, Germano Filho et al. 2000, Fiaschi & Pirani 2005, Sobral 2010, Acevedo-Rodriguez 2012) e ao registro de elevados níveis de diversidade e endemismo (por exemplo, Thomas et al. 1998, Amorim et al. 2005, Jesus & Rolim 2005, Thomas et al. 2008, Amorim et al. 2009, Wendt et al.

2010, Saiter et al. 2011).

Na região central do Domínio Atlântico, as florestas cobrem, de leste a oeste, trechos das planícies litorâneas arenosas (ou restingas), os sedimentos do Terciário (ou tabuleiros costeiros), as serras costeiras, as serras do interior e, por vezes, alguns vales úmidos da borda leste e do topo da Cadeia do Espinhaço, onde chegam a destoar da vegetação herbáceo-arbustivo dos campos rupestres. Nesse caminho, o relevo parte de uma condição plana e próxima ao nível do mar nas restingas, se eleva em algumas dezenas de metros (até cerca de 200 m) já sobre os tabuleiros costeiros, e passa à situação dissecada de colinas e montanhas, aumentando gradativamente a altitude até atingir a condição escarpada da borda leste da Serra do Espinhaço (> 1000 m) ou as zonas de transição com o Domínio da Caatinga (800-1000 m no planalto sul-baiano, ou menos que 600 m na bacia do rio Paraguaçu). Essa é apenas uma descrição simplificada do relevo na região, que se apresenta verdadeiramente mais complexo devido a um intricado conjunto geomorfológico marcado pelos vales dissecados por grandes rios como o Paraíba do Sul, o Doce, o Jequitinhonha e o Paraguaçu. Naturalmente, a complexidade geomorfológica se junta a fenômenos oceânicos e atmosféricos para determinar os padrões climáticos, sendo possível encontrar desde áreas muito úmidas, que recebem cerca de 2000 mm de chuva por ano, até áreas de clima semi-úmido a árido, onde a precipitação anual alcança apenas 800 mm. Áreas mais úmidas não necessariamente apresentam um montante de chuvas equilibradamente distribuído ao logo do ano, fato que, por sinal, pode ser constatado apenas na costa sul da Bahia.

Focando no determinismo ambiental sobre a composição da flora, seria possível prever o quanto toda essa complexidade ambiental poderia interferir na distribuição da flora, e como seriam diversos os padrões fitogeográficos. Nesse sentido, o meu principal estímulo na tese foi a possibilidade de investigação do papel de variáveis ambientais sobre a composição florística em uma região riquíssima em biodiversidade. Aqui faz-se necessário esclarecer que, devido à escassez de fontes de dados florísticos e ambientais, meus estudos foram restritos a dados de espécies arbóreas e a algumas variáveis climáticas e geográficas. Em se tratando de florestas, existem mais dados sobre o componente arbóreo do que qualquer outro grupo de plantas. Em relação a dados ambientais, existem bases de dados confiáveis apenas para um seleto grupo de variáveis climáticas e geográficas, isto é, variáveis climáticas ligadas à disponibilidade de energia e de água e ao balanço água-energia, bem como a variáveis do campo geográfico, como altitude, distância para o oceano, latitude e longitude. As duas últimas, por sinal, eu utilizei, especificamente, em análises espaciais destinadas a compreender o efeito da distância entre sítios amostrais em suas relações florísticas, um padrão já reconhecido para a Floresta Atlântica (Oliveira-Filho & Fontes 2000, Scudeller et al. 2001).

Nesse contexto, dividi a presente tese em cinco capítulos. O leitor certamente procurará por uma conexão entre eles, mas devo alertar que, embora algumas conexões diretas sejam possíveis, o escopo geral da tese foi, na verdade, norteado pela fragmentação das ideias. Com exceção do primeiro capítulo, no qual eu e meus colaboradores apresentamos uma análise mais ampla sobre a fitogeografia da região central do Domínio Atlântico, os demais correspondem a recortes do banco de dados visando a investigação de hipóteses ou temas mais específicos dentro dessa grande região. De qualquer forma, eu e meus diferentes colaboradores adotamos um mesmo plano de fundo nos capítulos, o qual permitiu uma certa integração temática em torno da conservação de florestas na região central do Domínio Atlântico brasileiro.

Como mencionei, o Capítulo I tem um caráter mais amplo, pois nele utilizamos grande parte do banco de dados para testar a hipótese de quebra da Floresta Atlântica em dois blocos florísticos, um ao sul e outro ao norte do rio Doce. Os resultados desse capítulo implicam diretamente sobre a forma como a Floresta Atlântica tem sido regionalizada para fins de conservação. No Capítulo I, entretanto, preferimos não incluir dados de florestas de restinga, uma vez que a baixa riqueza florística desses ambientes (pelo menos em relação a outros tipos florestais da costa atlântica brasileira) causou ruídos indesejáveis nas análises. Então, analisamos os dados de restingas em separado no Capítulo II, o qual serviu para confirmar a existência de um gradiente latitudinal de composição florística nas planícies arenosas do Quaternário e relevar uma região com alta prioridade de conservação, o trecho Regência-Prado. No Capítulo III, investigamos as causas da variação florística em uma região megadiversa – o leste da Bahia – e confirmamos, em parte, a consistência florística de uma classificação de florestas seguindo critérios de faixas altitudinais e de regime de renovação foliar. Destinamos o espaço do Capítulo IV para uma investigação das causas da variação florística ao longo da bacia hidrográfica do rio Doce, sem dúvida a área detentora da maior quantidade de inventários florísticos em toda a região central do Domínio Atlântico. Tal condição permitiu o estabelecimento de sub-regiões úteis para o planejamento regional da conservação de florestas. Por fim, no Capítulo V apresentamos um trabalho de revisão sobre a situação da Floresta de Linhares no contexto fitogeográfico do leste do Brasil. Houve, nesse capítulo, a oportunidade de também discutir uma controvérsia histórica envolvendo a classificação dessa floresta (se semidecidual ou perenifólia) e a influência das conexões florísticas com outras regiões sobre a elevada diversidade florística ali encontrada.

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Capítulo I – *Environmental and topographic correlates of floristic regions and tree species turnover in the Atlantic Forest hotspot*

Felipe Zamborlini Saiter, Jason Lee Brown, William Wayt Thomas, Ary Teixeira de Oliveira-Filho & Ana Carolina Carnaval

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Original Article (5,362 words)

Environmental and topographic correlates of floristic regions and plant turnover in the Atlantic Forest hotspot

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Key words: Biogeographic break, Doce River, floristic turnover, GDMs, Rio Doce, tree species.

ABSTRACT

Aim: Using a comprehensive floristic database (2,616 species, 36,004 occurrence records from 128 unique localities), we model species turnover along the central corridor of the Atlantic Forest hotspot to i) test whether local rivers, particularly the Rio Doce, are associated with marked biogeographic breaks, and ii) investigate how regional compositional changes correlate with geo-climatic variables.

Location: The central part of the Atlantic Forest in eastern Brazil (12°-22° S latitude).

Methods: We combine occurrence and geo-climatic data in a Generalized Dissimilarity Model, obtaining a continuous prediction of species turnover across space and identifying 12 significant geo-climatic predictors of community composition. We use a two-step cluster analysis to classify the turnover map into major floristic regions based on the natural subgroups observed. We further divide each major floristic region into smaller sub-regions based on natural subgroups statistically identified by the two-step cluster analyses.

Results: High levels turnover in species composition occurs around latitudes 18°-19° S, ca. 50-100 km north of the Rio Doce, and concurs with shifts in availability of both humidity and energy. We identify three major floristic regions in the central part of the Atlantic Forest, which we call Bahia Interior Forests, Bahia Coastal Forests, and the Krenák-Waitaká Forests – each of them divided into 2-4 sub-regions.

Main conclusions: Our results suggest that local climatic conditions, not riverine barriers, drive biogeographic shifts in this region – a finding that supports studies of current and historical determinants of the composition of the Atlantic Forest biota. Floristic composition in higher elevations (> 600 m) is clearly distinct from those in lower altitudes, likely as a result of physiological constrains imposed by cooler climates in the former. Floristic regions here identified from observed communities substantially improve the maps currently employed for conservation planning in a shrinking hotspot.

INTRODUCTION

Biogeography is central to conservation planning (Whittaker *et al.*, 2005). By mapping spatial biodiversity patterns, biogeographers identify regions of more or less heterogeneity in species composition, and provide evidence in support of conservation strategies and mobilization of funds (Brooks, 2010; Guisan *et al.*, 2013). Such mapping of compositionally similar areas can be further complemented whenever spatial changes in species composition, here referred to as species turnover, are modelled as a function of environmental variables. Areas of pronounced species turnover indicate concordant range limits across species, and help us to identify regions that are significantly distinct in their composition (Williams, 1996; Magnusson, 2004; Whittaker *et al.*, 2005).

Plant communities are particularly amenable to studies of species turnover given the abundance of complete or nearly complete inventory and floristic datasets for model training and validation (Ferrier *et al.*, 2002). Turnover of plant species is known to be influenced by both topographic elements (e.g. large rivers and mountain ranges) and ecological determinants (e.g. biotic interactions, climate, soil, and disturbance) that collectively impact individual dispersal, survivorship, and recruitment of each species (Cox & Moore, 2005). Although potentially acting at different scales, these elements function as filters and, in concert, define which taxa are able to occupy a certain area, given a regional species pool (Keddy, 1992).

The relative roles of topographical and ecological factors in constraining plant species ranges – and hence determining plant species turnover – remain highly controversial in phytogeographic studies, particularly in the megadiverse South American tropical forests. In great part, this is due to conflicting support to the effectiveness of rivers as biological barriers (e.g. Mori, 1990; Perret, 2006; but see Dexter *et al.*, 2012). Observations of community shifts across major South American rivers goes back to Wallace's expeditions (Wallace, 1853), and abundant data from animal groups – particularly birds, insects and mammals – identify major turnover across South American rivers at the species and lineage level (e.g. Costa *et al.*, 2003; Hayes & Sewlal, 2004; Haffer, 2008; Ribas *et al.*, 2011). On the other hand, large-scale studies based on reliable floristic datasets of well-known tropical forest plant groups (e.g. trees) and geo-climatic data provided by interpolated databases such as WorldClim (Hijmans, 2005) and CliMond (Kriticos *et al.*, 2012) demonstrate strong correlations between floristic composition and climatic and topographic shifts (e.g. Toledo *et al.*, 2012; Qian, 2013; Saiter *et al.* [upon acceptance]).

We investigate these questions in the biodiverse Atlantic Forest of Eastern Brazil. Biogeographic studies of multiple animals and plants support the existence of a biogeographic break around the Rio Doce (ca. 19° S latitude; Thomas *et al.*, 1998; Pellegrino *et al.*, 2005; Cabanne *et al.*, 2007; Brito & Arias, 2010; Ribeiro *et al.*, 2011; Carnaval *et al.*, 2014). Although a riverine barrier has been implied as possible cause of the break (e.g. Thomas *et al.*, 1998; Pellegrino *et al.*, 2005; Cabanne *et al.*, 2007), recent analyses suggest that climatic shifts may be responsible for this pattern (Ribeiro *et al.*, 2011; Carnaval *et al.*, 2014; Saiter *et al.*, [upon acceptance]). Irrespectively of the underlying mechanisms, the pervasiveness of the biogeographic break is leading to the recognition of two major blocks within the Atlantic Forest hotspot – one to the south, and one to the north of the Rio Doce (Fiaschi & Pirani, 2009; Carnaval *et al.*, 2014).

Combining extensive occurrence data from tree species (2,616 species, 36,004 occurrence records) and environmental information from 128 unique localities, here we modeled turnover in the floristic composition of the central corridor of the Atlantic Forest hotspot. These abundant and fine-scale data allow us to test whether plant communities support the view of the Rio Doce as a boundary between distinct communities, or alternatively, if local phytogeographic patterns are better explained by shifts in key environmental determinants (i.e., climate or geographic heterogeneity). Finally, we classify our turnover map into major and minor floristic regions to provide a basis for conservation planning.

MATERIALS AND METHODS

Study region

Our study encompasses the central part of the Atlantic Forest in eastern Brazil (Figures 1A and 1D), extending between the Recôncavo in the state of Bahia (ca. 12° S latitude) and the Rio Paraíba do Sul in the state of Rio de Janeiro (ca. 22° S latitude). The analyses, and resulting maps, exclude the forest patches and the riverine forests within the Espinhaço Range and Diamantina Plateau, which comprise diverse vegetation mosaics constituting the Cerrado (typical savannah in central Brazil), the Campos Rupestres (highland savannahs), and the Caatinga (semi-arid steppe in northeast Brazil).

Occurrence and Geo-climatic Data

We used a binary matrix of tree species occurrences for 128 sites throughout the study region (Figure 1A) taken from the NeoTropTree database (see http://www.icb.ufmg.br/treeatlan/ for database details; Oliveira-Filho, 2014). A total of 2,616 species and 36,004 presence records are included in the analyses.

Present-day climate data consist of Hijman's *et al*. (2005) 19 bioclimatic variables at 30-arc second resolution describing local temperature and precipitation (Bioclim, available at http://www.worldclim.org/), and 16 additional Bioclim variables at 2.5 arc-minute resolution pertaining to soil moisture and solar radiation (Kriticos *et al*., 2012; variables 20-35 downloaded from https://www.climond.org/; see Appendix S1 in Supporting Information for a complete list of environmental variables). Because the variables 20-35 were only available at a comparatively coarser resolution, we downscaled them to 30 arc-seconds using the ANUSPLIN method as per Hijmans *et al.* (2005). A digital elevation model was used as a covariate in all the ANUSPLIN analyses (Hijmans *et al.,* 2005). An additional covariate, annual precipitation, was used for the downscaling of variables pertaining to solar radiation (Bioclim 20-27); this incorporates the known dependences of solar radiation on cloud cover associated with rainfall, which gives rise to more complex solar radiation patterns in areas of topographic complexity (Hutchinson *et al*., 1984). Two additional covariates, slope and aspect, were used to downscale the variables pertaining to soil moisture (Bioclim 28-35). These were included because both affect the amount of solar radiation that habitats receive, hence directly influencing soil moisture and water retention (Geroy *et al*., 2011). The final downscaled variables are available for download at http://sdmtoolbox.org/ (Brown 2014) [upon acceptance].

Generalized Dissimilarity Modelling

Generalized Dissimilarity Modelling (GDM) is a statistical technique extended from matrix regressions designed to accommodate nonlinear data commonly encountered in ecological studies. A common use of GDM is to predict spatial patterns of turnover in community composition across large areas. Briefly, a GDM is fitted to available biological data (the absence or presence of species at each site), then compositional dissimilarity is predicted at unsampled localities throughout the landscape based on environmental data in the model. The output is a matrix of predicted compositional dissimilarities (PCD) between pairs of locations throughout the focal landscape. To visualize the PCD, multidimensional scaling is applied, reducing the data to three ordination axes and, in a Geographic Information System software, each axis is assigned a separate RGB color (red, green or blue).

To match the resolution of the community composition data, we upscaled the environmental data to 5 km^2 by averaging the higher resolution (30 arc-second) data. Both datasets (species presence and environmental data) were input into a generalized dissimilarity model following Rosauer *et al*. (2013). To select the best subset of geo-climatic predictors for our model, we used a stepwise backward elimination process as outline by Williams *et al.* (2012). Briefly, the model is initially built will all predictor variables and then iteratively, variables are removed that contribute less 0.1% to the deviance explained of the model, until all predictor variables in the model contribute more than 0.1% to the deviance explained. Using this method we went from 39 predictor variables down to 12 in the final model. The model built at 5 km^2 was subsequently projected into the full resolution (1 km^2) climate data. The continuous GDM was classified into three major regions, and each of these was then classified separately into 2-4 sub-regions. The numbers of regions and sub-regions were based on Two-Step Cluster Analyses in SPSS v21 (Banfield & Raftery, 1993; Zhang *et al.*, 1996; Theodoridis & Koutroumbas, 1999; IBM Corp., 2012).

RESULTS

A GDM explains 56% of the observed turnover in species composition in the central part of the Atlantic Forest. The continuous GDM framework (Figure 1F) can be split into three major floristic regions (hereafter referred to Bahia Interior Forests, Bahia Coastal Forests, and Krenák-Waitaká Forests; Figure 1C). The Bahia Interior Forests encompassed moist and dry forests of northeastern Minas Gerais and inland Bahia, and is further divided into four sub-regions (Figure 1E). The Bahia Coastal Forests include the wet forests north of 18-19° S, which can be further separated into three sub-regions (Figure 1E). In turn, the Krenák-Waitaká forest region encompasses two sub-regions of moist forest south of 18-19° S (Figure 1E). The term Krenák-Waitaká is a junction of the names of two main Amerindian groups that inhabited this region before the arrival of Europeans and Africans.

All major floristic regions have sub-regions that are distributed along distinct elevation belts: forests at low and mid-elevation (up to 500-600 m) are compositionally different from those in higher altitudes (> 600 m; see correspondence between Figure 1B and Figure 1E). In the

Bahia Coastal Forests, we further identify two sub-regions of low and mid-elevation: one extending south of the Rio Paraguaçu basin, and another encompassing the Rio Paraguaçu basin and Recôncavo. The Bahia Interior Forests also have two sub-regions of low and mid-elevation (the Jequitinhonha-Pardo region and Rio Paraguaçu basin) and other two sub-regions of high elevation (the Jequitinhonha-Pardo region and the Bahian plateau). The Bahia Coastal Forests and Bahia Interior Forests are more ecologically similar to each other than to the Krenák-Waitaká Forests (see dendogram in Figure 1 for relationships among regions and sub-regions).

The geographical limits of the main floristic regions fail to coincide with the Rio Doce valley, as the boundary between the Bahia Interior Forests and the Krenák-Waitaká Forests, and that between the Bahia Coastal Forests and the Krenák-Waitaká Forests, were located 50-100 km north of the river. These turnover regions also appear to have no correspondence with any other river in northern Espírito Santo or northeastern Minas Gerais (Figure 1). Instead, the GDM identifies 12 significant predictors of species composition turnover (see Appendix S2). Among the top five predictors in relative contribution are variables that describe the amount of insolation (Bio 24), moisture index (Bio 34), elevation, temperature (Bio10), and precipitation (Bio 14) – attesting to the role of availability of both water and energy in maintaining the floristic patterns observed.

DISCUSSION

Our results demonstrate that spatial patterns of climatic variation are intimately linked to the turnover in tree species composition in the central part of the Atlantic Forest. Instead of being imposed by a riverine barrier, the phytogeographic break near the Rio Doce seems to have a climatic basis. This result is not surprising, as the Rio Doce is not nearly as large as the Amazonian rivers previously reported to act as effective dispersal barriers to plants (e.g. Mori, 1990) and animals (e.g. Costa *et al.*, 2003; Hayes & Sewlal, 2004; Haffer, 2008; Ribas *et al.*, 2011). The river is no more than 1 km wide (observed at the lower basin), and its size has not changed significantly since the last transgression period (5.1 kyr BP; Suguio & Kohler, 1992).

However, floristic composition does changes significantly around latitude 18°-19° S (i.e., 50-100 km north of the Rio Doce), as reflected in the boundaries of three major floristic regions proposed here. The availability of both water and energy vary sharply between these latitudes (see below specific commentaries on each floristic region), suggesting that the current climate is working as a filter and limiting the distribution of tree species (Keddy, 1992).

The Krenák-Waitaká Forests are seasonal in terms of precipitation, solar radiation and temperature, in contrast with the Bahia Coastal Forests. This pattern of seasonality is known to result from seasonal atmospheric phenomena. In the winter, for instance, the South Atlantic Subtropical Anticyclone encroaches in southeastern Brazil, blocking the passage of humid air masses (Reboita *et al.*, 2010). In the summer, on the other hand, the South Atlantic Subtropical Anticyclone shifts to the west, towards the Atlantic Ocean. Thus, humid air masses commonly increase rainfall over continent. Such seasonal changes are, however, not observed north of latitudes 18°-19° S. In the Bahia Coastal Forests, two main atmospheric mechanisms bring great amounts of humidity and prevent the establishment of a dry season: the South Atlantic Convergence Zone works in spring-summer, whereas the Convergence Zone of the Eastern Coast of Northeast Brazil provides high amounts of monthly precipitation in autumn-winter (Molion & Bernardo, 2002).

In turn, the Bahia Interior Forests are known to be more seasonal and drier than Krenák-Waitaká Forests. For instance, the climate of the Mucuri and Jequitinhonha river valleys, in northeastern Minas Gerais, has indeed been described as seasonal sub-humid to semi-arid (Ferreira & Silva, 2012), whereas the climate in the Krenák-Waitaká Forests has been refereed as seasonal humid (Cupolillo *et al.*, 2008). Not surprisingly, some highly tolerant species typical of the dry forests of the Cerrado and Caatinga domains can be found in the Bahia Interior Forests, but not in the Krenák-Waitaká Forests (for additional details about interior dry forests, see Santos *et al.*, 2012; and Arruda *et al.*, 2013).

Our climate-based approach does not invalidate historical approaches to the study of the phytogeography of the Atlantic Forest, but rather complements them. Previous studies have, for instance, recognized the historical influence of the Subtropical-Andean flora on the composition of forests in a southern block of the Atlantic Forest, or flagged a stronger influence of the Amazonian flora in the northern block (e.g. Fiaschi & Pirani, 2009; Oliveira-Filho *et al.*, 2013; Duarte *et al.*, 2014). We can still recognize these influences in our analysis. Subtropical taxa such as *Araucaria angustifolia* (Bertol.) Kuntze and *Mimosa scabrella* Benth., as well as many species of Lauraceae, Melastomataceae, Myrtaceae, and tree ferns (Behling & Pillar, 2006; Duarte *et al.*, 2014) are solely observed in part of the Krenák-Waitaká Forests (the Mantiqueira Range, around the 20º S latitude). This compositional uniqueness matches existing hypotheses that such species, which survive in a few cooler and isolated mountains above 1000 m within the Mantiqueira Range, are relicts of a northward expansion of the subtropical flora during the Last Glacial Maximum (LGM), ca. 48-18 ka BP (Behling & Lichte, 1997). On the other hand, some of the tree species observed in the Bahia Coastal Forests and Krenák-Waitaká Forests have disjunct distributions in Amazonia (Mori *et al.*, 1981; Thomas *et al.*, 1998), such as *Anthodiscus amazonicus* Gleason & A.C.Sm., *Caraipa densifolia* Mart., *Erythroxylum macrophyllum* Cav., *Macoubea guianensis* Aubl., *Parkia pendula* (Willd.) Walp., and *Pagamea guianensis* Aubl. This pattern is predicted by hypotheses of a historical bridge between Amazonia and the Atlantic Forest through the gallery forests within the northeast-southwest corridor of open vegetation formations of central Brazil, through the Caatinga and the Cerrado (Oliveira-Filho & Ratter, 1995; Costa *et al.*, 2003; Oliveira-Filho *et al.*, 2013).

Historical climatic conditions may also provide an explanation for the number of endemic species shared between wet southern Bahia (e.g. *Beilschmiedia linharensis* Sa. Nishida & van der Werff, *Cariniana parvifolia* S. A. Mori, Prance & Menandro, *Hydrogaster trinervis* Kulhm., *Kielmeyera occhioniana* Saddi, *Mollinedia marqueteana* Peixoto, *Plinia stictophylla* G.M. Barroso & Peixoto, *Riodocea pulcherrima* DelPrete, *Simira grazielae* Peixoto, and *Trattinnickia mensalis* Daly) and the more seasonal coastal lowland forests of the Rio Doce region (usually referred to as the Linhares Forest). The coast of southern Bahia is a known center of plant diversity (Thomas *et al*., 1998), and it has been hypothesized that rainforest coverage has remained stable in this region for a long time (Carnaval & Moritz, 2008). Further, paleoclimate studies suggest that coastal Bahia was as wet in the Mid-Holocene (roughly 6 ka BP) as it is today (e.g. Melo & Marengo, 2008).

The Linhares Forest around the Rio Doce, although presently characterized by a seasonal climate, also experienced wetter and less seasonal climate during the Mid-Holocene (Buso Junior *et al*., 2013). It is possible that floristic exchanges across southern Bahia and the Linhares Forest were facilitated during the wet Mid-Holocene, and that humidity-associated species were able to persist around the Rio Doce until today in regions where drought can be offset by humid soils (e.g. riverine forests).

The sub-region identification process implemented by our approach clearly distinguishes the higher elevation forests of the central part of the Atlantic Forest from low and mid-elevation forests. This segregation, we argue, is a result of physiological constraints determined by cooler climates at higher elevations (see reviews in Grubb, 1977; and Körner, 2007). In the Bahia Interior Forests, however, the proximity of the Cerrado and Caatinga appears to additionally influence local tree composition. In this way, both low + mid-elevation and high-elevation forests of the Jequitinhonha-Pardo region have floristic affinities with dry forests enclaves within the Cerrado domain such as the interior semi-arid forests of northern Minas Gerais (Santos *et al*., 2012). Similarly, tree composition in the Rio Paraguaçu Basin and the Bahian plateau seems to be, in part, influenced by the Caatinga flora of the semi-arid regions farther west (Mori &

Mattos-Silva, 1979; Cardoso *et al*., 2009).

In Bahia's coastal region, a distinction between two lowland sub-regions is remarkable because some species commonly found in the Atlantic Forest-Caatinga transition (e.g. *Acrocomia intumescens* Drude, *Myrcia rosangelae* NicLugh., *Duguetia moricandiana* Mart., and *Gochnatia oligocephala* (Gardner) Cabrera) occur throughout the Rio Paraguaçu basin and the Recôncavo, but not south of them. This pattern may be related to subtle south-north changes in the water-energy balance during the critically warm summer months (Silva & Satyamurty, 2006), although it can also be the result of a dry and seasonal paleoclimate in such regions.

Through the use of GDMs, we are able to present an ecologically coherent and unbiased classification of floristic regions for the central Atlantic Forest, and demonstrate how these regions are strongly related to climatic variables. These results matter tremendously for the noteworthy effort of mapping of ecoregions worldwide (e.g. World Wildlife Fund-WWF global map of ecoregions; Olson *et al*., 2001). It is known that Olson *et al*. (2001) used the Brazilian vegetation map (IBGE, 1993) to generate WWF's ecoregion map. However, the IBGE map is essentially phytophysiognomic, because it was built solely from environmental data (particularly general climate and water deficit), information on vegetation structure, and leaf flush regime (IBGE, 1992). We argue that both the IBGE's (1993) vegetation map and Olson *et al*.'s (2001) ecoregion maps disregard important regional differences in forest composition that we are able to identify here, and expect that a biome-wide GDM will significantly improve mapping of biodiversity throughout the Atlantic Forest.

Our results reinforce the importance of employing robust and verified datasets of occurence records across different taxa and at finer scales, in lieu of on maps of environment and vegetation, to delimit biogeographic units (Magnusson, 2004; Whittaker *et al*., 2005; Brooks, 2010). In the Atlantic Forest, specifically, natural breaks in tree species distribution, such as those near the Rio Doce, provide important insights into key phytogeographic boundaries. It is arguably at mesoscale approaches, such as the one performed here, that improvements in the quantity and quality of biological data can lead to significant changes in biodiversity mapping – particularly for conservation planning in a shrinking hotspot.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Bioclim variables used to modelling turnover in tree species composition in the central part of the Atlantic Forest, Brazil.

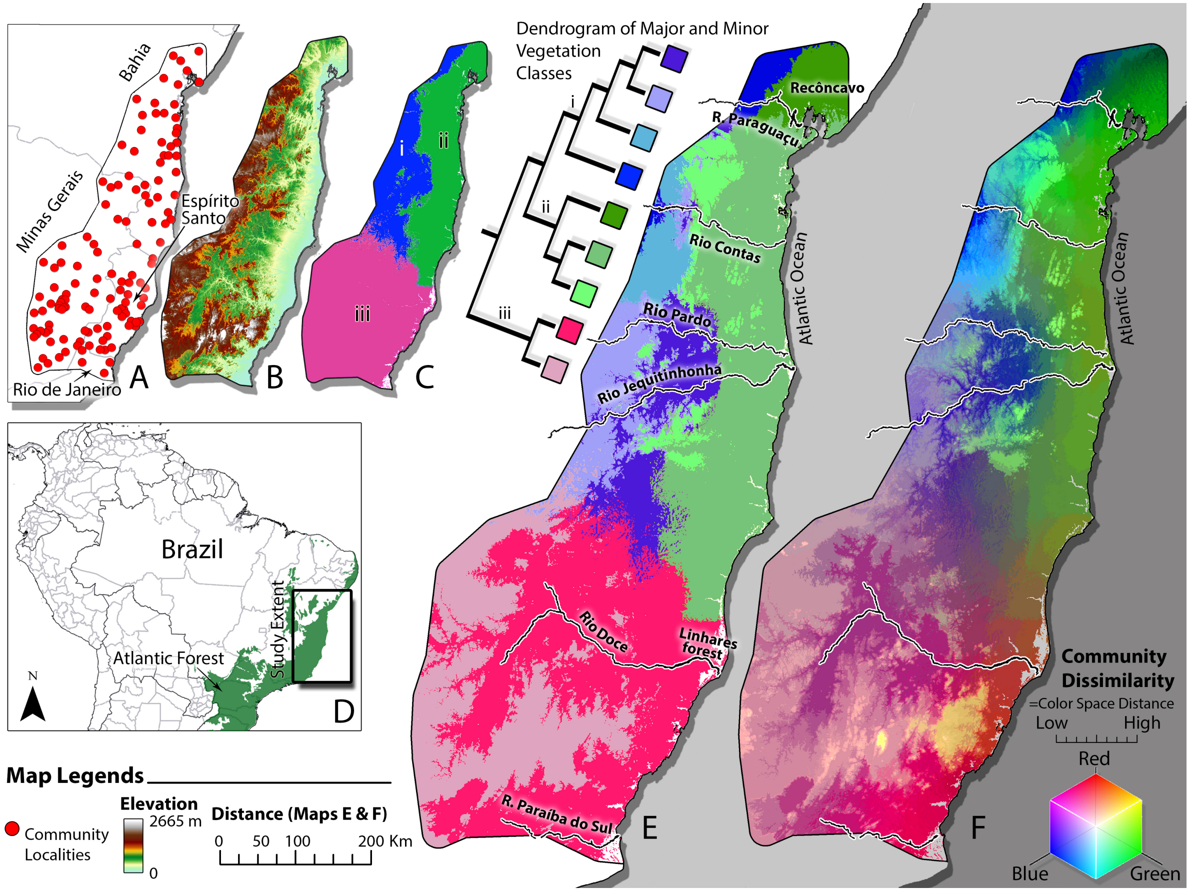
Appendix S2 Twelve significant geo-climatic predictors of turnover in tree species composition in the central part of the Atlantic Forest, eastern Brazil.

BIOSKETCHES

The authors are part of a broader interdisciplinary team funded by NSF, NASA and FAPESP to explain and predict of the distribution of animal and plant species in the endangered yet megadiverse Brazilian Atlantic forest. In pre-Columbian times, this ecosystem extended for 3000 km, forming a fringe of forests sandwiched between the Atlantic Ocean and the drier uplands of the Brazilian shield. Today, the forest is reduced to less than 11% of its historical range, yet its fragments harbor one of the largest percentages of endemic species in the world. Work by the team is enabling the reconstruction of historical and present-day factors influencing Atlantic forest biodiversity at three different dimensions (genetic, taxonomic and functional) and, given a range of climate change scenarios, will permit predictions of the composition of biodiversity under future conditions.

Author contributions: A.C.C. and F.Z.S. conceived the ideas; A.T.O.F., F.Z.S., and W.W.T. collected the data; F.Z.S. and J.L.B. analyzed the data; A.C.C., F.Z.S., and J.L.B. led the writing.

Figure 1 Prediction of turnover patterns in tree species composition in the central part of the Atlantic Forest, eastern Brazil. (A, D) Atlantic Forest domain, study extent, and 128 localities which provided data for a generalized dissimilarity model – GDM; (B) Elevation map; (C) Major floristic regions classified from GDM: i, Bahia Interior Forests, ii, Bahia Coastal Forests, and iii, Krenák-Waitaká Forests; (E) Floristic sub-regions and their interrelationships; (F) Continuous GDM framework.



Appendix S1 Bioclim variables used to modelling turnover in tree species composition in the central part of the Atlantic Forest, Brazil.

Geography: Elevation; Slope; Aspect; Geographic distance.

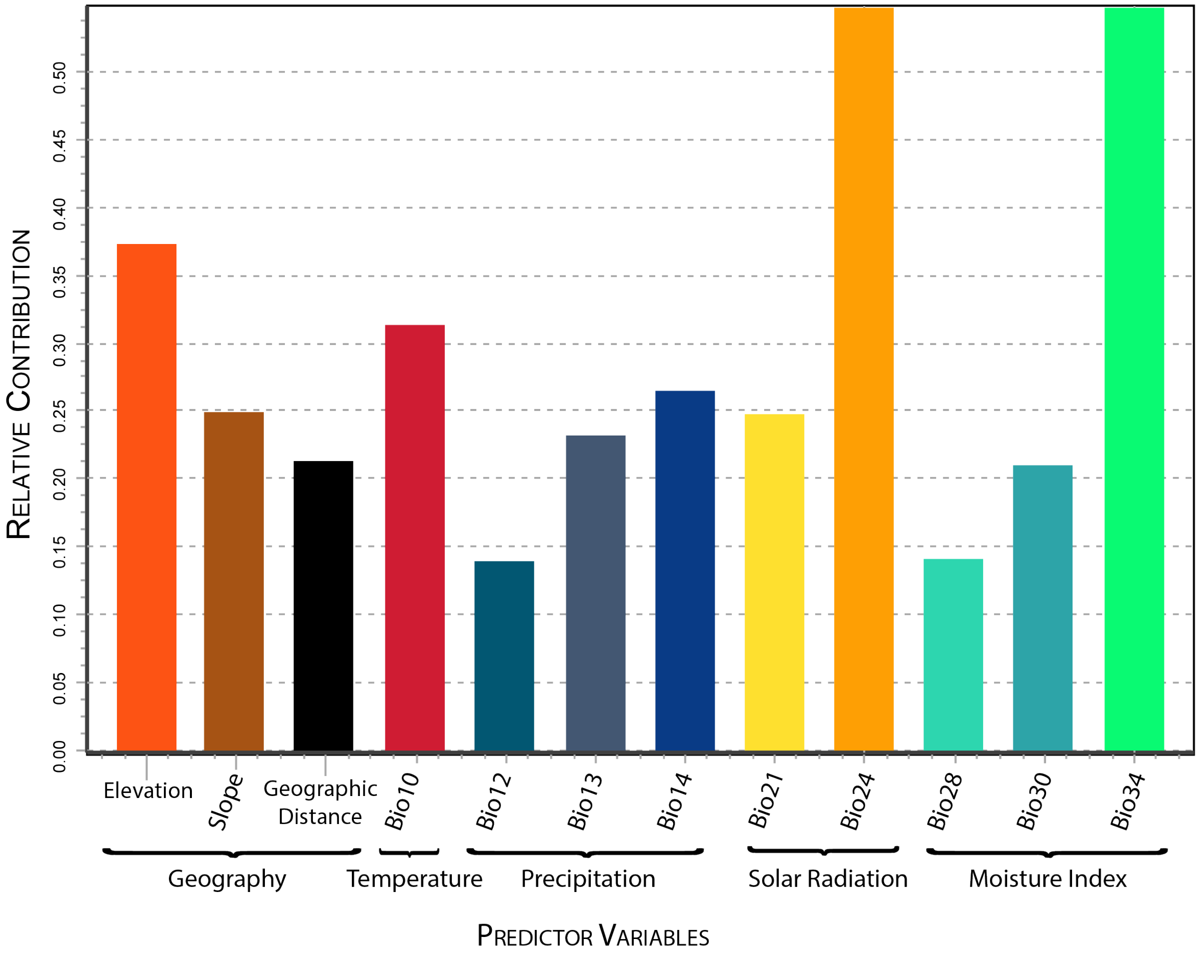
Temperature: Bio01, Annual mean temperature; Bio02, Mean diurnal temperature range; Bio03, Isothermality; Bio04, Temperature seasonality; Bio05, Maximum temperature; Bio06, Minimum temperature; Bio07, Temperature annual range; Bio08, Mean temperature of wettest quarter; Bio09, Mean temperature of driest quarter; Bio10, Mean temperature of warmest quarter; Bio11, Mean temperature of coldest quarter.

Precipitation: Bio12, Annual precipitation; Bio13, Precipitation of wettest month; Bio14, Precipitation of driest month; Bio15, Precipitation seasonality; Bio16, Precipitation of wettest quarter; Bio17, Precipitation of driest quarter; Bio18, Precipitation of warmest quarter; Bio19, Precipitation of coldest quarter.

Radiation: Bio20, Annual mean radiation; Bio21, Highest weekly radiation; Bio22, Lowest weekly radiation; Bio23, Radiation seasonality; Bio24, Radiation of wettest quarter; Bio25, Radiation of driest quarter; Bio26, Radiation of warmest quarter; Bio27, Radiation of coldest quarter.

Moisture: Bio28, Annual mean moisture index; Bio29, Highest weekly moisture index; Bio30, Lowest weekly moisture index; Bio31, Moisture index seasonality; Bio32, Mean moisture index of wettest quarter; Bio33, Mean moisture index of driest quarter; Bio34, Mean moisture index of warmest quarter; Bio35, Mean moisture index of coldest quarter.

Appendix S2 Twelve significant geo-climatic predictors of turnover in tree species composition in the central part of the Atlantic Forest, eastern Brazil.



Capítulo II – *Recognizing climatic seasonality and geographical location as causes of a latitudinal floristic gradient: implications for conservation of Restinga forests in the central part of the Atlantic forest*

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ORIGINAL ARTICLE

Recognizing climatic seasonality and geographical location as causes of a latitudinal floristic gradient: implications for conservation of Restinga forests in the central part of the Atlantic forest

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Abstract

Restinga forests are one of the most endangered and neglected ecosystems of the South America and their pythogeographic patterns are poorly known. Here, we submitted climatic and occurrence data of tree species from Restinga sites in the central part of the Atlantic forest to numerical analyses in order to determine the role of climate and geographical location of sites in a latitudinal floristic gradient, and to discuss the implications of such patterns for conservation. We confirmed the existence of such a gradient, one that was strongly related to climatic seasonality, and especially to temperature seasonality. Within this gradient, we noticed a stronger variation in composition in a region known for its transitional climate, from seasonal to non-seasonal. The shifts in climatic seasonality can be explained by a set of atmospheric and oceanographic phenomena and by geographical relief inland. Geographical location influences species composition because spatial proximity means similarity in climatic conditions, although dispersal difficulties can also limit the distribution of some species. Within the study region, we recognize the Regência-Prado stretch as the most relevant area for conservation of Restingas, because of the paucity of reserves and the high floristic variation within a relatively short distance along the coast.

Key words: climatic gradient; coastal sandy plains; macroecology; species distribution; spatial autocorrelation

Introduction

The causes of mesoscale variation in floristic composition are still poorly understood in South American forests (ter Steege *et al.*, 2006). Several studies have demonstrated that floristic gradients are related to shifts in availability of water and energy (e.g., Oliveira-Filho *et al.*, 2005; ter Steege *et al.*, 2006; Toledo *et al.*, 2011). In turn, the effect of geographical distance on changes in tree species composition has also been noticed by many studies (e.g., Oliveira-Filho *et al.*, 2005; Macía etal., 2007; Saiter *et al.*, 2015). This effect can be simply a result of spatial structuring of environmentor limited dispersal of some species (Legendre & Legendre 2012).

An interesting region for investigation of causes of floristic gradients is the central part of the Atlantic Forest (CCAF). This is a priority area for biodiversity conservation in the South American tropics that stretches in the Brazilian coast from southern Espírito Santo (ca. 21° S) to southeastern Bahia (ca. 13° S; Ayres *et al.*, 2005). Here, several studies have found some of the highest levels of plant diversity and endemism in the world (e.g., Thomas *et al.*, 1998; Martini *et al.*, 2007; Saiter *et al.*, 2011). In the shoreland of the CCAF, there are sandy coastal plains, also named Restingas, which originated from deposition of fluvial-marine quartzic sandy during the Quaternary (Martin *et al.*, 1996). Plant colonization in these plains is, therefore, a relatively recent event with the source of species provided mainly by the Atlantic forest over adjacent, more ancient geological formations (Rizzini 1979; Scarano 2002), such as the coastal tablelands formed of Tertiary sediments, and the hills of the Precambrian basement.

At local scale, structure and composition of vegetation in Restingas are driven by edaphic features, such as water table depth, amount of organic matter, and salt content, which lead to vegetation mosaics of forest, shrubby, and herbaceous physiognomies (Pereira 2003; Martins 2012). Forest physiognomies can occur in non-flooded areas over sand ridges as well as in flooded depressions located between two consecutive ridges (Pereira 2003). The Restinga forests within the CCAF are generally characterized by trees with < 20 cm diameter at breast height, canopy ca. 10 m height, and great abundance of lianas and shrubs (Amorim *et al*., 2008; Giaretta *et al*., 2013).

Given that Restinga forests have lower richness and endemism levels than other forest types within the Atlantic forest, little attention has been paid to their protection against urban and industrial expansion, beach-front development, mining (mainly of sand and oil), and illegal collection of ornamental plants and wood (Zamith & Scarano 2006). When Restingas are degraded by such activities, the restoration of communities becomes extremely expensive and difficult due to edaphic, microclimatic, and biological factors (Zamith & Scarano 2006; Saiter *et al*., 2012). Thus, the current scenario in the coastal zone shows a few Restingas with natural communities (although often subjected to some human impacts) and large areas of degraded sandy plains covered by invasive species or occupied by urban settlements and industrial sites (Saiter *et al*., 2012). Unfortunately, degradation is likely to worsen because few studies (e.g. Scarano 2009) have provided useful scientific knowledge for the formulation of appropriate strategies for Restinga conservation.

Although Restingas are highly endangered, the phytogeographic relationships among their forests within the CCAF are still poorly known. The sole attempt was performed by Giaretta *et al*. (2013) in a study about floristic relationships among coastal forests found in Restingas, tablelands, and ‘muçunungas’ (patches of sandy soils within the coastal tablelands) between southernmost Bahia and southern Espírito Santo (17°30’-20°30’ S). These authors provided biological evidences of a latitudinal floristic gradient along the coast, but did not discuss its possible drivers.

Understanding the phytogeographic patterns of Restinga forests in the CCAF and their implications for conservation is an important challenge of our study. To that end, we submitted climatic and occurrence data of tree species from Restinga sites to ordination and spatial analyses in order to answer the following questions: [1] Which climatic variables are the most related to a latitudinal gradient of tree species composition in Restingas of the CCAF? [2] Does geographical location influence the floristic relationships among Restinga sites in the CCAF?

Materials and Methods

Study region

The study region comprises Restingas of the CCAF occurring discontinuously between the Itabapoana River, in southern Espírito Santo, and the Bahia de Todos os Santos, south of Salvador, in Bahia (Fig. 1). Restingas can be broken up by Tertiary tablelands or crystalline Precambrian formations extending all the way to the Atlantic (Martin 1996; Dillenburg & Hesp 2009). We included the sandy tablelands of the Olivença region (Bahia) in this study region due to their proximity to the ocean and their structural and floristic similarity to typical Restinga forests (Araujo *et al*., 2008; Amorim *et al*., 2008). The sandy tablelands are constituted by a deep layer (> 2 m) of podzolized sand over sandy-clay soils (variety Cururupe; Santana *et al*., 2002) and their origin due to deposition of quartzic sand by wind remains speculative (Araujo *et al*., 2008).

Preparing the dataset

The dataset was composed of a binary matrix of tree species occurrence records and a climatic matrix of 23 sites of Restinga forest in the CCAF (Fig. 1 and Table 1). The matrices were extracted from the database NeoTropTree, which comprises checklists of tree species occurrence records and geoclimatic data of previously selected sites of the Neotropical Region (http://prof.icb.ufmg.br/treeatlan/; Oliveira-Filho 2014). The NeoTropTree uses three data sources for checklists: [a] Floristic and quantitative inventories; [b] Taxonomic studies; and [c] Herbarium reports available in the INCT – Herbário Vitual da flora e dos fungos (http://inct.splink.org.br/), being prioritized those records determined by taxonomists.

Because NeoTropTree adopts circular sampling units with 5 km radius, our dataset included all tree species recorded in the Restinga sites, regardless their occurrence over non-flooded sand ridges or in flooded depressions. We emphasize that forest physiognomies are only a portion of the vegetation mosaic in Restingas, and that we are considering treelike plants (e.g. some palms and cacti) within a broad concept of tree species due their importance in characterization of Restinga forests.

The binary matrix had 596 tree species and 3196 presence records, but we excluded 168 singletons (species with only one occurrence data point) because they could not contribute to ordination patterns (Lepš & Šmilauer 2003). Thus, the final matrix comprised 428 species, 23 sites, and 3028 occurrence records.

The environmental matrix comprised 25 variables. A total of 19 bioclimatic variables were obtained from WorldClim 1.4, including a set of layers with high resolution (1 km^2) organized by Hijmans *et al.* (2005). Three other variables, potential evapotranspiration, actual evapotranspiration, and an aridity index, were produced by Zomer *et al.* (2007) from WorldClim's data. The percentage of cloud coverage was obtained from Harris (2014), and the mean duration (in days) and severity of water deficit (amount in mm) were extracted from Walter's diagrams (Walter 1985).

Data analyses

We used the Nonmetric Multidimensional Scaling (NMS) ordination in the software PC-ORD 6 (McCune & Mefford 2011) to create a dimension that could represent the main gradient of species composition within the dataset. The significance of this dimension was tested using Monte Carlo test ($p \leq 0.05$) and the stress stability was verified through successive iterations (McCune & Grace 2002).

We undertook correlations *a posteriori* among NMS dimension and climatic variables using Pearson's correlation and a linear regression model (OLS). Redundant variables were excluded when the variance inflation factor (VIF) of each variable was greater than 10 (e.g., Quinn & Keough 2002). We considered the best linear regression model to be the one having the lowest AICc value (Burnham & Anderson 2002). Assumptions of this model were confirmed according suggestions provided by Eisenlohr (2013) and Eisenlohr (2014).

In order to recognize any spatial structure in the variables and residuals of the model, we created correlograms with Moran's I coefficient in the software SAM 4.0 (Rangel *et al.*, 2010). We tested the global significance of the correlogram using Bonferroni's sequential correction, and confirmed the existence of spatial structure when at least one distance class was significant (Fortin & Dale 2005). Spatial structures need to be checked because, although they improve our understanding of ecological patterns, they may also violate statistical assumptions (Diniz-Filho *et al.*, 2003).

Because we found spatial structure in climatic variables and NMS scores, and this structure can inflate the type I error (Legendre *et al.*, 2002), we modeled the spatial component to confirm previous decisions based on p-values. These models were built through the addition of spatial filters (Moran's Eigenvector Maps; Dray *et al.*, 2006) that were forward selected under a RDA (Canonical Redundancy Analysis) scheme followed by a variance partitioning, thereby discounting the effect of spatial structures (Peres-Neto & Legendre 2010). Here, we used the R-code suggested by Eisenlohr (2014). Since the significance of previous models was supported, we opted to show the results of the simplest models, i.e., without inclusion of spatial filters.

We performed an additional variance partitioning considering the overall floristic data to unveil the contribution of each driver set (climate, space, and the spatially structured fraction of climate variables) on the variation of species distribution along Restinga sites.

Before this variance partitioning, however, we excluded the three variables less related to NMS scores (mean annual temperature, potential evapotranspiration, and actual evapotranspiration) in order to respect an assumption of RDA (number of predictors < number of sites) adopted in the aforementioned protocol. In this way, we used a climatic matrix with only 22 variables in the partitioning. We also tested the significance of pure fractions of climate and space by permutation-based ANOVA. We conducted variance partitioning analyses using the packages ‘vegan’, ‘spacemakeR’, ‘packfor’ and ‘spdep’ in R (R Core Team 2011). Finally, the correlation between floristic and geographic distance matrices was tested using Mantel test, followed by the Monte Carlo test with 999 permutations.

Results

The NMS provided a one-dimensional solution with a final stress of 18.66 and explained 78.4% of variation in relation to the similarity in the original *n*-dimensional space. The southern and northern sites were placed, respectively, at left and right sides of the ordination diagram (Fig. 2). In the central portion of the diagram, there were large gaps among the sites Regência, Conceição da Barra, Caravelas, and Prado, indicating that floristic turnover is stronger in a coastal stretch with ca. 200 km between northern Espírito Santo and southernmost Bahia (hereafter named as Regência-Prado stretch). This unexpected pattern instigated us to inspect the whole dataset and, thus, we found that distribution range of several tree species is discontinued in this part of the CCAF. For instance, around 60% of 70 species of Fabaceae, one of the most important families in the tree stratum of the Atlantic forest (Rizzini 1979), have their distribution ranges discontinued somewhere in the Regência-Prado stretch (see Table S1).

The variables most strongly related to the NMS dimension ($r > 0.70$) are shown in Table 2. The top five variables were temperature seasonality ($r = -0.95$), annual temperature range ($r = -0.93$), precipitation of coldest quarter ($r = 0.92$), maximum temperature ($r = -0.92$), and precipitation of driest quarter ($r = 0.88$). The NMS dimension was effective in segregate sites along a latitudinal gradient of climatic seasonality, so that the more seasonal sites (southern sites) were positioned to the left and the less seasonal sites (northern sites) to the right in the ordination diagram (Fig. 2).

The best linear regression model (AICc = 19.91; r^2 adjusted = 0.90; F = 185.93; $p < 0.001$) had only temperature seasonality as a predictor. Both pure fractions of environment (3%) and space (2.5%) were significant ($p \leq 0.05$) in the variance partitioning. The Mantel test indicated a positive correlation between floristic and geographic distance matrices ($r = 0.81$, $p < 0.01$), reinforcing the role of space in determining tree species composition. The spatially structured fraction of climate (12%) was greater than the pure fractions. The unexplained fraction was high (82.5%).

Discussion

Our results indicated a latitudinal gradient of tree composition in Restingas of the CCAF, with floristic turnover stronger in the Regência-Prado stretch than in other parts of the study region. This phytogeographic pattern confirms the findings of Giaretta et al. (2013) and reveals remarkable implications for conservation of Restingas, an issue that we will return later in this paper.

The latitudinal gradient of tree composition is, in part, supported by climatic shifts along the CCAF. The climate is progressively more seasonal to south (Feitoza *et al.*, 2001) and becomes non-seasonal to north (Thomas *et al.*, 1998). In fact, the best predictor of variation in tree composition was a variable directly related to seasonality (i.e. temperature seasonality). This variable is a measure of temperature shifts over the course of a year; however, its specific role in plant distribution remains speculative (Raes *et al.*, 2009). O'Brien (1993) and O'Brien *et al.* (1998), for instance, suggested that climatic seasonality changes the duration of the growing season for plant species, thus affecting the distribution of the southern Africa's woody flora. Such an approach is corroborated by studies that found a direct relationship between seasonal variation in temperature and a decrease in productivity in forests worldwide (e.g., Larjavaara & Muller-Landau 2012).

Because we have recognized that temperature seasonality was strongly collinear to variables representing seasonal distribution of rain (such as precipitation of coldest quarter, precipitation of driest quarter, and precipitation seasonality), thus, it should be reasonable to state that thermal shifts concur with changes in rainfall regime along the CCAF. In this sense, temperature seasonality is lower where there is no dry season, specifically north of Prado. On the other hand, thermal seasonality reaches its maximum in Itapemirim and Praia das Neves, where the dry season can last up to 3 months and precipitation of the coldest quarter is only 10-15% of the annual total.

The congruence of thermal and rainfall regimes can be explained by a set of atmospheric and oceanographic phenomena and by the inland geographical relief. In coastal Bahia, the absence of a dry season is caused mainly by two atmospheric mechanisms carrying great amounts of humidity. The South Atlantic Convergence Zone works in spring-summer, whereas the Convergence Zone of the Eastern Coast of Northeast Brazil provides the highest amounts of monthly precipitation in autumn-winter (Molion & Bernardo 2002). In coastal Espírito Santo, however, the South Atlantic Subtropical Anticyclone encroaches on the continent during the winter, blocking the passage of humid air masses that cause weather fronts (Cupolillo *et al.*, 2008).

The southern coast of Espírito Santo (Itapemirim and Praia das Neves) is also affected by an oceanic upwelling of deep, cold water during the summer (Aguiar *et al.*, 2014). This phenomenon leads to lower evaporation over the ocean and reduced cloud formation. As a consequence of a sky with low cloudiness, the higher insolation increases both temperature (maximum > 31 °C) and evaporation levels over the continent, decreasing the water storage in soil and contributing to the water deficit during the winter (Coe & Carvalho 2013). Geographical relief has a role in diminishing drought severity only in the small stretch between Vitória and Guarapari, where slopes of the Castelo Range are only 20 km from the coast, contributing to moisture retention windward.

Summarizing, annual thermal range is higher, and drought is more severe in the southernmost of the CCAF (Itapemirim and Praia das Neves), and both climatic features are sharply attenuated in the Regência-Prado stretch, changing to more thermally stable and moister conditions in the northern part of the CCAF. Indeed, it was in the Regência-Prado stretch where we found the stronger turnover in tree species composition. Thus, the occurrence of a seasonal climate in such part of the CCAF may represent an important ecological filter to a more southern distribution of typical pluvial species from coastal Bahia. Such a pattern is similar to that proposed by Saiter (2015) to explain a biogeographic break of the Atlantic forest in two blocks (southern and northern blocks) around the latitude 19° S.

Here, it is necessary to restate that the Atlantic forest over coastal hills and tablelands was the main source of species for the colonization of the emerging Quaternary sandy plains (Rizzini 1979; Scarano 2002). In this way, it is reasonable to assume that differences in tree composition among Restinga forests are effects of floristic variation along more ancient geological formations in the CCAF. Despite sandy coastal plains are interrupted by cliffs in some places, it is even possible to suppose that Restingas are not pockets isolated from each others. Instead, adjacent ecosystems are certainly the way for floristic interchange at least where modern anthropogenic action does not represent a barrier. That is why the connection of Restinga forests with other forest types in CCAF is probably a critical problem for biodiversity conservation in sandy coastal plains. Thus, conservation programs should ensure it.

The discussions up to this point demonstrate a partial determinism of climate on tree species distribution along the CCAF. This is supported by a significant fraction of floristic variation explained purely by environment. Additionally, the high shared fraction indicated that the majority of climatic variables here analyzed are spatially structured. In turn, the pure fraction of space, although lower than other fractions, also suggests that intrinsic features of the species, such as limited dispersal, can also influence the tree composition in Restingas of the CCAF.

The high unexplained fraction of floristic variation can be attributed to undetermined component related to variables not included in the analyses. For example, we chose not to use soil variables here because in all Restinga sites, the soils are sandy and very oligotrophic (Bonilha *et al.*, 2012). We also did not use variables related to disturbance regime and biological interactions, since these processes are poorly understood in tropical regions (Zimmermann *et al.*, 2010).

Regardless of this, the high percentage of uncertainty does not invalidates the explanatory power of the climatic variables (see also Gasper *et al.*, 2015), because the regression model revealed clear relationship between climate and tree species distribution. In this way, the predictive power of other variables, such as those mentioned above, should be tested in order to complement our results.

We conclude that there is a latitudinal gradient of tree species composition along Restingas in the CCAF, which matches with a gradient of climatic seasonality (especially of temperature seasonality). Not surprisingly, geographical position indirectly influences tree species composition because spatial proximity means similarity in climatic conditions. However, dispersal limitations can also play a role in the distribution of some species. The floristic gradient becomes stronger in the Regência-Prado stretch, as well as the variation in climatic seasonality. Thus, investigating how climatic seasonality has limited the distribution of plant species in Restingas in the Regência-Prado stretch is a new challenge for ecologists.

Some knowledge has been achieved about the processes affecting the occurrence of plants in Restingas. It is suggested that colonization of these Quaternary sands by species from mesic environments of the Atlantic forest was enabled by morphological, physiological and ecological adjustments to edaphic severity (Scarano 2006). Such adjustments are manifestations of a diverse genetic richness, perhaps as important as endemisms (Scarano 2006). In addition, the high floristic variation in the Regência-Prado stretch can lead to more diversity in functional aspects, such as those related to facilitation processes already found in Restingas (for instance, those involving nurse species; see Scarano 2009).

Therefore, we recognize the relatively short Regência-Prado stretch as the most relevant region for conservation of Restinga forests in the CCAF. Despite this relevance, there is only one reserve effectively protecting Restinga ecosystems in the Regência-Prado region, the Parque Estadual de Itaúnas (ca. 3,500 ha). Some extensive areas of Restinga with preserved native vegetation are still unprotected, such as along the Degredo Beach, or included in areas of sustainable land use with insufficient surveillance, as in the Caravelas coastal plain. In this way, it is urgent that we improve the protection of Restingas in northern Espírito Santo and southernmost Bahia through systematic conservation planning and controlling land use and through the creation of additional reserves.

Acknowledgments

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Figure 1. Location of 23 sites of Restinga forest in the central part of the Atlantic forest, eastern Brazil. The correspondence between codes and site names can be found in Table 1.

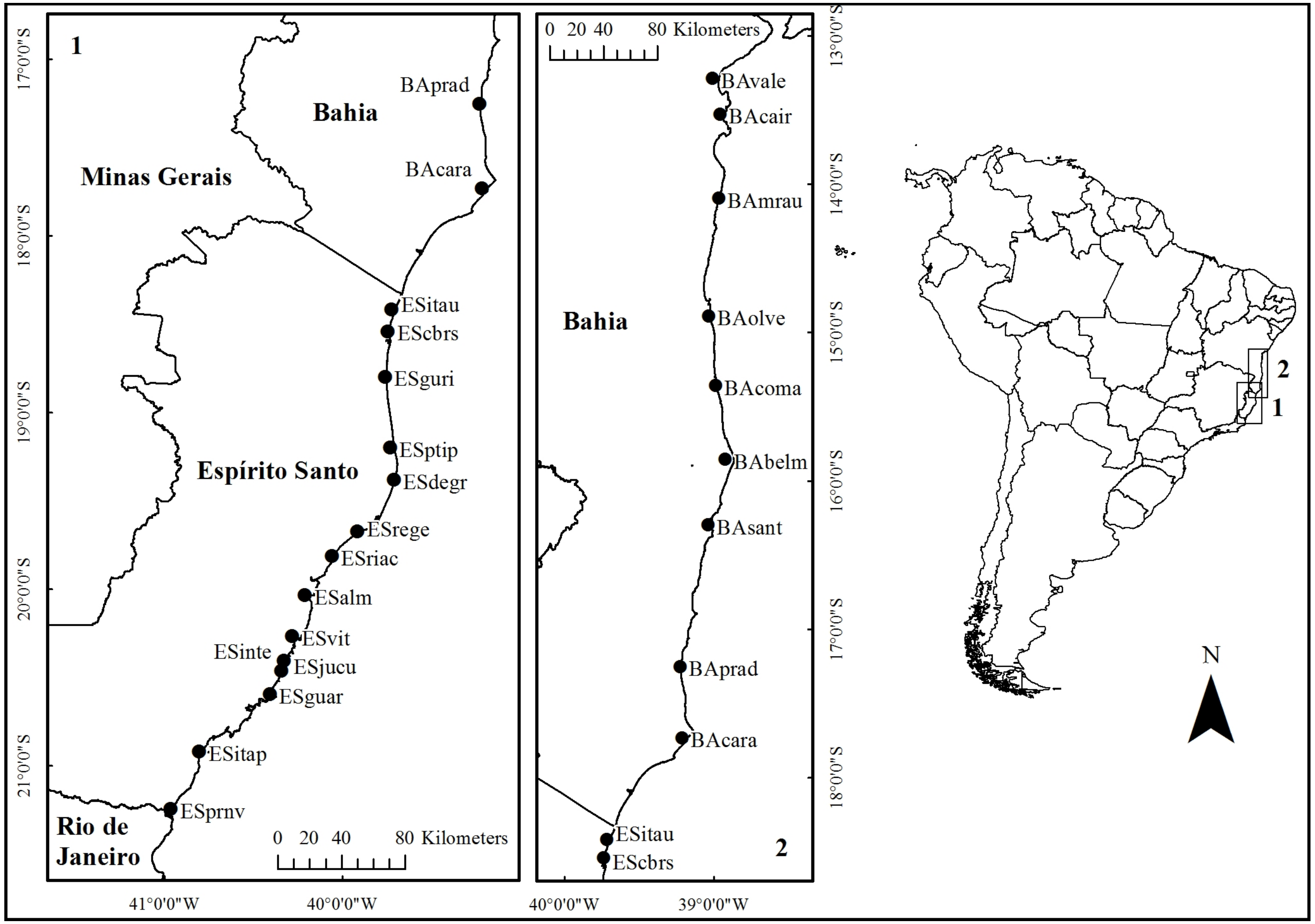

Figure 2. One-dimensional diagram of ordination analysis (NMS) produced from floristic data of 23 sites of Restinga forest in the central part of the Atlantic forest, eastern Brazil. The sites codes are showed in Table 1**.** The symbol size of each Restinga site is proportional to its temperature seasonality value.

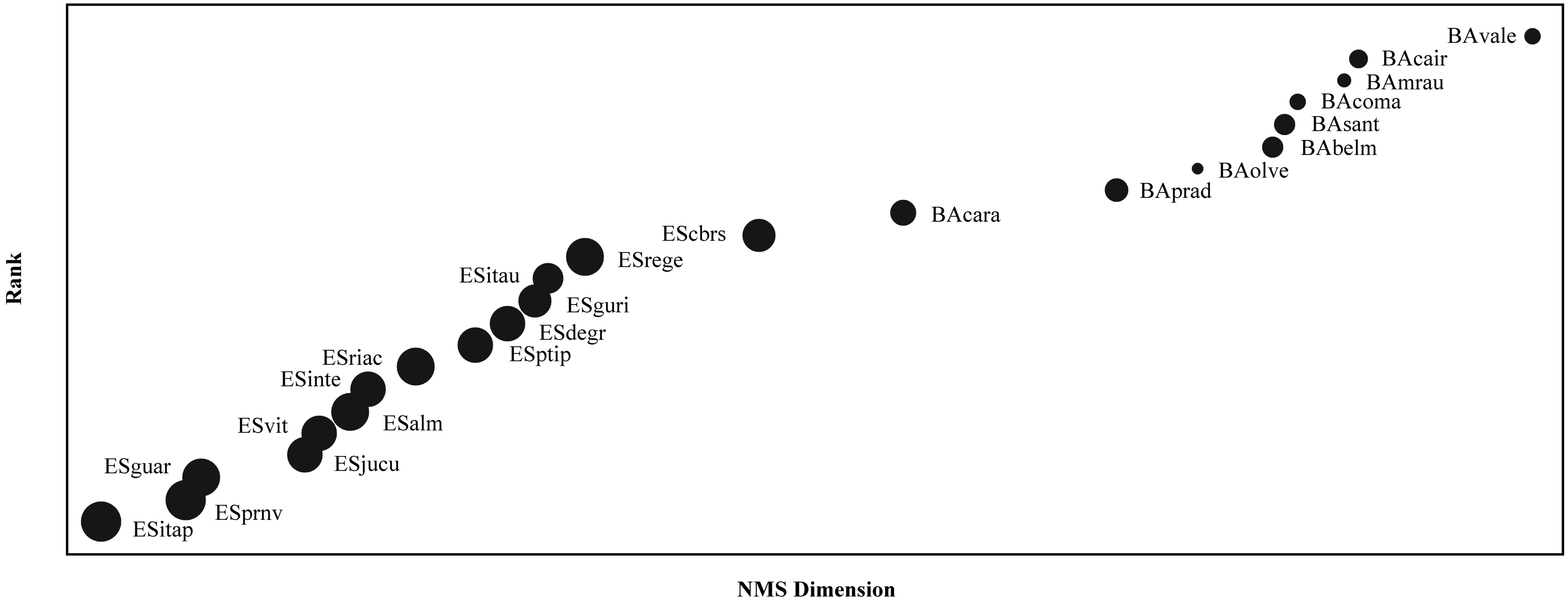

Table 1. Codes, names and geographical coordinates of 23 sites of Restinga forest in the central part of the Atlantic forest, eastern Brazil

Code	**Locality**	**Latitude**	**Longitude**
BAvale	Valença, Bahia	13°17’20”S	39°00’23”W
BAcair	Cairu, Bahia	13°31’40”S	38°57’28”W
BAmrau	Maraú, Bahia	14°05’43”S	38°57’55”W
BAolve	Olivença, Bahia	14°53’19”S	39°01’51”W
BAcoma	Comandatuba, Bahia	15°21’35”S	38°59’02”W
BAbelm	Belmonte, Bahia	15°51’30”S	38°55’21”W
BAsant	Santa Cruz Cabrália, Bahia	16°18’03”S	39°02’09”W
BAprad	Prado, Bahia	17°15’17”S	39°13’29”W
BAcara	Caravelas, Bahia	17°44’05”S	39°12’38”W
ESitau	Itaúnas, Espírito Santo	18°25’13”S	39°43’08”W
EScbrs	Conceição da Barra, Espírito Santo	18°32’40”S	39°44’24”W
ESguri	Guriri, Espírito Santo	18°48’04”S	39°45’25”W
ESptip	Pontal do Ipiranga, Espírito Santo	19°12’08”S	39°43’40”W
ESdegr	Cacimbas-Degredo, Espírito Santo	19°23’09”S	39°42’25”W
ESrege	Regência, Espírito Santo	19°40’45”S	39°54’45”W
ESriac	Barra do Riacho, Espírito Santo	19°48’58”S	40°03’25”W
ESalm	Nova Almeida, Espírito Santo	20°02’19”S	40°12’28”W
ESvit	Vitória, Espírito Santo	20°16’14”S	40°16’45”W
ESjucu	Barra do Jucu, Espírito Santo	20°24’35”S	40°19’32”W
ESinte	Interlagos, Espírito Santo	20°27’56”S	40°20’36”W
Esguar	Guarapari, Espírito Santo	20°35’55”S	40°24’26”W
ESitap	Itapemirim, Espírito Santo	20°55’30”S	40°48’16”W
ESprnv	Praia das Neves, Espírito Santo	21°14’55”S	40°57’57”W

Table 2. Environmental variables most correlated ($r > 0.7$) to one-dimensional solution created from floristic data of 23 sites of Restinga forest in the central part of the Atlantic forest, eastern Brazil.

Climatic variables	**r**	**r^2**
Temperature seasonality	-0.95	0.90
Annual temperature range	-0.93	0.87
Precipitation of coldest quarter	0.92	0.85
Maximum temperature	-0.92	0.84
Precipitation of driest quarter	0.88	0.77
Isotherm	0.87	0.75
Precipitation seasonality	-0.84	0.71
Precipitation of driest month	0.83	0.70
Aridity index	0.82	0.67
Annual precipitation	0.82	0.67
Daily temperature range	-0.82	0.67
Potential evapotranspiration	-0.79	0.63
Actual evapotranspiration	0.79	0.62
Temperature of driest quarter	0.77	0.59
Temperature of wettest quarter	-0.74	0.55
Temperature of warmest quarter	-0.73	0.54

Table S1. Occurrence of species of Fabaceae in Restinga sites along the central part of the Atlantic Forest. Dark cells mean occurrence. Sites within the Regência-Prado stretch are in bold. The correspondence between codes and site names can be found in Table 1.

	BAvale	BAcair	BAmrau	BAolve	BAcoma	BAbelm	BAsant	**BAprad**	**BAcara**	**ESitau**	**EScbrs**	**ESguri**	**Esptip**	**ESdegr**	**ESrege**	ESriac	ESalm	ESvit	ESjucu	ESinte	ESguar	ESitap	ESprnv
Abarema barnebyana													■	■	■								
Abarema brachystachya												■									■		
Abarema cochliacarpos									■														
Abarema filamentosa	■	■	■	■	■	■	■	■	■	■	■	■	■		■								
Abarema jupunba			■		■			■				■		■	■			■			■		
Abarema turbinata	■		■						■														
Acosmium lentiscifolium														■		■					■		
Albizia pedicellaris	■								■		■	■		■		■						■	■
Albizia polycephala									■							■						■	
Andira fraxinifolia		■			■		■		■	■	■	■	■	■	■	■		■	■	■		■	■
Andira legalis																■				■			
Andira nitida	■	■		■		■	■		■	■	■	■				■		■	■	■	■		■
Brodriguesia santosii	■	■		■	■		■																
Chamaecrista aspidiifolia			■	■		■	■	■			■												
Chamaecrista bahiae		■	■		■	■	■	■															
Chamaecrista blanchetii			■					■													■		
Chamaecrista ensiformis	■		■	■	■		■	■		■	■	■	■	■	■	■	■	■	■	■			■
Copaifera lucens																						■	
Exostyles venusta									■							■	■	■	■	■	■	■	
Hymenaea courbaril														■					■	■	■		■
Hymenaea rubriflora											■						■	■	■		■	■	

Hymenolobium alagoanum	■																						
Inga capitata	■	■	■	■	■	■	■	■		■	■	■	■		■			■	■	■	■	■	■
Inga edulis		■	■	■	■	■	■	■	■		■						■		■				
Inga exfoliata										■	■												
Inga hispida									■				■										
Inga ingoides	■	■		■	■	■			■			■											
Inga laurina	■	■		■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	
Inga marginata						■							■										
Inga pleiogyna	■	■	■	■	■	■	■	■					■										
Inga sessilis														■					■				
Inga striata													■	■									
Inga subnuda	■	■				■			■	■	■	■	■	■	■	■	■			■		■	■
Inga suborbicularis									■														
Inga thibaudiana					■											■						■	
Inga vera																							■
Leptolobium bijugum			■	■		■	■	■	■	■	■		■	■	■					■	■		
Leptolobium tenuifolium												■											
Libidibia ferrea														■									■
Lonchocarpus sericeus									■			■		■									
Machaerium incorruptibile																	■				■	■	
Machaerium lanceolatum												■	■						■				■
Macrolobium latifolium	■	■	■	■	■	■	■	■	■	■	■												
Macrolobium rigidum	■		■																				
Melanoxylon brauna											■					■							
Mimosa bimucronata			■		■			■	■														
Moldenhawera blanchetiana		■			■	■																	

Ormosia arborea											■						■						■
Ormosia fastigiata	■																						
Ormosia nitida									■														
Parapiptadenia pterosperma																							■
Piptadenia paniculata																							■
Pseudopiptadenia contorta																■							
Pterocarpus rohrii										■	■		■							■		■	■
Senna affinis												■	■			■	■		■	■	■		
Senna appendiculata									■							■				■		■	■
Senna pendula									■						■		■			■			■
Senna silvestris																■							
Senna splendida																■							
Stryphnodendron pulcherrimum		■	■		■	■	■																
Swartzia apetala		■	■	■		■	■	■	■	■	■	■	■	■	■	■	■	■	■	■		■	■
Swartzia capixabensis																					■		
Swartzia dipetala	■		■	■	■	■																	
Swartzia macrostachya									■														
Swartzia pickelii	■																						
Swartzia simplex									■	■									■				
Tachigali densiflora	■																						
Vatairea heteroptera																						■	
Zollernia glabra										■		■		■	■		■	■	■	■	■	■	■
Zollernia ilicifolia																						■	

Capítulo III – *From evergreen to deciduous tropical forests: how energy-water balance, temperature, and space influence the tree species composition in a high diversity region*

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From evergreen to deciduous tropical forests: how energy-water balance, temperature, and space influence the tree species composition in a high diversity region

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Abstract

Background: Understanding floristic and geographic patterns in one of the highest biodiverse regions in the world – the Atlantic forest of eastern Bahia, Brazil – can identify the drivers of diversity in tropical forests and provide useful information for biological conservation.

Aims: To understand the role of both climate and geographical location on variation in tree species composition in a region characterised by an abrupt transition from wet forests to semi-arid thorn-woodlands. To test whether a regional classification of forests according to elevation belts and leaf flush pattern is consistent with floristic composition.

Methods: We submitted 14,094 tree species occurrence records and 31 geo-climatic variables prepared for 57 sites in eastern Bahia, Brazil, to multivariate and regression analyses and variance partitioning.

Results: Climate and space were both significantly ($P \leqslant 0.05$) contributing to explaining floristic variations. Actual evapotranspiration, duration of water deficit, and minimum temperature of coldest month were the main predictors. Floristic differences were significant except when comparing evergreen lower plains and upper plains forests.

Conclusions: Although distance among sites may play an important role, species composition is chiefly influenced by environmental gradients. This highlights environmental heterogeneity as a key factor in the planning of biodiversity conservation in tropical forests.

Key words: Atlantic forest, phytogeographic patterns, floristic gradient, geo-climatic variables, spatial autocorrelation

Introduction

South American tropical forests are recognised for their high species diversity (Gentry 1988) and some of them are among the most diverse in the world (the Brazilian Atlantic coast (Martini et al. 2007; Thomas et al. 2008; Saiter et al. 2011); the Colombian Chocó (Faber-Langendoen and Gentry 1991); eastern Ecuador (Valencia et al. 1994; Pitman et al. 2002); and the Peruvian Amazon (Gentry 1988)). The high diversity of these regions has been associated to environmental heterogeneity at several spatial scales (e.g. Oliveira-Filho and Fontes 2000; Pitman et al. 2002; Homeier et al. 2010; Hernández et al. 2012).

At a regional scale, variation in tree composition in tropical forests has been related mainly to water and energy availability, and energy-water balance (Oliveira-Filho and Fontes 2000; Pausas and Austin 2001; Qian 2013). Such patterns are based on the physiological requirements of species (Hawkins et al. 2003). Decreasing availability of both water and energy may limit the distribution of a given species because water scarcity directly affects root absorption of minerals, sap transportation, and leaf metabolism, whereas low temperature and low radiation (both energy-related variables) affect not only leaf metabolism but also flowering and fruiting (Grubb 1977). In turn, energy-water balance variables (e.g. potential and actual evapotranspiration), which depend on temperature, solar radiation, water availability in the soil, and properties of the vegetation, summarise the effect of environmental constraints on plant survival and development (Pausas and Austin 2001; Zomer et al. 2007).

The shifts in availability of both water and energy are influenced by several factors across large-scale regional environmental gradients. For instance, water availability gradients are related to surface roughness, distance to large water sources (oceans, inland seas and lakes) and air mass features (Wulf et al. 2010; Qian 2013). On the other hand, energy availability gradients are mainly influenced by both cloudiness and latitudinal shifts in solar radiation (Homeier et al. 2010; Qian 2013). Distance among sampled sites is also an important factor in the floristic relationships among tropical forests, since species dissimilarity generally increases with distance (e.g. Oliveira-Filho and Fontes 2000; Scudeller et al. 2001; Macía et al. 2007). As a result, the modelling of spatial components has been used in recent phytogeographic analyses of tropical forests to improve the interpretation quality of relationships among taxa distribution and their predictors (Legendre and Legendre 2012).

The Atlantic forest of coastal Bahia, Brazil, provides a special opportunity to study the causes of floristic variation in highly biodiverse forests. In this region there is a unique and abrupt transition from evergreen to semideciduous, and then to deciduous forests encompassing plains, hills, and plateaux up to a distance of 200-250 km inland, from the coast (Thomas et al. 2008). This transition ends in the contact zone with the caatinga, a deciduous, thorny and xerophytic vegetation type that covers most of the hinterlands of north-eastern Brazil (Mori and Silva 1979). The forests of eastern Bahia are a high priority region for conservation in the Atlantic forest (Martini et al. 2007; Thomas et al. 2008), which has been recognized as a biodiversity hotspot (Myers et al. 2000).

We analysed an extensive dataset compiled from tree species occurrence records and geo-climatic data for Bahian Atlantic forest sites. Our goal was to address phytogeographic questions of general interest for high diversity tropical regions and for regional planning of forest conservation. Considering the main environmental factors that are related to floristic patterns at regional scales in tropical forests, we expected that both geo-climatic and distance-related variables would be important for proposing phytogeographic hypotheses. Specifically for regional conservation, these questions should provide basis for assessing effectiveness of the current system of conservation through the comparison of totals of protected area among different forest types. Our questions were: [1] Which geo-climatic variables are most strongly correlated with variations in tree species composition across the region from coast to inland? [2] Is variation in tree composition influenced by the spatial proximity of sampled forest sites? [3] Is the existing classification of eastern Bahian forests according to elevation belts and leaf flush pattern consistent with tree species composition?

Materials and Methods

Study region

The study region encompassed the forests of eastern Bahia, Brazil (Figure 1), with the northern limit along the Inhambupe River (latitude 12° S) about 120 km north of Salvador and the southern limit along the Mucuri River (latitude 18° S) near the border of Espírito Santo state. It included part of northeastern Minas Gerais where forests with similar physiognomy to those of southern Bahia are found. According to the updated world map of the Köppen-Geiger climate classification (Peel et al. 2007), the coastal zone of Bahia has a tropical rainforest climate (Af) with monthly precipitation above 60 mm year-round. Farther away from the coast, there is a narrow strip of tropical monsoon climate (Am) and then a zone of tropical wet and dry climate (Aw). In both Am and Aw zones, the monthly rainfall is below 60 mm during the Austral winter months, but in Aw the driest month has precipitation (in mm) less than 100 subtracted of annual rainfall and then divided by 25 (see details in Peel et al. 2007). Table S1 summarises the geo-climatic shifts across eastern Bahia.

The coastal zone comprises a band 50-70 km wide where annual rainfall is around 1600 mm and there is typically no dry season (Thomas and Barbosa 2008). In the Prado region, however, annual rainfall reaches only 1100-1300 mm. Despite this, we considered such a region as a part of the coastal zone because precipitation is regularly distributed year-round. Such climatic conditions allow the growth of evergreen forests that are known for their particularly high levels of plant diversity and endemism (Amorim et al. 2009; Thomas et al. 2008) and have been grouped according to their elevation into lower plains, upper plains, and lower highlands forests (Oliveira-Filho 2009).

The lower plains forests comprise all evergreen forests up to 200 m elevation, regardless of the dominant geomorphology (Oliveira-Filho 2009). Thus, both forests of sedimentary plains originating in the Pliocene (the Barreiras Formation) and forests on low hills from the Proterozoic were included in this type. The upper plains forests cover hills from 200 to 600 m (Oliveira-Filho 2009). In turn, the lower highlands forests cover hills at elevations above 600 m (Oliveira-Filho 2009).

Seasonal forests predominate inland. In the basins of both the Mucuri and Jequitinhonha Rivers, semideciduous forests are found up to 200-250 km away from the coast. Deciduous forests also show their maximum extension in the Jequitinhonha River basin, originally comprising a band 80-100 km wide (Mori and Silva 1979). To the north, the band of seasonal forests is narrower (IBGE 2004), indicating a sharper transition zone to the Caatinga Domain where annual precipitation is less than 800 mm and dry season lasts 5 months or more (Mori and Silva 1979).

Semideciduous forests often grow in areas that receive around 1000 mm of rainfall per year and have a well-defined dry period of over two months (Thomas and Barbosa 2008). Such forests are found at 200-1,000 m, and they are classified by Oliveira-Filho (2009) as upper plains (200-600 m) or lower highlands forests (600-1,000 m).

Deciduous forests receive 800-1000 mm of rainfall per year and generally are adjacent to caatinga vegetation. The dry season can lasts 5-6 months in both the southern Bahian plateau and valley of the Jequitinhonha River (commonly from April to September according to Murta et al. 2005), or three months (from August to October) in the Paraguaçu River basin where rainfall does not exceed 100 mm per month over the rest of the year (Santos and Andrade 2008). The upper plains deciduous forests (200-600 m) are found mainly in the Paraguaçu and Jequitinhonha river valleys. The lower highlands deciduous forests show a greater extension on the southern Bahian plateau where they are called 'matas de cipó' due to the high density of lianas (Mori and

Silva 1979). We also considered in this type all deciduous forests located above 600 m whether or not their physiognomy resembled that of the 'matas de cipó'.

The dataset used

The dataset was composed of a binary matrix of species occurrence and geo-climatic data for 57 sites in the eastern Bahia (see Figure 1 and Table S1 for location of sites). The matrices were extracted from the NeoTropTree database (http://www.icb.ufmg.br/treeatlan/; Oliveira-Filho 2014).

The binary matrix comprised 2002 tree species and 14,094 presence records. The geo-climatic matrix was composed of the forest type code and 31 quantitative variables, including three geographic variables (latitude, longitude and distance to ocean), one topographic (elevation) extracted from HYDRO1k Elevation Derivative Database (US Geological Survey 2012) with spatial resolution of 1 km^2, and 27 climatic variables. Nineteen of these climatic variables were obtained from WorldClim 1.4, including a set of layers with high resolution (1 km^2) organized by Hijmans et al. (2005). Three other variables – potential evapotranspiration, actual evapotranspiration, and an aridity index – were produced by Zomer et al. (2007) from the WorldClim data. The mean duration (in days) and severity of water deficit (amount in mm) were extracted from Walter's diagrams (Walter 1985). The mean frequency of frost (in days) and the percentage of cloud coverage were obtained from Harris (2014). The cloud interception (amount in mm) was created for the NeoTropTree database through a linear regression model with measured points (response variable) and the following predictors: elevation, annual mean temperature, cloud coverage, distance to ocean, and annual mean precipitation. We also incorporated a correction factor in this model which attributed zero to cloud interception of sites below 500 m (Oliveira-Filho 2014).

Data analyses

Presets.

We undertook an initial outlier analysis (McCune and Grace 2002; cut-off of 2.0) and removed three sites: Jequié II (BAjeqc), Maracás II (Bamrcc), and Ipirá (BAipir). We also excluded species with a single occurrence data point since they could not contribute to the ordination patterns (Lepš and Šmilauer 2003). Thus, the final matrix comprised 54 sites, 1559 species, and 13,297 occurrence records.

Correlations among floristic gradients and geo-climatic variables.

We used Non-metric Multidimensional Scaling (NMS) in PC-ORD 6 (McCune and Mefford 2011) to create axes that could represent the main gradients of species composition within the dataset. The significance of axes was tested through Monte Carlo tests ($P \leqslant 0.05$) and the stress stability was verified through progressive iterations (McCune and Grace 2002).

We undertook correlations *a posteriori* among NMS axes and geo-climatic variables using simple correlations and linear regression models (OLS). We did not use latitude and longitude in the regressions, since the influence of space on floristic gradients was checked through Moran's correlograms and spatial filters (see below). We pre-selected some variables which had clear relationships with floristic patterns along each axis (visual analysis), then we eliminated collinearities, excluding redundant variables with lower explanatory power along each axis.

We considered the existence of collinearity when the variance inflation factor (VIF) of each variable was greater than 10 (e.g., Quinn and Keough 2002). Then we selected the models adopting the best balance between parsimony and accuracy of data description (i.e., lower AICc value; Burnham and Anderson 2002). We confirmed assumptions of the models following Eisenlohr (2013, 2014). Specifically, for normality of residuals we used the D'Agostino test.

Since spatial structure in both response variables and predictors can inflate the Type I error (Peres-Neto and Legendre 2010), we also prepared correlograms for the predictors of each OLS model, regardless of residuals independence assumption (Landeiro and Magnusson 2011). Correlograms were created by the software SAM 4.0 (Rangel et al. 2010) adopting Moran's I coefficient (Legendre and Fortin 1989) and followed the default options. We tested the global significance of correlograms using Bonferroni's sequential correction, and confirmed the existence of spatial structure when at least one distance class was significant (Fortin and Dale 2005). As we found spatial structure in all variables, we also prepared spatial models to confirm the significances found. These models were built through the addition of MEM spatial filters (Moran's Eigenvector Maps; Dray et al. 2006), which were created by the 'spacemakeR' package and selected progressively (Blanchet et al. 2008) by the package 'packfor' in R (R Development Core Team 2011). We created the MEMs from a matrix of Delaunay's triangular connectivity, including weighing ‘min-max’ to intensiveness of connection in the calculation of the matrix-product (Borcard et al. 2011). Since the significance of these models was supported, we opted to show the results of the simplest models, i.e., without inclusion of MEMs.

Aiming to evaluate the gradients of species composition as a function of geographic distance, we verified the spatial structure of scores of each significant axis of NMS also through Moran's I correlograms.

Differentiation of forest types.

We evaluated the distinction among forest types through ANOVA permutation-based with gradients scores (NMS axes 1 and 2) as response variables, and then Tukey's *post hoc* test adapted for unequal samples (Smith 1971) when the F test was significant. The spatial structure of ANOVAs was considered through the addition of MEM spatial filters, which were created as previously described for OLS models. The fraction that was explained by the treatment (i.e. the forest type) was partitioned out from the explained fraction by selected MEMs with the aim of controlling the inflation of Type I error (Peres-Neto and Legendre 2010). In the *post hoc* tests, the selected MEMs were held as covariables. We followed the R script provided by Eisenlohr (2014).

Variance partitioning.

Following the protocol suggested by Eisenlohr (2014), based on references such as Peres-Neto and Legendre (2010) and Legendre and Legendre (2012) and using the packages 'vegan', 'spacemakeR', 'packfor', and 'spdep' in R (R Development Core Team 2011), we undertook a partitioning of the explanation provided by: [a] only climatic variables + elevation, [b] the spatially structured fraction of climatic variables + elevation, [c] only spatial components, and [d] unmeasured factors.

The occurrence data were Hellinger-transformed (Legendre and Gallagher 2001) and both environmental variables and MEMs were forward-selected in separate models. Environmental variables were standardised by the adjustment to standard deviation (McCune and Grace 2002). We then processed two Canonical Redundancy Analyses (RDAs), the first involving species and environment, and the second involving environment and space (MEMs). This allowed us to partition the floristic variance (R^2 adjusted) among the four fractions mentioned above. We also tested the significance of pure fractions [a] and [c] by ANOVA permutation-based.

Results

Correlations among floristic gradients and geo-climatic variables

The NMS provided a two-dimensional solution (Figure 2), with final stress value of 15.31. Axes 1 and 2 explained, respectively, 62.7% and 16.9% of the variation. The most correlated variables ($r > 0.6$) with the NMS axes are shown in Table 1.

Axis 1 was related to an energy-water gradient since the most correlated climate-related variable with such an axis was actual evapotranspiration ($r = -0.79$). Axis 2 represented a thermal gradient following elevation changes because the most correlated variables were minimum temperature of coldest month ($r = 0.70$) and elevation ($r = -0.69$).

The best model created with axis 1 scores (r^2 adjusted = 0.65; F = 49.39; $P < 0.001$) had actual evapotranspiration and water deficit duration as predictors. The best model for axis 2 (r^2 adjusted = 0.49; F = 49.47; $P < 0.001$) had minimum temperature of coldest month as sole predictor.

Differentiation of forest types

The ANOVA indicated significant differences among forest types in ordination axis 1 (F = 64.83; $P < 0.001$) and axis 2 (F = 10.82; $P < 0.001$). The results of the Tukey's *post hoc* test showed that differences were significant among all forest types at least on one axis, except between evergreen lower plains and upper plains forests (Table 2).

Variance partitioning

The fractions of variance partitioning were significant ($P < 0.01$) for both climate and space, although the former explained a greater fraction of variance (Figure 3). The variance explained by the shared fraction between climate and space was greater than the individual fractions; the unexplained fraction was high (78.4%).

Discussion

Our results indicated that tree species distribution in eastern Bahia is strongly influenced by evapotranspiration levels and water deficit duration, both closely related to changes in precipitation from the Atlantic coast to inland areas. From coast to inland, evapotranspiration levels tend to decrease due to water deficit during the dry season, which induces deciduousness in vegetation. In the coastal zone itself, however, the sites do not have a typical dry season, comparable to that in the inland zone. There, the wetter climate allows water storage in the soil, maintaining the evergreen forests and leading to high evapotranspiration levels.

Even in the coastal sites where the annual rainfall is lower (i.e. Prado, 1121 mm; Itamaraju, 1113 mm; Teixeira de Freitas, 1048 mm; Eunápolis, 1146 mm; Serra da Jibóia, 1179 mm; Wenceslau Guimarães, 1191 mm; Camacan, 1098 mm; and Santa Maria do Salto, 1020 mm), the evapotranspiration commonly reaches levels above 900 mm year^{-1}. The absence of significant differences in species composition between evergreen lower plains and upper plains forests can be justified by the resemblances of actual evapotranspiration among their sites. Indeed, sites of evergreen upper plains forests had tree compositions strongly related to those of evergreen lower plains forests sites. These include Ibirapitanga and Nazaré (1120-1160 mm year^{-1}), Uruçuca, Ilhéus and Canavieiras (1230-1270 mm year^{-1}), and Eunápolis, Itamaraju, and Prado (950-960 mm year^{-1}).

We noticed that changes in climatic conditions following an elevation gradient also contribute to floristic differentiation between forests sites in eastern Bahia. This pattern was not surprising, because it has also been reported for other sites in north-eastern (Ferraz et al. 2004) and south-eastern Brazil (Oliveira-Filho and Fontes 2000; Scudeller et al. 2001), northe-astern Ecuador (Homeier et al. 2010), the Peruvian Amazonia (Gentry 1988), and the Venezuelan Guayana Shield (Hernández et al. 2012).

Elevation is intrinsically correlated with geophysical factors that directly affect plant growth, among them wind, air humidity, solar radiation and temperature (Grubb et al. 1977; Körner 2007). Although we did not consider in our analyses all environmental factors under the influence of elevation, the best model created for axis 2, with minimum temperature of coldest month being a predictor, indicates that in the study region tree species composition is in part determined by thermal variation along elevation gradients. This condition corroborates reviews about the influence of temperature on structure and composition of vegetation (Grubb et al. 1977; Pausas and Austin 2001; Hawkins et al. 2003).

In fact, the differences in tree composition were significant between lower plains or upper plains and lower highlands forests. Lower highlands forests of eastern Bahia have some genera typical of Neotropical mountains that are adapted to ‘cold’ climates (e.g. *Clethra*, *Drimys*, *Hedyosmum*, *Ilex*, *Laplacea*, *Meliosma*, *Meriania*, *Myrceugenia*, *Prunus*, *Roupala*, and *Weinmannia*; Amorim et al. 2009; Rocha and Amorim 2012), and do not show high species richness of Euphorbiaceae, Fabaceae and Sapotaceae such as that can be found in lower plains and upper plains forests (Amorim et al. 2005; Amorim et al. 2008). In this sense, low temperature is crucial for survival of cold-adapted species in the lower highlands of eastern Bahia, and the persistence of such taxa there tells us part of an interesting biogeographic history of the Atlantic forest.

Besides, floristic studies in the eastern Bahia have reported many new, endemic plant species at elevations above 600 m (Martini et al. 2007; Amorim et al. 2009; Leme and Kollman 2011). However, it is alarming that of the total of protected area in such a region (ca. 230,000 ha whether areas of both governmental and private reserves and parks are incorporated; see data at http://www.icmbio.gov.br/), around 60% is in lower plains or upper plains of the coastal zone. Remnants of all other forest types, especially the lower highlands forests, remain largely endangered. This is a critical hurdle for conservation in one of the most diverse regions in the world.

In the inland zone, we also noticed that rainfall distribution pattern together with temperature and relief influenced the features of transition among seasonal forests and the caatinga vegetation. Deciduous forests cover a large area on the southern Bahian plateau where the transition to the caatinga is probably abrupt due to a sharp increasing in both temperature and water deficit following the decreasing in elevation northwestward (from 900 to 400 m). On the other hand, the transition in the valley of the Paraguaçu River is characterised by a mosaic of shrubby caatinga occupying lower, warmer areas, and seasonal forests covering hills at higher elevation (around 500 m) where temperatures are lower, thereby diminishing water deficit. Examples of this sort of transition were reported by Cardoso and Queiroz (2008) in the 'Serra do Orobó' (Itaberaba and Ruy Barbosa sites) and Cardoso et al. (2009) in the 'Serra da Fazenda Retiro' (Feira de Santana site). In the Serra do Orobó, the seasonal forests occur at 450 m and above, and a shrubby caatinga covers areas at lower elevation. In the Serra da Fazenda Retiro, a dense caatinga occurs up to 250 m and seasonal forests reach the hilltop at about 500 m. Cardoso and Queiroz (2008) and Cardoso et al. (2009) also reported that the seasonal forests in that region have a stronger relationship with the flora of the Atlantic forest domain than with the caatinga flora, which has only spotty representation (such as the presence of *Cavanillesia umbellata*).

The transitional mosaic between the Atlantic forest and Caatinga domains also encompasses areas immediately to the south of the Paraguaçu River, in the Jequiriçá River basin. According to Carvalho-Sobrinho and Queiroz (2005), caatinga vegetation can be found at the base of the Serra da Jibóia, while evergreen forest generally occupies slopes from 400 to 800 m. This contrasting situation can be explained by both diminishing temperature and meteorological events, such as orographic precipitation and fog formation, which increase humidity on slopes.

Records provided by Barbosa et al. (2009) regarding the diversity of fungi associated with litter from *Clusia* species in the Serra da Jibóia, indicated that substantial changes in diversity were related to fog created by humid coastal winds. Thus, increasing humidity is probably an additional effect of elevation in the inland zone. Amorim et al. (2005) and Thomas et al. (2009) described differences in vegetation structure and plant species composition along a gradient from 350 to 750 m in the Serra do Teimoso (Jussari site). According to these studies, semideciduous forests occur at lower elevation (350-550 m) due to a hotter and dryer climate, while at elevations above 600 m, cooler and more humid conditions allowed the establishment of an evergreen forest. A similar gradient exists in the Alto Cariri region (Santa Maria do Salto and Guaratinga sites) where typical semideciduous forests are replaced by evergreen forests at around 800 m. The greater humidity in this region maintains assemblages of bromeliads with a high percentage of endemic species (Leme and Kollman 2011).

In agreement with the aforementioned examples, the usual classification of sites using leaf flush pattern was supported by distinct sets of species for evergreen, semideciduous, and deciduous forests. On the other hand, the classification based on elevation belts was not fully consistent with floristic data because evergreen forests below 600 m had apparently similar tree compositions. This reveals that the distinction of evergreen lower plains and upper plains forests is too subtle for our methods to resolve.

The discussions up to this point demonstrate the influence of climate and elevation on tree species distribution along a transition from moist to seasonal forests. Indeed, the fractions of floristic variation explained by climate plus elevation and by the spatially structured component of climate and elevation exceeded the fraction explained purely by space. However, the individual fraction of space was also significant and we assumed that it was not overestimated because an extensive and suitable set of environmental predictors has been used. In this way, we suggest that the distribution of tree species in eastern Bahia could be determined in part by their limited dispersal.

The high unexplained fraction of floristic variation can be attributed to undetermined residuals related to variables not included in the analyses. For example, we chose not to use soil variables here because studies (e.g. Homeier et al. 2010; Hernández et al. 2012) reported the importance of soil variables for plant distribution only at scales finer than the radius of 5 km adopted by NeoTropTree sampling units (Oliveira-Filho 2014). We did not use variables related to disturbance regime and biological interactions, since these processes are poorly known in tropical regions (Zimmermann et al. 2010). In turn, it has been hypothesised that historical processes influenced the current floristic composition in Bahian forests. For instance, disjunct patterns in spatial distribution of 7% of plant species found in the evergreen forest of the 'Reserva Biológica de Una' (see a floristic list provided by Amorim et al. 2008, which includes tree species) offer support for the hypothesis of a historical bridge between Amazonia and the Atlantic forest through gallery forests within the northeast-southwest corridor of open vegetation formations of central Brazil (Oliveira-Filho and Ratter 1995).

However, the high percentage of uncertainty does not invalidate the explanatory power of the predictors, because we used two complementary approaches in our statistical analyses: (1) regression models, based on summarised floristic variance in NMS axes, and (2) the overall floristic variation captured by variance partitioning analysis. This second approach indicated the statistical significance ($P \leqslant 0.05$) of environmental and spatial factors. Regression models also showed clear relationships among some environmental gradients and tree species distribution. It is clear, therefore, that environmental and spatial components constitute significant predictors, that environment spatially structured is crucial for explaining floristic variation, and that new investigations on tree composition should complement these results, testing the predictive power of other variables, such as those above mentioned.

Such discussions, although performed in the context of eastern Bahia forests, could be extrapolated to other tropical regions with high diversity. Therefore, focusing on the importance of environmental gradients for floristic variation, we could indicate environmental heterogeneity as a key factor in the planning of biodiversity conservation in tropical forests. As we mentioned, parks and reserves are not suitably distributed among all forest types along environmental gradients in eastern Bahia, suggesting that some ecosystems, as well as endemic species, have not been sufficiently protected. This is certainly a critical problem for conservation in most of tropical regions, and it should be part of debates for amelioration in systems of protected lands. Particularly in eastern Bahia, the need of increment in number of parks or reserves is distressing. It remains only 11-12% of natural forests, which originally covered around 160,000 km^2 according our estimates using data provided by Fundação SOS Mata Atlântica and INPE (2015), and no more than 1.5% of them have been effectively protected. Unfortunately, this situation is common in biodiversity hotspots and it is expected that scientific efforts, such as that here presented, may support wiser strategies for the global biodiversity conservation.

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Table S1. Codes, names, and general geo-climatic features of 57 sites distributed for forest types in eastern Bahia, Brazil. Dist Ocean, distance to ocean (km); TempAnn, mean annual temperature (°C); PrecAnn, mean annual precipitation (mm); PET, potential evapotranspiration (mm); AET, actual evapotranspiration (mm).

Forest type	**Site**	**Site code**	**Latitude**	**Longitude**	**Elevation**	**Dist Ocean**	**TempAnn**	**PrecAnn**	**PET**	**AET**
Evergreen lowland forest	Santo Amaro	BAamar	12°36’51”S	38°46’25”W	180	8	24,1	1610	1435	1126
	Pituaçu	BApitu	12°57’17”S	38°25’05”W	29	2	24,9	1711	1336	1082
	Nazaré	BAnaza	13°01’53”S	39°02’33”W	106	24	24	1540	1325	1119
	Nilo Peçanha	BAnilo	13°37’48”S	39°09’09”W	144	20	23,7	2066	1271	1266
	Camamu	BAcama	14°01’45”S	39°07’09”W	85	18	24,4	2241	1276	1275
	Itacaré	BAfaze	14°20’56”S	39°04’24”W	131	8	24	2049	1265	1259
	Ilhéus	BAilhe	14°46’51”S	39°05’01”W	103	3	24,5	1815	1272	1262
	Itabuna	BAitab	14°53’51”S	39°15’59”W	157	26	23,8	1368	1298	1153
	Una	BAuna	15°10’31”S	39°05’42”W	69	10	23,2	1304	1320	1262
	Canavieiras	BAcana	15°40’08”S	39°06’21”W	21	18	24,1	1571	1372	1273
	Porto Seguro	BAport	16°21’11”S	39°08’34”W	87	12	24	1501	1379	1201
	Monte Pascoal	BAmont	16°52’48”S	39°20’31”W	98	21	24,5	1241	1440	1062
	Prado	BAprdo	17°05’30”S	39°15’56”W	69	8	24,4	1121	1416	955
	Teixeira de Freitas	BAteix	17°36’22”S	39°40’38”W	103	45	24,6	1048	1442	891
	Caravelas	BAcrvl	17°47’00”S	39°34’40”W	54	23	24,4	1372	1421	1166
	Serra da Jibóia	BAjibo	12°50’32”S	39°28’27”W	590	72	21,1	1179	1229	809

Evergreen submontane forest	Wenceslau Guimarães	BAwenc	13°35’11”S	39°44’47”W	598	83	20	1191	1261	936
	Ibirapitanga	BAibta	13°53’23”S	39°27’43”W	511	51	22,2	1539	1226	1162
	Itamari	BAitam	13°53’46”S	39°42’33”W	524	78	22,1	1448	1252	1128
	Uruçuca	BAuruc	14°29’24”S	39°06’24”W	358	8	23,5	1874	1240	1228
	Eunápolis	BAeuna	16°25’34”S	39°39’39”W	215	63	24	1146	1490	957
	Itamaraju	BAitju	17°10’33”S	39°50’14”W	201	66	24,6	1113	1520	953
Evergreen montane forest	Barro Preto	BAbprt	14°46’19”S	39°32’05”W	787	51	20,4	1260	1264	1065
	Arataca	BAarat	15°09’53”S	39°19’53”W	906	36	19,6	1299	1231	1084
	Camacan	BAcamc	15°22’55”S	39°34’30”W	929	64	19,7	1098	1279	961
	Santa Maria do Salto	MGsmst	16°21’51”S	40°01’36”W	839	99	21,5	1020	1444	885
Semideciduous submontane forest	Alagoinhas	BAalag	12°01’34”S	38°25’14”W	265	71	22,8	1257	1421	1012
	Jussari	BAjuss	15°09’51”S	39°28’02”W	442	51	22,3	1199	1328	996
	Itapetinga	BAitpt	15°02’26”S	40°21’25”W	467	143	23,1	941	1473	818
	Itapebi	BAitap	15°55’09”S	39°38’19”W	432	76	23,2	983	1403	859
	Guaratinga	BAguar	16°35’42”S	39°55’03”W	338	84	24,2	984	1553	848
	Águas Formosas	MGagfo	17°04’54”S	40°51’18”W	431	175	23,7	983	1644	838
	Machacalis	MGmach	17°09’17”S	40°36’10”W	371	143	24	1025	1614	907
	Nanuque	MGnanu	17°49’56”S	40°16’51”W	224	124	24	981	1550	834
	Teófilo Otoni	MGteof	17°50’03”S	41°34’12”W	558	210	22,5	1112	1625	945
Semideciduous montane forest	Maracás I	BAmara	13°28’05”S	40°17’21”W	853	147	19,7	755	1280	648
	Jequié I	BAjeqm	13°56’58”S	40°06’50”W	718	122	20,4	861	1304	735

	Bandeira-Macarani	MGband	15°46’49”S	40°31’11”W	876	160	20,9	942	1460	879
	Almenara	MGalm	16°03’27”S	40°50’40”W	848	191	21,5	973	1511	829
	Jequitinhonha	MGjqnh	16°07’37”S	41°03’53”W	904	209	21,2	948	1499	803
	Joaíma	MGjoai	16°38’19”S	41°13’14”W	891	216	21,1	932	1546	796
	Ladainha	MGlada	17°36’51”S	41°46’41”W	666	235	21,9	1052	1646	891
Deciduous sub-montane forest	Serra Preta	BAsrpr	12°09’13”S	39°21’47”W	524	95	21,6	701	1349	636
	Angüera	BAangu	12°09’45”S	39°11’09”W	467	124	22	759	1362	672
	Feira de Santana	BAfeir	12°18’58”S	38°58’02”W	214	53	23,5	928	1404	788
	Itaberaba	BAitbr	12°28’49”S	40°22’03”W	600	182	21,9	727	1515	606
	Salto da Divisa	MGsdiv	16°03’29”S	40°02’29”W	225	113	24,6	808	1582	683
	Jacinto	MGjaci	16°11’30”S	40°18’12”W	283	140	24,6	806	1642	684
Deciduous montane forest	Ipirá	BAipir	12°09’02”S	39°41’37”W	646	158	21,5	716	1378	623
	Ruy Barbosa	BArbrb	12°22’33”S	40°31’07”W	641	195	21,8	706	1502	590
	Maracás II	BAmrcc	13°25’43”S	40°31’26”W	884	169	19,9	687	1362	608
	Jequié II	BAjeqc	13°48’31”S	40°20’38”W	650	145	21,5	687	1362	608
	Boa Nova-Poções	BAboan	14°23’52”S	40°08’55”W	830	120	19,2	773	1405	627
	Vitória da Conquista	BAvito	14°50’46”S	40°43’47”W	950	180	19,8	723	1407	612
	Cândido Sales	BAcand	15°10’39”S	41°12’04”W	870	235	20,9	810	1490	680
	Ninheira	MGninh	15°23’37”S	41°34’39”W	829	266	21,2	882	1548	739
	Pedra Azul	MGpedr	15°57’16”S	41°18’03”W	731	235	21,7	902	1554	780

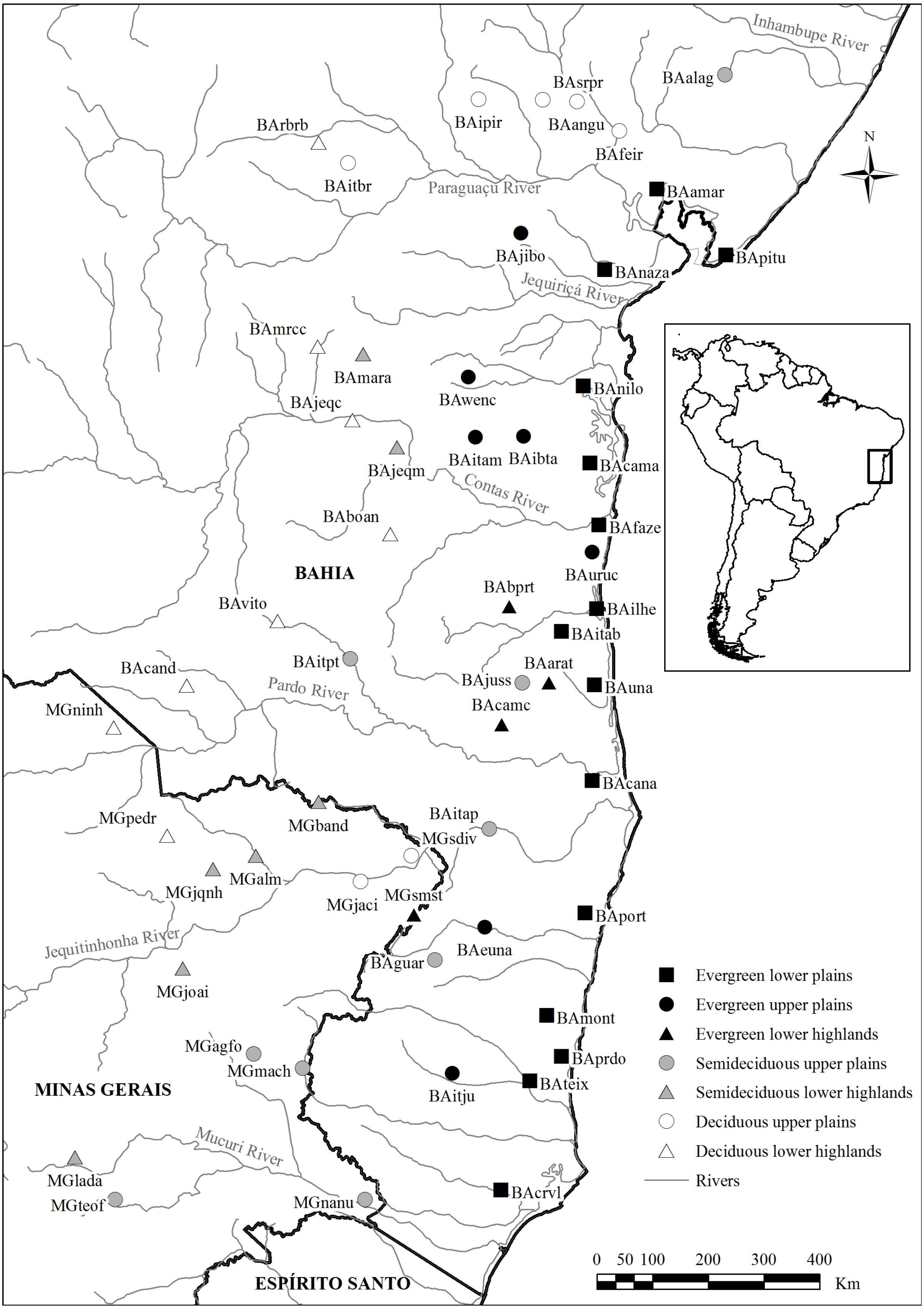
Table 1. Geo-climatic variables most correlated ($r > 0.6$) to NMS axes created from floristic data of 54 sites in eastern Bahia, Brazil. Bold numbers are correlation values of pre-selected variables for construction of linear models. Variables were pre-selected by excluding redundant variables with lower explanatory power along each axis.

	Axis 1		**Axis 2**	
Geo-climatic variables	**r**	**r^2**	**r**	**r^2**
Elevation	0.40	0.16	**-0.69**	**0.48**
Distance to ocean	**0.64**	**0.41**	-0.44	0.19
Minimum temperature of coldest month	-0.50	0.25	**0.70**	**0.49**
Mean temperature of driest quarter	-0.39	0.15	**0.65**	**0.42**
Mean temperature of coldest quarter	-0.41	0.16	0.62	0.38
Annual precipitation	-0.71	0.50	0.36	0.13
Precipitation of driest month	-0.73	0.53	0.29	0.08
Precipitation of driest quarter	**-0.74**	**0.54**	0.34	0.12
Precipitation of coldest quarter	-0.60	0.36	0.50	0.25
Duration of water deficit	**0.65**	**0.42**	-0.17	0.03
Cloud interception	0.09	0.01	**-0.64**	**0.41**
Actual evapotranspiration	**-0.79**	**0.63**	0.25	0.06
Aridity index	**-0.70**	**0.48**	0.35	0.12

Table 2. Differences among averages of scores of ordination axes for seven forest types (*sensu* Oliveira-Filho 2009) in eastern Bahia, Brazil. Letters superscripted indicate differences by Tukey's test adapted for unequal samples ($P \leqslant 0.05$).

Forest types	**Axis 1**	**Axis2**
Evergreen lower plains forests	-0.64^{a}	0.33^{a}
Evergreen upper plains forests	-0.72^{a}	0.08^{a}
Evergreen lower highlands forests	-0.78^{a}	-0.91^{b}
Semideciduous upper plains forests	0.10^{b}	0.07^{a}
Semideciduous lower highlands forests	0.37^{c}	-0.41^{b}
Deciduous upper plains forests	1.52^{d}	0.44^{a}
Deciduous lower highlands forests	1.16^{d}	-0.39^{b}

Figure 1. Study region of the vegetation in the eastern Bahia, Brazil. BAalag, Alagoinhas; BAangu, Anguera; BAamar, Santo Amaro; BAarat, Arataca; BAboan, Boa Nova-Poções; BAbprt, Barro Preto; BAcama, Camamu; BAcamc, Camacan; BAcana, Canavieiras; BAcand, Cândido Sales; BAcrvl, Caravelas; BAeuna, Eunápolis; BAfaze, Itacaré; BAfeir, Feira de Santana; BAguar, Guaratinga; BAibta, Ibirapitanga; BAilhe, Ilhéus; BAipir, Ipirá; BAitab, Itabuna; BAitam, Itamari; BAitap, Itapebi; BAitbr, Itaberaba; BAitju, Itamaraju; BAitpt, Itapetinga; BAjeqm, Jequié I; BAjeqc, Jequié II; BAjibo, Serra da Jibóia; BAjuss, Jussari; BAmara, Maracás I; BAmont, Monte Pascoal; BAmrcc, Maracás II; BAnaza, Nazaré; BAnilo, Nilo Peçanha; BApitu, Pituaçu; BAport, Porto Seguro; BAprdo, Prado; BArbrb, Ruy Barbosa; BAsrpr, Serra Preta; BAteix, Teixeira de Freitas; BAuna, Una; BAuruc, Uruçuca; BAvito, Vitória da Conquista; BAwenc, Wenceslau Guimarães; MGagfo, Águas Formosas; MGalm, Almenara; MGband, Bandeira-Macarani; MGjaci, Jacinto; MGjqnh, Jequitinhonha; MGjoai, Joaíma; MGlada, Ladainha; MGmach, Machacalis; MGnanu, Nanuque; MGninh, Ninheira; MGpedr, Pedra Azul; MGsdiv, Salto da Divisa; MGsmst, Santa Maria do Salto; MGteof, Teófilo Otoni.


Inhambupe River
BAalag
BAsrpr
BAipir
BAangu
BArbrb
BAfeir
BAitbr
Paraguaçu River
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BAjibo
BApitu
BAnaza
Jequiriçá River
BAmrcc
BAmara
BAwenc
BAnilo
BAjeqc
BAitam
BAibta
BAjeqm
BAcama
Contas River
BAboan
BAfaze
BAuruc
BAHIA
BAbprt
BAvito
BAilhe
BAitab
BAitpt
BAarat
BAcand
Pardo River
BAjuss
BAuna
MGninh
BAcamc
BAcana
MGpedr
MGband
BAitap
MGsdiv
MGalm
MGjqnh
MGjaci
MGsmst
BAport
Jequitinhonha River
BAeuna
BAguar
MGjoai
Evergreen lower plains
Evergreen upper plains
Evergreen lower highlands
Semideciduous upper plains
Semideciduous lower highlands
Deciduous upper plains
Deciduous lower highlands
Rivers
BAmont
MGagfo
BAprdo
MGmach
BAteix
MINAS GERAIS
BAitju
Mucuri River
MGlada
MGteof
MGnanu
BAcrvl
0 50 100 200 300 400
Km
ESPÍRITO SANTO

Figure 2. Diagram of ordination analysis (NMS) produced from floristic data of 54 sites in eastern Bahia, Brazil. Symbol legend is available in Figure 1. Elev, elevation; DistOce, distance to ocean; TempMin, minimum temperature of the coldest month; TempDry, mean temperature of the driest quarter; TempCold, mean temperature of coldest quarter; PrecAnn, annual precipitation; PrecDryP, precipitation of driest month; PrecDryQ, precipitation of driest quarter; PrecCold, precipitation of coldest quarter; WaterDef, duration of water deficit; CloudItc, cloud interception; AET, actual evapotranspiration; AridI, aridity index.

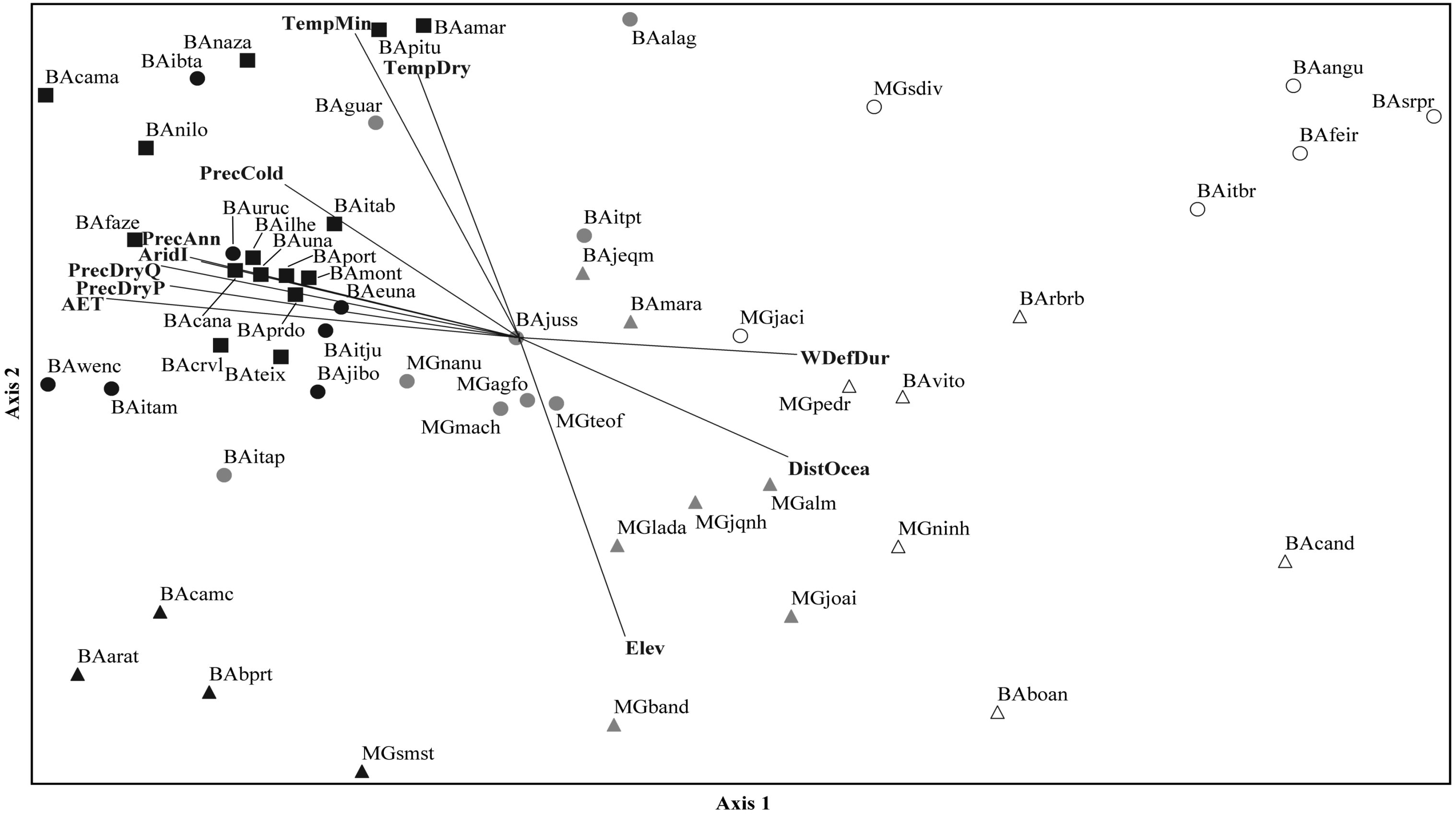
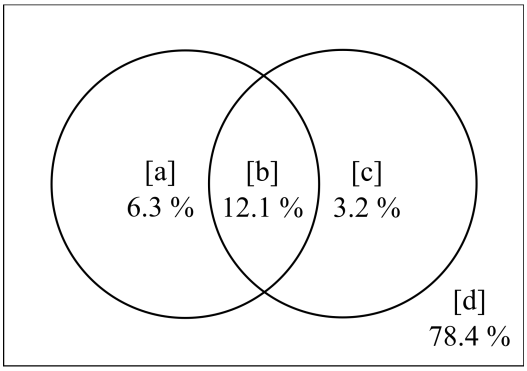


Figure 3. Venn diagram showing the variance partitioning for [a] climatic variables + elevation only, [b] the spatially structured fraction of climatic variables + elevation, [c] spatial components only, and [d] unmeasured factors



Capítulo IV – *Floristic units and their predictors unveiled in part of the Atlantic Forest hotspot: implications for conservation planning*

Felipe Zamborlini Saiter, Pedro V. Eisenlohr, Glauco Santos França, João Renato Stehmann, William Wayt Thomas & Ary Teixeira de Oliveira-Filho

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Floristic units and their predictors unveiled in part of the Atlantic Forest hotspot: implications for conservation planning

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Keywords: Phytogeographic patterns, environmental gradients, spatial autocorrelation, Doce River basin

Running Title: Floristic units in the Atlantic Forest

Academy section: Biological Sciences

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Abstract

We submitted tree species occurrence and geoclimatic data from 59 sites in a river basin in the Atlantic Forest of southeastern Brazil to ordination, ANOVA, and cluster analyses with the goals of investigating the causes of phytogeographic patterns and determining whether the six recognized subregions represent distinct floristic units. We found that both climate and space were significantly ($p \leq 0.05$) important in the explanation of phytogeographic patterns. Floristic variations follow thermal gradients linked to elevation in both coastal and inland subregions. A gradient of precipitation seasonality was found to be related to floristic variation up to 100 km inland from the ocean. The temperature of the warmest quarter and the precipitation during the coldest quarter were the main predictors. The subregions Sandy Coastal Plain, Coastal Lowland, Coastal Highland, and Central Depression were recognized as distinct floristic units. Significant differences were not found between the Inland Highland and the Espinhaço Range, indicating that these subregions should compose a single floristic unit encompassing all interior highlands. Because of their ecological peculiarities, the ferric outcrops within the Espinhaço Range may constitute a special unit. The floristic units proposed here will provide important information for wiser conservation planning in the Atlantic Forest hotspot.

Introduction

The patterns of geographic distribution of plant taxa are directed by a complex set of variables and interrelationships (Rizzini 1997). Among these, climatic variables deserve to be highlighted in mesoscale approaches because, in several studies, they are indicated as the main predictors of phytogeographic patterns (e.g., Engelbrecht et al. 2007, Oliveira-Filho et al. 2005, Scudeller et al. 2001).

Climatic variables, especially those related to temperature and precipitation, are important because they directly influence plant development and are responsible for floristic changes along gradients (Grubb et al. 1977, Pausas and Austin 2001). Precipitation gradients are quite complex and are influenced by factors such as surface roughness, distance to large water sources (oceans, inland seas and lakes) and air mass features (Wulf et al. 2010). The equally complex temperature gradients are linked to latitudinal changes in solar radiation (Breckle 2002, Kessler et al. 2011) and altitudinal changes in air pressure, humidity, and cloud cover (Körner 2007, Homeier et al. 2010).

Geographic location is also a relevant factor in floristic relationships among sites because floristic similarity is likely to increase with the spatial proximity (e.g., Scudeller et al. 2001, Oliveira-Filho et al. 2005, White and Hood 2004). Because of this, recent studies (e.g., Chain-Guadarrama et al. 2012, Gasper et al. 2013) have added spatial filters in statistical analyses to minimize the effect of spatial autocorrelation on the interpretation of the relationship among species distributions and environmental variables (Eisenlohr 2013, Legendre and Legendre 2012, Zimmermann et al. 2010).

In the Atlantic Forest of southeastern Brazil, a region with high diversity and endemism (França and Stehmann 2013, Rolim et al. 2006, Saiter et al. 2011), phytogeographic studies indicate that changes in tree composition are related to at least three major climatic gradients: a coastal-inland gradient of precipitation seasonality (Oliveira-Filho and Fontes 2000, Oliveira-

Filho et al. 2005, Santos et al. 2011), a latitudinal gradient of temperature (Oliveira-Filho and Fontes 2000, Oliveira-Filho et al. 2005), and an altitudinal gradient of temperature and humidity (Torres et al. 1997, Oliveira-Filho and Fontes 2000, Oliveira-Filho et al. 2005, Bertoncello et al. 2011, Kamino et al. 2008). Such phytogeographic patterns, however, are generalizations for a large and environmentally complex region (see Oliveira-Filho et al. 2005) and it is possible that they do not accurately explain the floristic variation in finer mesoscales. Understanding subregional floristic patterns is still a challenge to elucidate the phytogeography of southeastern Brazil, taking into account that the Brazilian flora, as a whole, remains undercollected (Sobral and Stehmann 2009). Furthermore, policies for forest conservation, such as those related to the creation of parks and reserves, restoration of ecosystems, and sustainable use of natural products, can be more appropriately planned when biological-environmental changes throughout the region are better known (McShea et al. 2014).

Within southeastern Brazil, the Doce River Basin (DRB) is an interesting region for investigating subregional phytogeographic patterns because of its high number of forest inventories and botanical collections. The DRB also shows high environmental heterogeneity, with three coastal subregions (Sandy Coastal Plain, Coastal Lowland, and Coastal Highland) and three inland subregions (Central Depression, Interior Highland, and Espinhaço Range) recognized through geomorphology and climatic features (Cupolillo et al. 2008, Instituto Mineiro de Gestão das Águas 2010, Nascimento et al. 2012).

Our goals were to answer the following questions using floristic and geoclimatic data: [1] Which climatic variables better explain subregional phytogeographic patterns in the DRB? [2] Does spatial proximity among sites influence these patterns? [3] Do the subregions of the DRB deserve to be treated as distinct floristic units? We addressed such questions considering, in particular, the implications for biological conservation in the Atlantic Forest hotspot.

Materials and Methods

Study area

The Doce River Basin (DRB) encompasses approximately 87,000 km^2 in the eastern region of the state of Minas Gerais and the central and northern portions of the state of Espírito Santo in southeastern Brazil (Instituto Mineiro de Gestão das Águas 2010). The DRB is limited to the north by the Negra and Aimorés Mountains, to the west by the Espinhaço Range, to the southwest by the Mantiqueira Range, to the southeast by the Caparaó Range, and to the east by the Atlantic Ocean (Instituto Mineiro de Gestão das Águas 2010; Fig. 1). We added the small Barra Seca River Basin to the final stretch of the DRB in order to include Sandy Coastal Plain and Lowland sites of northern Espírito Santo into the dataset.

For this study, in agreement with the geoclimatic features (see Table 1) shown by Cupolillo et al. (2008), Instituto Jones dos Santos Neves (2012), Instituto Mineiro de Gestão das Águas (2010), and Nascimento et al. (2012), we divided the DRB into six subregions: Sandy Coastal Plain or Restinga (SP), Coastal Lowland or Tabuleiro (CL), Coastal Highland (CH), Central Depression (CD), Interior Highland (IH) and Espinhaço Range (ER).

Preparing the dataset

The dataset was composed of a binary matrix of occurrence records of tree species and a geoclimatic matrix of 59 sites within the DRB (Fig. 1 and Table 1). Although five sites are located outside the boundaries of the DRB, they were included in the database due to their proximity to headwaters of tributaries (i.e., Santa Teresa, Santa Maria de Jetibá, Venda Nova do Imigrante, and Caparaó) or to the mouth of the Doce River (i.e., Regência). The matrices were extracted from the database NeoTropTree (see details at http://www.icb.ufmg.br/treeatlan/; Oliveira-Filho 2014).

The binary matrix had 2,021 tree species and 16,835 occurrence records. The geoclimatic matrix was composed of the subregion code and 31 quantitative variables: three spatial variables (latitude, longitude and distance to ocean), plus raster data at 1-km resolution including one topographic (elevation) extracted from U.S. Geological Survey's HYDRO1k Elevation Derivative Database (http://eros.usgs.gov/), and 27 climatic variables. Nineteen climatic variables were obtained from WorldClim 1.4 at approximately 1-km resolution (Hijmans et al. 2005), and three other variables – potential evapotranspiration, actual evapotranspiration, and an aridity index – from Zomer et al. (2007) based on WorldClim's data. The mean duration (in days) and severity of water deficit (amount in mm) were extracted from Walter's diagrams (Walter 1985). The mean frequency of frosts (in days), the percentage of cloud coverage, and the cloud interception (amount in mm) were obtained from Jones and Harris (2008).

Data analyses

Presets

We undertook a previous outliers analysis (McCune and Grace 2002; cut-off 2.0) and removed three sites in the SP subregion and one site located in 'canga' (a type of ferric outcrop) of the southernmost ER (Ouro Preto). We also excluded 510 singletons (species with only one occurrence data point) as they could not contribute to the most important ordination patterns (Lepš and Šmilauer 2003). After these procedures, the final matrix comprised 55 sites, 1518 species, and 15,959 occurrence records.

Floristic differentiation of subregions

We used the Nonmetric Multidimensional Scaling (NMS) ordination techniques adopting the Sørensen's similarity coefficient to create dimensions representing the main gradients of species composition within the dataset. The NMS analysis was performed in the software PC-ORD 6 (McCune and Mefford 2011).

We evaluated the dissociation among five of six subregions through ANOVA with gradients scores (dimensions 1 and 2) that emerged from NMS, and then Tukey's *post hoc* test adapted for unequal samples (Smith 1971) when the F test was significant. The assumptions of normality of residuals and homoscedasticity were confirmed, respectively, by D'Agostino and Levene tests (Zar 2010).

The spatial structure of ANOVA was considered through the addition of MEM spatial filters (Moran's Eigenvector Maps; Dray et al. 2006), which were created by 'spacemakeR' package and selected progressively (Blanchet et al. 2008) by the package 'packfor' in R (R Core Team 2011). We created the MEMs from a matrix of Delaunay's triangular connectivity, including weighing 'min-max' to intensiveness of connection in the calculation of the matrix-product (Borcard et al. 2011, Kelejian and Prucha 2010). The fraction explained by the treatment (i.e. the five subregions) was partitioned from the fraction explained by selected MEMs with the aim of controlling the inflation of Type I error (Peres-Neto and Legendre 2010). In the *post hoc* tests, the selected MEMs were held as covariates.

As a solution for interpreting the identity of SP (in which all sites are excluded as outliers) and CL (a small sample size reduced statistical power, diminishing the chance of finding significant results) subregions, we performed a cluster analysis (Unweighted Pair Group Method – UPGMA) using Sørensen's similarity coefficient available in PC-ORD 6 (McCune and Mefford 2011). We obtained the cophenetic correlation coefficient and conducted the Mantel test (999 permutations) to check the consistency between cophenetic values and original similarity values. By doing so, we verified the reliability of groups (floristic units) that emerged from the dendrogram.

Complementary, indicator species were obtained by calculating the Phi coefficient (Tichý and Chytrý 2006) in each floristic unit using the PC-ORD 6.0 software (McCune and Mefford 2011). The significance of Phi coefficient was tested using 999 Monte Carlo permutations. In order to obtain a set of the most representative indicator species, we selected only those with Phi coefficient ≥ 0.95 and/or $p \leq 0.001$.

Correlations among floristics and geoclimatic variables

We undertook correlations *a posteriori* among NMS dimensions and geoclimatic variables using Pearson's correlation and linear regression models (OLS). Here we did not use latitude and longitude, since their influence on floristic gradients was checked through Moran's correlograms (see below). We pre-selected some variables that showed clear relationships with floristic patterns in each dimension (visual analysis), and then eliminated co-linearities, excluding redundant variables with lower explanatory power. We considered the existence of co-linearity when the variance inflation factor (VIF) of each variable was greater than 10 (e.g., Quinn and Keough 2002). Then, we selected the models adopting the best balance between parsimony and accuracy of data description (i.e., lower AICc – corrected Akaike Information Criteria – value; Burnham and Anderson 2002). We confirmed the models' assumptions considering the cautions indicated by Eisenlohr (2013). Specifically for normality of residuals, we used the D'Agostino-Pearson test (Zar 2010). Since we detected the absence of normality in models, we excluded outliers identified among studentized residuals (values > 2).

To evaluate gradients of species composition as a function of geographical distance, we verified the spatial structure of scores of each significant dimension of NMS through correlograms created by the software SAM 4.0 (Rangel et al. 2010) adopting Moran's I coefficient (Legendre and Fortin 1989) and following the default options. We tested the global significance of correlograms using Bonferroni's sequential correction, and confirmed the existence of spatial structure when at least one distance class was significant (Fortin and Dale 2005).

Since spatial structure in both response variables and predictors can inflate the Type I error (Peres-Neto and Legendre 2010), we also prepared correlograms for each individual variable, regardless of the residuals independence assumption (Landeiro and Magnusson 2011). Because we found spatial structure in all variables, we also prepared spatially explicit models to confirm the significances found. We also prepared partitioned models in the same manner as described above. Because the significance of these models was supported, we opted to show the results of the simplest models, i.e., without inclusion of MEMs.

Variance partitioning

Following the protocol suggested by Eisenlohr (2014), we performed a variance partitioning of the explanation provided by: [a] only climatic variables + elevation, [b] the spatially structured fraction of these variables, [c] only spatial components, and [d] factors not measured. Here we used the packages ‘vegan’, ‘spacemakeR’, ‘packfor’ and ‘spdep’ in R (R Core Team 2011).

To achieve this goal, the occurrence data were Hellinger transformed (Legendre and Gallagher 2001) and the MEMs were forward selected. We then processed two Canonical Redundance Analyses (RDA), the first involving species and environment, and the second involving environment and space (MEMs). Note that the variance partitioning makes the removal of co-linear variables unnecessary (Oksanen et al. 2013). We also tested the significance of pure fractions [a] and [c] by permutation-based ANOVA.

Results

Floristic differentiation of subregions

The NMS provided a two-dimensional solution (Fig. 2), with final stress value of 16.97. The dimensions 1 and 2 reproduced 56.3% and 24.6%, respectively, of the variation in relation to the similarity in the original space *n*-dimensional. We found significant differences among CL, CH and CD subregions (Table 2). The differences, however, were not significant between IH and ER (with the Canga site excluded), indicating a floristic similarity of the whole set of inland sites located at higher elevations (Table 2).

The floristic identity of IH plus ER was confirmed by UPGMA (Fig. 2; cophenetic correlation coefficient = 0.90; Mantel bi-lateral test, $p = 0.001$), because sites of IH and ER were integrated in the same group (with the exception of the Conselheiro Pena and Serra do Ambrósio sites), in the middle portion of the dendrogram. The UPGMA also confirmed the floristic identity of the SP subregion and CL subregion through the emergence of discrete groups (floristic units). The Canga site of the southernmost ER constituted a floristic unit separated from other localities in the Espinhaço Range. Indicator species of six floristic units (i.e. SP, CL, CH, CD, IH plus ER, and Canga) emerged from the analyses and are listed in Table 4. Such indicator species are the most frequent and exclusive species in each floristic unit.

Correlations among floristic composition and geoclimatic variables

The most highly correlated variables ($r^2 > 0.6$) with the NMS dimensions are shown in Table 3. The first dimension was effective in the segregation of sites along a thermal gradient, so that warmer sites were positioned to the right and colder sites to the left in the ordination diagram (Fig. 3). The variable most highly correlated with this dimension was mean temperature of the warmest quarter ($r^2 = 0.803$), which was strongly co-linear with elevation ($r < - 0.9$), the aridity index ($r < - 0.9$), and the following thermal variables ($r > 0.9$): mean temperature of the coldest quarter, mean temperature of the driest quarter, mean temperature of the wettest quarter, minimum temperature of the coldest month, and maximum temperature of the warmest month. Note that co-linearity is not critical here because we are dealing with an initial exploratory analysis instead of any inferential test.

The second NMS dimension summarizes the segregation of sites along a gradient of precipitation seasonality, with sites showing lower seasonality (1-3 months) occupying the upper portion of the diagram, and sites with higher seasonality (4-5 months) occupying the lower portion of the diagram (Fig. 2). The variable most highly correlated with this dimension was precipitation of the coldest quarter ($r^2 = 0.718$), which had strong co-linearity with precipitation of the driest month ($r > 0.9$), precipitation of the driest quarter ($r > 0.9$), and seasonality of precipitation ($r < - 0.9$). The second dimension was only moderately correlated with longitude ($r^2 = 0.53$) and distance to ocean ($r^2 = 0.51$).

The best OLS models for each dimension were generated with only one significant climatic variable. The model that explains the scores variation of NMS Dimension 1 (adjusted $r^2 = 0.803$; $F = 216.181$; $p < 0.001$) had temperature of the warmest quarter as a predictor ($p < 0.001$), while the model for scores variation of NMS Dimension 2 (adjusted $r^2 = 0.718$; $F = 134.704$; $p < 0.001$) had precipitation in the coldest quarter as a predictor ($p < 0.001$).

Variance partitioning

We summarized the results of variance partitioning in a Venn diagram shown in Figure 4. The fractions were significant ($p < 0.01$) for both environment (climate + elevation) and space, although the first explains a greater fraction of variance than the second. The fraction explained in the intersection of environment and space was also greater than the fraction of “pure” space. The unexplained fraction was high (80%).

Discussion

Our results indicate that both precipitation and thermal variables were important for the distribution of tree species in the Doce River Basin (DRB). Precipitation variables related to seasonality were more correlated to NMS Dimension 2 (Table 2) and contributed to explaining the differences between two floristic sets: the coastal (CL and CH) and the inland subregions

(CD, IH, and ER). Nevertheless, such variables were not strongly correlated to longitude or distance to ocean, as suggested by Oliveira-Filho and Fontes (2000) and Oliveira-Filho et al. (2005) for forests of southeastern Brazil, and by Santos et al. (2011) specifically for DRB. The absence of direct relationships among precipitation variables and longitude or distance to ocean in the DRB can be explained by the intense subsidence of dry air provided by the South Atlantic Subtropical Anticyclone, which encroaches on southeastern Brazil in winter and blocks humid air masses that cause frontal rain (Cupolillo et al. 2008). Due to this atmospheric blockage, the duration of the dry seasons tends to be uniform throughout the interior of the DRB (Cupolillo et al. 2008).

In fact, most inland sites in our dataset have a dry period of 4-5 months and precipitation in the driest quarter of less than 70 mm. These conditions induce deciduousness in 20-50% of trees, an important physiognomic feature used in the classification of forests in these three subregions (Veloso et al. 1991). On the other hand, in coastal portions of the DRB (subregions SP, CL, and CH), humidity from the ocean can influence the winter rain patterns, promoting shorter and wetter dry periods (Cupolillo et al. 2008). The absence of pronounced droughts in the CH promotes the occurrence of tropical moist forests (Saiter et al. 2011), but in the CL some studies reported levels of deciduousness in the tree stratum that suggest the occurrence of semideciduous forests (Rolim et al. 2005, Rolim et al. 2006).

Although diminished, the ocean's influence seems to continue up to ca. 100 km from the coast, encompassing the CD sites in Espírito Santo (Colatina, São João de Petrópolis, Itaguaçu, Águia Branca, Alto Liberdade, Pancas, and São Gabriel da Palha). These sites have a shorter dry period (2-3 months) and a higher amount of precipitation in the driest quarter (ca. 100 mm) than other CD sites. There is a linear gradient of precipitation seasonality from the coast, west to the border of Espírito Santo and Minas Gerais. Farther west, the variables related to seasonal distribution of rainfall do not appear to vary with distance from the ocean.

In the ordination diagram (Fig. 3), the disruption of floristic gradients was also noted, because some CD sites in Espírito Santo were closer to CL sites than to other inland sites. Besides, the majority of inland sites were aligned along NMS Dimension 1, indicating that floristic variations among subregions were more correlated to temperature associated with elevation than with seasonal distribution of precipitation.

We noticed that the strong correlation of NMS Dimension 1 with elevation and temperature variables suggests a thermal control in the species distribution following elevational gradients in both coastal and inland portions of the DRB. The ecological effect of elevation is related to its influence on geophysical factors that directly affect plant growth, such as air pressure, wind, humidity, insolation, and temperature (Grubb et al. 1977, Körner 2007). Adaptations of species to different levels of these factors drive the floristic composition along altitudinal gradients (Grubb et al. 1977, Pausas and Austin 2001, Scarano 2002, Kessler et al. 2011).

Studies have reported the high elevation characteristics of the tree flora in the Atlantic Forest of southeastern Brazil. High richness of Asteraceae, Lauraceae, Myrtaceae, Melastomataceae, Rubiaceae and Solanaceae (França and Stehmann 2004, Saiter et al. 2011), and occurrence of genera such as *Clethra*, *Clusia*, *Drimys*, *Hedyosmum*, *Ilex*, *Meliosma*, *Meriania*, *Miconia, Myrceugenia, Podocarpus*, *Prunus, Roupala,* and *Weinmannia* (Giulietti and Pirani 1988, Oliveira-Filho and Fontes 2000) are considered diagnostic of highland forests in such region. In fact, we noticed several species of these families and genera among the indicator species of highland floristic units (i.e. CH, IH plus ER, and Canga, see Table 4).

At lower elevations (in general < 600 m), Euphorbiaceae, Leguminosae, and Sapotaceae are the richest and most abundant families, although some genera of Lauraceae (mainly *Ocotea*) and Myrtaceae (*Eugenia, Marlierea*, and *Myrcia*) are still represented by many species (Guedes-Bruni et al. 2006, França and Stehmann 2013, Lombardi and Gonçalves 2000, Rolim et al.

2006). In turn, indicator species of low-elevation units (SP, CL, and CD) mostly belong to these families and genera (see Table 4).

These characteristics support the significant differences found in NMS Dimension 1 between the CL and the CH, and between the CD and the IH plus ER. Considering this last case, we were unable to find significant differences between the IH and ER, despite some distinctive environmental conditions in our dataset, such as the fact that ER sites are located at higher elevations and in colder and rainier places than the IH sites. Physiognomic differences are remarkable between the IH, where forests predominate, and the ER, where shallow, sandy and dry soils, induce the dominance of savannas ('campos rupestres'; Giulietti and Pirani 1988, Kamino et al. 2008). In the ER, forests occur in islands ('capões') or are connected to valley forests, where deeper and moister soils allow the development of trees 7-15 meters in height (Giulietti and Pirani 1988, Kamino et al. 2008).

The absence of significant differences, however, indicates that forests in the ER share many tree species with the IH forests, i.e., those able to tolerate low temperatures and shallow, dry soils; these are probably the indicator species of the unit IH plus ER. The resemblance among the IH and ER forest sites agrees with Carmo and Jacobi (2013), Giulietti and Pirani (1988), and Kamino et al. (2008) regarding strong influences of Atlantic Forest Domain on the tree flora in forest patches and gallery forests of Espinhaço Range.

The SP was treated differently because the sites, due to their lower floristic richness when compared to other subregions, were considered outliers. The flora of the SP was derived from the migration of taxa from the mesic coastal forests (Rizzini 1997), but its floristic poverty may be explained by the insufficient time for speciation (Scarano 2002), since its origin is the Upper Quaternary after the last transgression occurred ca. 5,100 yr BP (Martin et al. 1993). Despite this, the three sites of the SP formed a distinct group in cluster analysis, supporting the floristic identity of this subregion.

Another outlier case involved the Canga site of the southernmost ER that hosts forest patches on ironstone outcrops. This site comprises a group separated from other ER sites in the dendrogram (Fig. 2). Here, the richness of the tree stratum is lower than in other ER forests (Kamino et al. 2008), and can be explained by evolutionary selection for taxa that can tolerate low temperatures and substrates with a high percentage of toxic metals (metalophyte functional group; Carmo and Jacobi 2013). In fact, some indicator species of the Canga belong to metalophyte genera recognized by Carmo and Jacobi (2013), such as *Eremanthus*, *Ilex*, *Trembleya*, and *Weinmannia.* Notwithstanding this poverty in tree species, high levels of both richness and endemism have been recorded in the herbaceous and shrubby strata of Canga (Jacobi and Carmo 2008, Carmo and Jacobi 2013).

The influence of spatial proximity in the patterns reported here cannot be disregarded. Although environmental factors have been very important in the explanation of floristic variation, the fraction explained purely by space was significant as well. We also assumed that the fraction explained by spatial processes was not overestimated because an extensive set of environmental predictors were also used. Therefore, the distribution of tree species along the DRB could be determined in part by their dispersal limitation. In addition, an important portion of the floristic variation can be attributed to environmental resemblances among sites that are geographically close (the spatially structured environment).

The high unexplained fraction (80%) of the floristic variation can be attributed to undetermined residuals related to variables that were not included in the analyses. In general, biotic interactions (including anthropogenic effects) and historical events are not included in biogeographical analyses due to the difficulty of quantifying them (Zimmermann et al. 2010); this exclusion is relatively common in vegetation studies (ter Braak 1987).

We can conclude, therefore, that: [1] Thermal variables (particularly temperature of the warmest quarter), associated with precipitation variables (particularly precipitation of the coldest quarter), were the most important factors for determining tree species distribution in the DRB; [2] Site spatial proximity significantly influenced the explanation of patterns due to the limited dispersal of species and spatially structured climatic variables; [3] Considering floristic and environmental features, the subregions SP, CL, CH and CD can be treated as distinct floristic units. The subregions IH and ER, however, should be recognized as a single floristic unit encompassing most of interior highlands. Furthermore, the 'cangas' of the southernmost ER should be considered as a distinct unit due to their unique ecological features as suggested by Jacobi and Carmo (2008).

Although general phytogeographic patterns can provide theoretical support for conservation planning in the Atlantic Forest at a coarse level, the stakeholders (mainly the government and conservation organizations) should always be aware of the ecological criteria determining discrete floristic units within a given region. Even if the floristic knowledge is insufficient, consideration of geomorphology and climate at finer scales in subregions defined for other purposes (e.g., geopolitics or water management) can lead to wiser biodiversity conservation planning. Parks and reserves should be created in each of these subregions, in order to protect most of the plant species, especially the endemic and indicator ones. In forest restoration, species selection should respect the tree composition in nearby forests that are floristically similar.

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Resumo

Submetemos dados de ocorrência de espécies arbóreas e dados geoclimáticos de 59 sítios de uma bacia hidrográfica na Mata Atlântica do sudeste do Brasil a análises de ordenação, ANOVA e agrupamento com os objetivos de investigar as causas dos padrões fitogeográficos e determinar se seis sub-regiões reconhecidas constituem unidades florísticas distintas. Nós descobrimos que clima e espaço foram significativamente ($p \leq 0,05$) importantes na explicação dos padrões fitogeográficos. As variações florísticas seguiram gradientes térmicos ligados a altitude tanto em sub-regiões costeiras, como em sub-regiões interioranas. Um gradiente de sazonalidade da precipitação esteve relacionado com a variação florística até cerca de 100 km de distância do oceano. Temperatura no trimestre mais quente e precipitação no trimestre mais frio foram as principais variáveis preditoras. As sub-regiões Planície Arenosa Costeira, Terra Baixa Costeira, Montanha Costeira, e Depressão Central foram reconhecidas como unidades florísticas distintas. Diferenças significativas não foram encontradas entre Montanha do Interior e Cadeia do Espinhaço, indicando que essas sub-regiões devem compor uma única unidade florística abrangendo todas as áreas elevadas do interior. Tendo em vista suas peculiaridades ecológicas, os campos ferruginosos da Cadeia do Espinhaço podem constituir uma unidade especial. As unidades florísticas aqui propostas fornecerão informações importantes para o sábio planejamento da conservação no *hotspot* Mata Atlântica.

Palavras-chave: Padrões fitogeográficos, gradientes ambientais, autocorrelação espacial, bacia do rio Doce

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Table 1. Sites and general characteristics of six subregions within the Doce River Basin, southeastern Brazil. AT, Annual mean temperature; AP, Annual mean precipitation.

Subregion	**Sites**	**AT (°C)**	**AP (mm/yr)**	**Elevation (m)**	**Geomorphology**
Sandy Coastal Plain	**ESlirs** (Degredo), **ESptip** (Pontal do Ipiranga), **ESrege** (Regência)	24	1,200-1,300	0-50	Plains formed by sandy sediments from Quaternary
Coastal Lowland	**ESlinh** (Linhares), **ESflon** (FLONA Goytacazes), **ESsoor** (Sooretama)	24	1,200-1,250	< 200	Flattened loamy-sandy sediments (Barreiras Group) from Tertiary
Coastal Highland	**ESjtba** (Santa Maria de Jetibá), **ESsant** (Santa Teresa), **ESvnim** (Venda Nova do Imigrante), **MGarap** (Araponga), **MGcapa** (Caparaó)	18-21	1,300-1,800	600-2,000	Dissected Precambrian plateaus
Central Depression	**ESagbr** (Águia Branca), **ESalib** (Alto Liberdade), **EScola** (Colatina), **ESitag** (Itaguaçu), **ESpalh** (São Gabriel da Palha), **ESpanc** (Pancas), **ESsjpt** (São João de Petrópolis), **MGaimo** (Aimorés), **MGanto** (Antônio Dias), **MGbaix** (São Geraldo do Baixio), **MGbrau** (Braúnas), **MGcart** (Caratinga), **MGdion** (Dionísio), **MGipan** (Ipanema), **MGipat** (Ipatinga), **MGitam** (Itambé do Mato Dentro), **MGgove** (Governador Valadares), **MGguar** (Guaraciaba), **MGipab** (Ipaba), **MGmrlc** (Marilac),	24-25	1,000-1,200	< 600	Hills and fluvial plains with deep soils within a inter-plateaus zone

	MGmarl (Marliéria), **MGping** (Pingo d'Água), **MGpont** (Ponte Nova), **MGptqm** (Ponte Queimada), **MGrdoc** (Rio Doce), **MGsilv** (Lagoa Silvano), **MGsped** (São Pedro do Suaçuí), **MGtimo** (Timóteo), **MGvinh** (Vinhático)				
Interior Highland	**MGdiog** (Diogo de Vasconcelos), **MGevan** (São João Evangelista), **MGmari** (Mariana), **MGmonl** (João Monlevade), **MGpena** (Conselheiro Pena), **MGpinh** (Pinheiro Alto), **MGpira** (Piranga), **MGrver** (Rio Vermelho), **MGsgra** (São Gonçalo do Rio Abaixo), **MGvico** (Viçosa)	19-21	1,200-1,400	600-1,000	Dissected Precambrian plateaus
Espinhaço Range	**MGcboi** (Cabeça de Boi), **MGcata** (Catas Altas da Noruega), **MGmtdr** (Conceição do Mato Dentro), **MGpila** (Morro do Pilar), **MGcara** (Santuário do Caraça), **MGrioa** (Serra da Gandarela), **MGsamb** (Serra do Ambrósio), **MGserr** (Serro), **MGopnn** (Ouro Preto)	18-20	1,400-1,800	1,000-1,600	Peaks, ridges and escarpments of quartzic or ferric rocks from Precambrian (Brazilian Crystalline Shield)

Table 2. Differences among averages of scores of ordination dimensions for five subregions of the Doce River Basin, southeastern Brazil. Letters superscripted indicate differences by Tukey test adapted for unequal samples ($p \leq 0.05$).

Subregions	**Dimension 1**	**Dimension 2**
Coastal Lowland	0.71^{a}	0.99^{a}
Coastal Highland	-1.24^{b}	0.79^{a}
Central Depression	0.54^{a}	-0.12^{b}
Interior Highland	-0.38^{c}	-0.21^{b}
Espinhaço Range	-0.96^{bc}	-0.19^{b}

Table 3. Environmental variables more correlated ($r^2 > 0.6$) to ordination dimensions created from floristic data of 55 sites within the Doce River Basin, southeastern Brazil. Bold numbers are correlation values of pre-selected variables for construction of linear models.

	Dimension 1		**Dimension 2**	
Environmental variables	**r**	**r^2**	**r**	**r^2**
Elevation	**-0.891**	**0.795**	-0.041	0.002
Annual mean temperature	0.895	0.801	0.028	0.001
Max temperature of the warmest month	0.873	0.763	-0.094	0.009
Min temperature of the coldest month	0.859	0.738	0.268	0.072
Mean temperature of the wettest quarter	0.881	0.777	-0.006	0.000
Mean temperature of the driest quarter	0.883	0.780	0.130	0.017
Mean temperature of the warmest quarter	**0.896**	**0.803**	-0.004	0.000
Mean temperature of the coldest quarter	0.885	0.783	0.127	0.016
Precipitation of the driest month	0.174	0.030	0.831	0.691
Precipitation seasonality	-0.257	0.066	-0.802	0.644
Precipitation of the driest quarter	0.151	0.023	0.832	0.693
Precipitation of the coldest quarter	0.054	0.003	**0.847**	**0.718**
Severity of the water deficit	0.213	0.045	**-0.781**	**0.610**
Aridity index	**-0.792**	**0.627**	0.119	0.014

Table 4. Indicator species of six floristic units within the Doce River Basin, southeastern Brazil.

Sandy Coastal Plain: *Abarema filamentosa, Aspidosperma pyricollum, Calyptranthes brasiliensis, Clusia hilariana, Clusia spiritu-sanctensis, Eugenia astringens, Leptolobium bijugum, Maytenus obtusifolia, Myrsine parvifolia, Ocotea cernua, Protium icicariba.*
Coastal Lowland: *Amphirrhox longifolia, Annona acutiflora, Aspidosperma camporum, Aspidosperma discolor, Byrsonima cacaophila, Campomanesia espiritosantensis, Couepia carautae, Couepia schottii, Diplotropis incexis, Eugenia copacabanensis, Exellodendron gracile, Exostyles venusta, Glycydendron espiritosantense, Guazuma crinita, Henriettea succosa, Hirtella bahiensis, Inga tripa, Licania salzmannii, Manilkara salzmannii, Marlierea strigipes, Marlierea suaveolens, Maytenus samydaeformis, Miconia mirabilis, Micropholis guyanensis, Myrcia isaiana, Neomitranthes obtusa, Ocotea aniboides, Ocotea confertiflora, Ormosia nitida, Parkia pendula, Pilocarpus grandiflorus, Plinia stictophylla, Pouteria bapeba, Simira grazielae, Tabernaemontana salzmannii, Tovomita brevistaminea, Xylopia ochrantha.*
Coastal Highland: *Baccharis dentata, Byrsonima ligustrifolia, Clusia lanceolata, Clusia organensis, Drimys brasiliensis, Matayba sylvatica, Meliosma chartacea, Meliosma sellowii, Miconia pusilliflora, Psychotria suterella, Solanum megalochiton, Solanum pseudo-quina, Solanum rufescens, Tibouchina arborea, Vantanea compacta.*
Central Depression: *Carpotroche brasiliensis, Casearia guianensis, Gallesia integrifolia, Joannesia princeps, Machaerium incorruptibile, Machaerium pedicellatum, Miconia calvescens, Pseudopiptadenia contorta, Sparattosperma leucanthum.*
Interior Highland plus Espinhaço Range: *Blepharocalyx salicifolius, Callisthene major, Casearia obliqua, Eremanthus incanus, Ixora brevifolia, Lamanonia ternata, Matayba mollis, Tapirira obtusa, Vochysia tucanorum.*
Canga of southernmost Espinhaço Range: *Athenaea pereirae, Baccharis lychnophor*a, *Cinnamomum erythropus, Eremanthus crotonoides, Hololepis pedunculata, Ilex pseudobuxus, Myrceugenia myrcioides, Pseudobrickellia angustissima, Schefflera varisiana, Trembleya laniflora, Weinmannia humilis.*

Figure 1. Location of the Doce River Basin encompassing portions of Minas Gerais and Espírito Santo states in southeastern Brazil. Sites of the six subregions adopted in this study are highlighted.

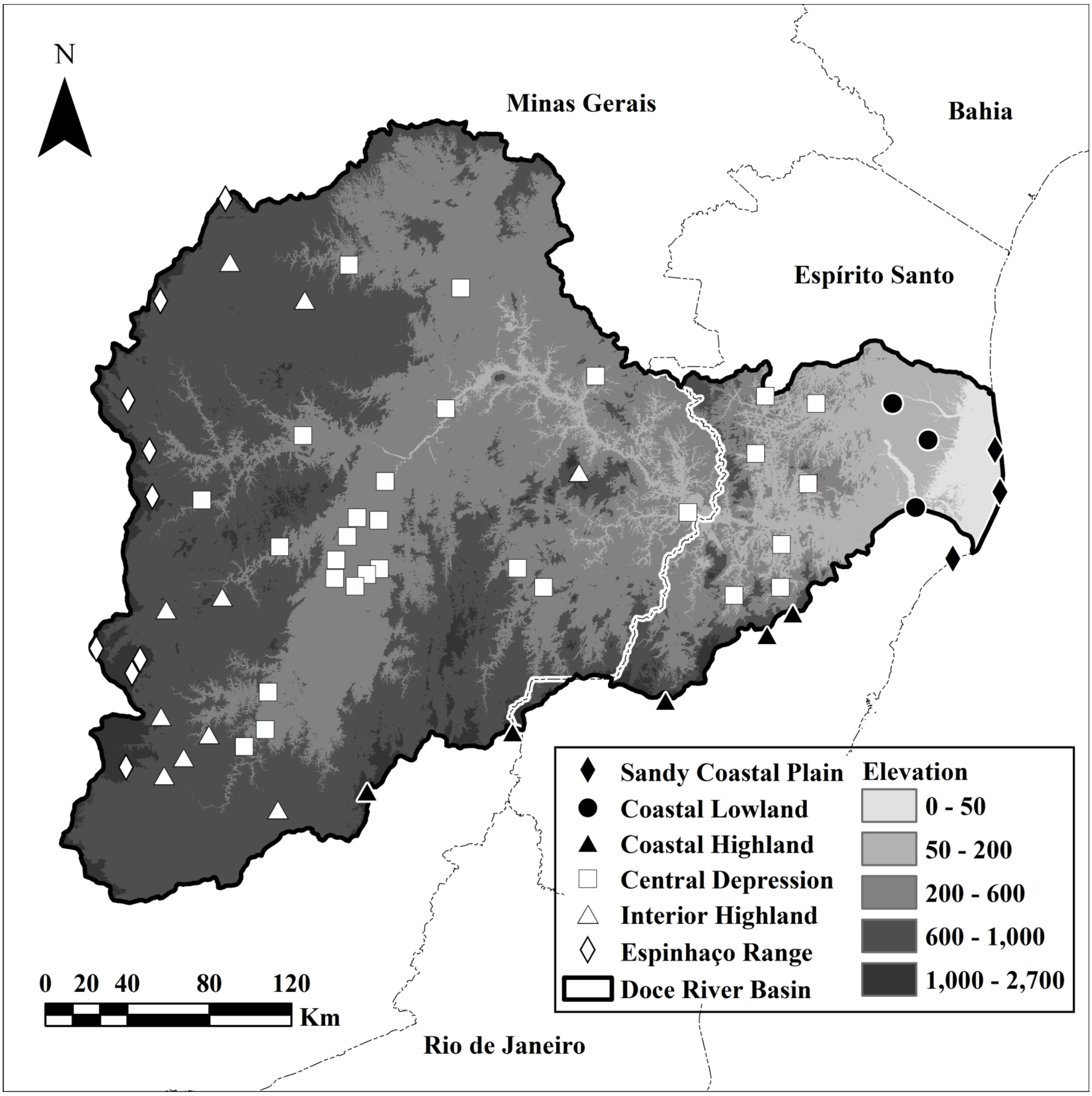


Figure 2. Cluster analysis (UPGMA) for 59 sites (including outliers) within the Doce River Basin, southeastern Brazil. The codes of sites are described in Table 1.

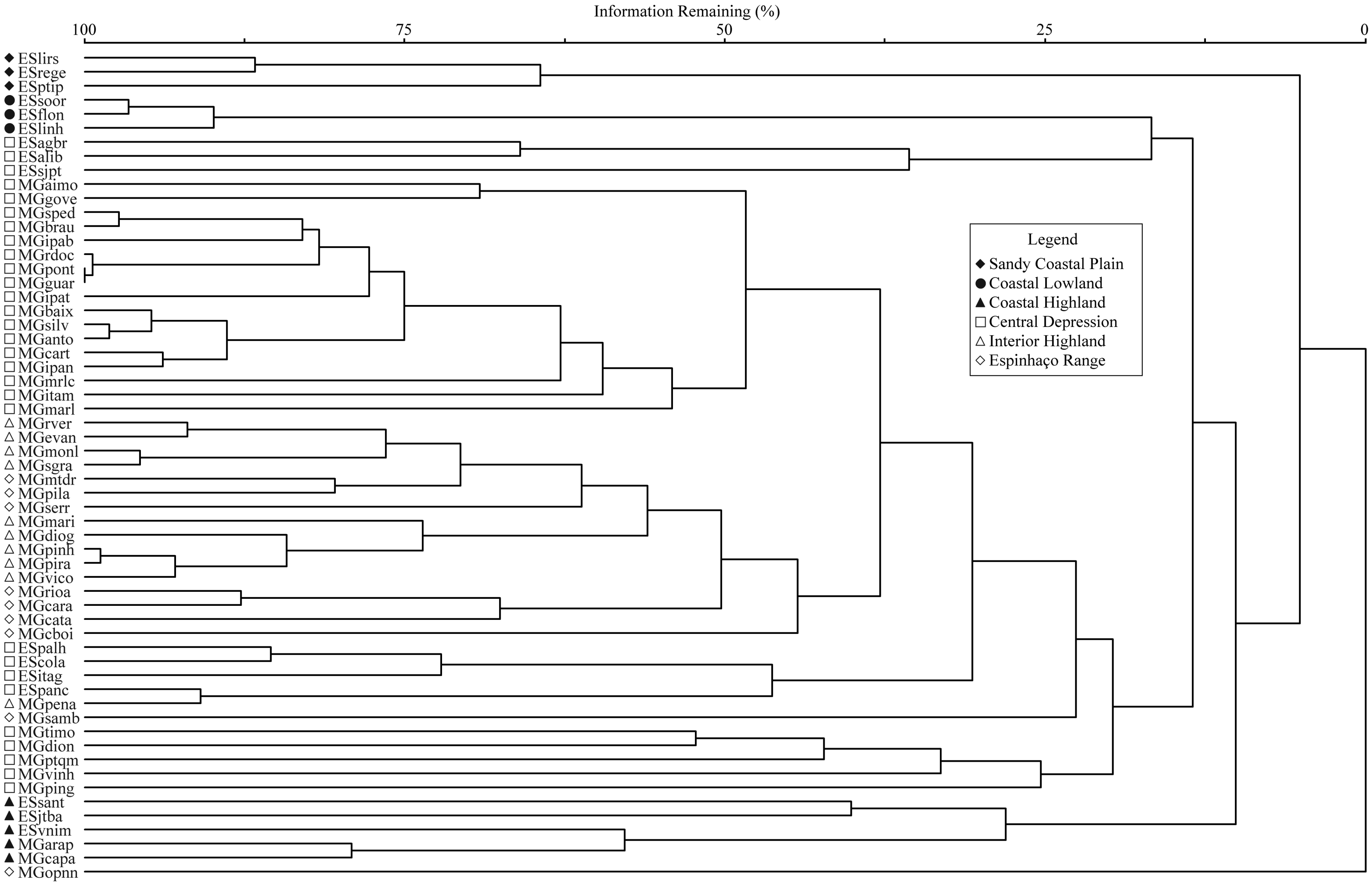


Figure 3. Diagram of ordination analysis (NMS) produced from floristic data of 55 sites within the Doce River Basin, southeastern Brazil. Symbol legend is available in Figure 1. The sites codes are shown in Table 1.

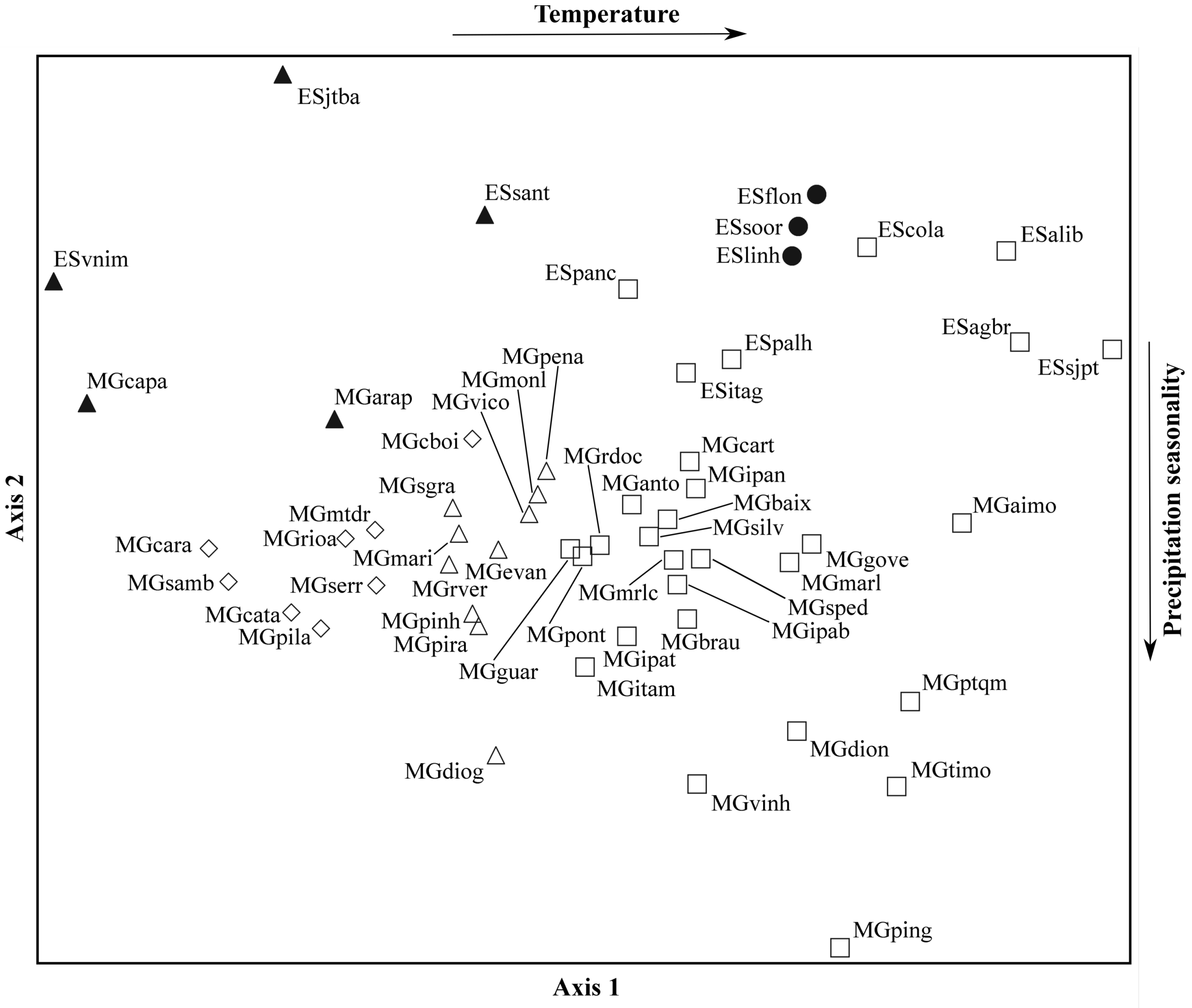
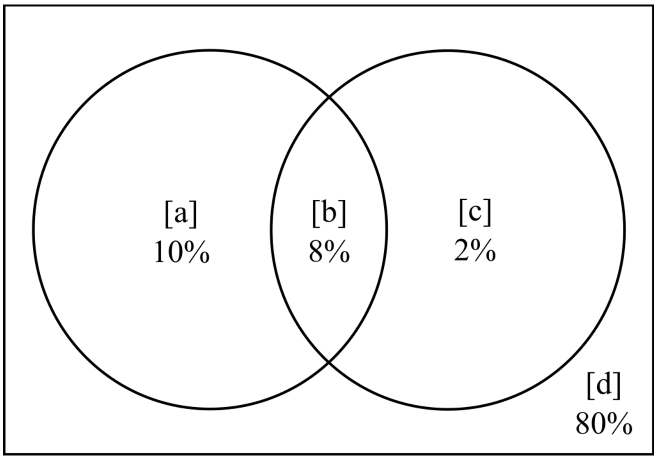


Figure 4. Venn diagram with variance partitioning between environment (climate + elevation) and space in the Doce River Basin, southeastern Brazil.



Capítulo V – A Floresta de Linhares no contexto fitogeográfico do leste do Brasil

Felipe Zamborlini Saiter & Ary Teixeira de Oliveira-Filho

Capítulo em fase de avaliação para publicação no livro intitulado “Reserva Natural Vale: Centro de Endemismo, Diversidade e Conservação da Mata Atlântica”. Organizadores: Samir Rolim, Ana Carolina Srbek Araújo e Luis Fernando Tavares de Menezes.

A Floresta de Linhares no contexto fitogeográfico do leste do Brasil

Felipe Zamborlini Saiter & Ary Teixeira de Oliveira-Filho

Introdução

A exuberante floresta que cobria os extensos tabuleiros costeiros existentes entre os rios Doce e Barra Seca foi uma barreira intransponível para os primeiros colonizadores do norte do Espírito Santo até o início do século XX (Soares 1943; Egler 1951). Contribuiu para isso, não só a expressiva largura do rio Doce e o leito intransitável do rio Barra Seca, mas também o medo de ataques das tribos indígenas (sobretudo de Botocudos) e de "febres" (como a malária), além da falta de contingente humano para a colonização (Soares 1943; Egler 1951; Ruschi 1954).

A "luta" contra a floresta só começou a ser vencida pelos colonizadores a partir das décadas de 1920 e 1930, quando uma ponte sobre o rio Doce foi construída na cidade de Colatina e uma estrada ligando a então vila de Linhares e a cidade de São Mateus foi aberta (Soares 1943; Egler 1951). Esses são marcos históricos de um período de grandes transformações na paisagem natural da região, com tribos indígenas sendo rapidamente exterminadas por doenças e a floresta sucumbindo à exploração madeireira e às queimadas para a abertura de áreas para a agricultura (Egler 1951; Ruschi 1954).

Atualmente, a floresta de tabuleiros entre os rios Doce e Barra Seca, que chamaremos a partir daqui de Floresta de Linhares, está reduzida a um bloco florestal com cerca de 48.000 ha e a pequenos fragmentos florestais inseridos em uma matriz de áreas com atividades agropecuárias (especialmente pastagens, silvicultura de eucalipto e plantios de café e mamão) nos municípios de Linhares e Sooretama (Vicens *et al.*, 2004; Magnago et al. 2014). O bloco florestal acima referido é composto pela Reserva Natural Vale (21.787 ha), pela Reserva Biológica de Sooretama (24.000 ha), e por duas Reservas Particulares do Patrimônio Natural (RPPN Recanto das Antas, com 2.212 ha, e RPPN Mutum Preto, com 379 ha) constituindo o maior remanescente de floresta de tabuleiro do sudeste do Brasil (Germano Filho *et al.*, 2000).

A diversidade florística na Floresta de Linhares é elevada (Peixoto & Silva 1997). Dados mais recentes indicam a ocorrência de cerca de 2300 espécies de plantas vasculares, dentre as quais destacam-se algumas dezenas de espécies novas para a ciência (Germano Filho *et al.*, 2000; Peixoto *et al.*, 2008). O número de endemismos também é relativamente alto e muitas espécies amplamente distribuídas apresentam biotipos distintos nessa região (Peixoto & Silva 1997).

Embora o conhecimento botânico na Floresta de Linhares tenha sido impulsionado nas últimas quatro décadas pelos vários inventários florísticos e estudos taxonômicos ali desenvolvidos (por exemplo, Peixoto & Gentry 1990; Barroso & Peixoto 1995; Jesus & Rolim 2005; Lopes & Mello-Silva 2014), a literatura científica sobre essa região apresenta apenas discussões rasas sobre sua situação no contexto fitogeográfico do leste do Brasil. Há uma carência, sobretudo, de abordagens mais detalhadas sobre sua tipologia florestal e suas relações florísticas com outras regiões. Apoiados nessa realidade, propomos aqui uma revisão sobre o que alguns autores pensaram sobre esses aspectos ao longo do tempo e aproveitamos para acrescentar algumas de nossas impressões sobre o tema, na expectativa de que elas possam contribuir para uma melhor interpretação do cenário fitogeográfico regional.

Começamos reunindo informações sobre o ambiente de tabuleiros na região de Linhares e depois relacionando o efeito da sazonalidade do clima com aspectos fisionômicos úteis no mapeamento e classificação da vegetação. Passamos a uma discussão sobre a relação florística da Floresta de Linhares com as florestas do sul da Bahia (ou Hileia Baiana), do Médio Vale do rio Doce e do sul do Espírito Santo e norte do Rio de Janeiro (ou Falha de Campos dos Goytacazes). Por fim, as características dessas relações florísticas também serviram para a busca de justificativas para a elevada diversidade florística da Floresta de Linhares.

O ambiente de tabuleiros em Linhares

Os tabuleiros costeiros que ocorrem em Linhares correspondem a planícies sedimentares originadas no Plioceno (Formação Barreiras) que são entrecortadas por vales amplos e rasos. As altitudes variam entre 28 e 65 m e predominam solos Podzólicos Vermelho-Amarelo, distróficos, com horizonte B textural de atividade baixa (não hidromórfico) e horizonte A moderado com textura variável de argilosa a areno-argilosa (Jesus *et al*., 1992). O clima é quente e úmido, com verões chuvosos e invernos secos, sendo classificado como Awi de acordo com o sistema de Köppen (Jesus 1987).

Dados meteorológicos de uma série histórica de 26 anos (1975-2000) mostram que a temperatura média anual é de 23,3 ºC e a precipitação média anual é de 1202 mm (Jesus & Rolim 2005). Fevereiro é o mês mais quente, com média de 25,6 ºC, e julho o mais frio, com média de 19,9 ºC. As temperaturas médias máxima e mínima são, respectivamente, 34,2 ºC e 14,8 ºC (Jesus & Rolim 2005). As médias mensais de precipitação variam, aproximadamente, entre 200 mm (Janeiro) e 30 mm (junho). Cerca de 80% da precipitação anual está distribuída entre outubro e março (Engel & Martins 2005; Jesus & Rolim 2005). O balanço hídrico permite reconhecer uma estação úmida de verão (dezembro a fevereiro) e uma estação seca de outono-inverno (maio a meados de setembro) separadas entre si por estações de transição (Peixoto *et al*., 1995; Engel & Martins 2005).

Sabe-se também que a precipitação anual na Floresta de Linhares tem variado entre 800 a 2000 mm nas últimas quatro décadas (ver dados em Jesus & Rolim 2005, e em http://hidrometeorologia.incaper.es.gov.br) e que a precipitação acumulada na estação seca, por vezes, pode cair para menos de 50 mm em anos de estiagem extrema causada por eventos de El-

Niño (Jesus & Rolim 2005; Rolim *et al*., 2005). O balanço hídrico também pode ser prejudicado quando veranicos causados por bloqueios atmosféricos derrubam os totais de precipitação na estação úmida (para detalhes, ver Cupolillo *et al*., 2008).

A semideciduidade ou a perenidade da Floresta de Linhares

Em primeiro lugar, consideramos interessante que o leitor conheça a Figura 1 antes de iniciarmos essa seção. Tal figura revela a fisionomia semidecídua da Floresta de Linhares no início do período de transição seco-úmido dos anos de 2010 e 2014, mas devemos informar que o regime de renovação foliar dessa floresta é um tema há muito tempo controverso na literatura científica. Existem motivos para isso, e pretendemos esclarecê-los por meio de uma discussão contendo o tratamento do tema por diversos autores.

Partimos do trabalho pioneiro de Ruschi (1950) sobre a fitogeografia do Estado do Espírito Santo, no qual o autor chamou de “mata pluvial dos tabuleiros” ou “floresta perenifólia dos tabuleiros” o conjunto de florestas cobrindo os sedimentos do Terciário no norte do Espírito Santo. Nesse mesmo trabalho, entretanto, encontramos um mapa fitogeográfico onde duas tipologias de florestas de tabuleiro podem ser identificadas, uma sempre-verde e outra caducifólia (ver reprodução na Figura 2). Apesar de Ruschi (1950) não destacar em seu texto as características das “florestas dos tabuleiros caducifólias”, percebemos que no mapa elas estão distribuídas em áreas mais interioranas, tal como a oeste da Lagoa Juparanã e no trecho inicial da bacia do rio Barra Seca. Por outro lado, as “florestas dos tabuleiros sempre-verdes” ocupam uma parte mais próxima da costa, na qual é possível reconhecer junto ao paralelo 19° S o bloco florestal correspondente ao “Parque de Refúgio e Criação de Animais Silvestres Sooretama”, atual Reserva Biológica de Sooretama.

Um ano mais tarde, e demonstrando desconhecer o mapa fitogeográfico de Ruschi

(1950), Egler (1951) relata a ocorrência de florestas semidecíduas ao norte do rio Doce por meio de um estudo sócio-ambiental sobre o avanço da colonização de terras durante a primeira metade do século XX. Nas palavras do autor "... *Um fato, porém, parece que passou despercebido à maioria dos antigos viajantes: o caráter semidecíduo de uma grande parte da vegetação do rio Doce* (...) *O que não resta dúvida é que acima do paralelo de 20° ocorrem, como partes integrantes da chamada "mata costeira" ou "mata atlântica", extensas e contínuas áreas de matas de caráter indiscutivelmente semidecíduo e que não foram ainda devidamente assinaladas, delimitadas e estudadas*".

Na década seguinte, Azevedo (1962) caracterizou os tipos de vegetação do Espírito Santo, denominando de "floresta mesófila de tabuleiros" a vegetação sobre sedimentos da série Barreiras ao norte do rio Doce. Heinsdijk *et al.* (1965) sugeriu classificar a Floresta de Linhares como floresta pluvial, mas assumiu que "... *Algumas vêzes essa formação poderá ser uma floresta sasonal sempre verde* (grafia original do autor)". Em seguida, Ruschi (1969) revisou o mapa fitogeográfico do Espírito Santo proposto por Ruschi (1950), confirmando em um segundo mapa (ver reprodução na Figura 3) a existência de florestas de tabuleiro sempre-verdes e ampliando a distribuição das florestas de tabuleiro caducifólias para parte da bacia do rio São Mateus.

No entanto, em um tratado fitogeográfico do Brasil elaborado por Rizzini (1979) o termo "floresta pluvial" reaparece vinculado ao conjunto de florestas de tabuleiros do norte do Espírito Santo. Em sequência, o estudo fitogeográfico da Folha SE.24 Rio Doce elaborada pelo Projeto RADAMBRASIL (Jordy Filho 1987) utilizou a classificação de Velloso & Góes-Filho (1982) para descrevê-las como "floresta ombrófila densa", embora características de espécies do dossel da floresta ao sul do paralelo 18° 30' S (onde está localizada a Floresta de Linhares) tenham lançado dúvidas sobre o seu verdadeiro regime de renovação foliar. Segundo o autor, quando comparadas com a floresta ao norte do paralelo 18° 30' S "... *esta floresta destaca-se pelas diferenças estruturais que algumas espécies do estrato dominante apresentam, como brotos protegidos, folhas coriáceas e troncos de casca grossa, o que cause justa preocupação quanto à sua classificação, se ombrófila ou estacional.*"

Em um trabalho contemporâneo ao anterior, Jesus (1987) descreveu aspectos florestais da Floresta de Linhares, dentre eles um período muito curto de semideciduidade ocorrendo na estação seca. Pouco tempo depois, Peixoto & Gentry (1990) descreveram a diversidade e composição de um trecho da Floresta de Linhares, trazendo à tona o termo "floresta ombrófila semidecídua" (mais tarde esse termo seria recordado por Kindel *et al.*, 1999; e Kindel & Garay 2001). Tal denominação, entretanto, causa certa estranheza pois mistura conceitos flagrantemente opostos segundo os sistemas de classificação da vegetação brasileira que eram usados naquela época (principalmente os de Velloso & Góes-Filho 1982; e Veloso *et al.*, 1991). Nesses sistemas, as florestas ombrófilas são caracterizadas por elevada precipitação, que é bem distribuída ao longo do ano, e por ausência de período biologicamente seco. As florestas estacionais semideciduais são marcadas por uma distribuição sazonal de chuvas, com ocorrência de uma estação seca pronunciada.

Ainda que até o início da década de 1990 alguns estudos já tivessem indicado o caráter estacional e semidecíduo da Floresta de Linhares, os resultados do Projeto RADAMBRASIL (Jordy Filho 1987) levaram à publicação do Mapa da Vegetação do Brasil (IBGE 1993) mostrando a região como parte integrante da tipologia de floresta ombrófila densa. Todavia, na contramão desse mapa oficial, estudos ecológicos posteriores basearam-se em observações de campo para adotar o termo "floresta estacional semidecidual" (por exemplo, Rolim & Nascimento 1997, Rolim *et al.*, 1999, Kindel & Garay 2002) disponível no sistema de Veloso *et al.* (1991).

Nesse contexto, Engel (2001) realizou um estudo fenológico que revelou os efeitos da distribuição sazonal de chuvas sobre a Floresta de Linhares. Tal estudo monitorou por 11 anos (1982-1992) a fenologia de 41 espécies de dossel (205 árvores no total, sendo cinco de cada espécie) e descobriu que 44% delas são brevidecíduas (totalmente sem folhas por até um mês) e 12% são decíduas (totalmente sem folhas por mais de um mês). O máximo de queda foliar ocorreu na transição da estação seca para a chuvosa, quando uma média de 30% das espécies e 15% dos indivíduos monitorados mostraram queda total de folhas. A autora, entretanto, classificou a Floresta de Linhares como "floresta estacional perenifólia" seguindo critérios de Longman & Jeník (1987), e indicou que essa seria uma tipologia transicional entre os conceitos de "floresta ombrófila densa" e "floresta estacional semidecidual" propostos por Veloso *et al.* (1991). Para Longman & Jeník (1987) no dossel de uma floresta tropical estacional perenifólia predominam espécies sempre-verdes, das quais um máximo de 30% apresentam desfolha durante a época seca do ano.

Posteriormente, Vicens *et al.* (2004) baseou-se na variação sazonal de um índice de vegetação (NDVI – *Normalized Difference Vegetation Index*) ao longo do ano de 1997 para sugerir o caráter semicaducifólio da Floresta de Linhares. Nesse ponto devemos ressaltar que o biênio 1997-1998 foi considerado pelo Instituto Nacional de Pesquisas Espaciais (CPTEC-INPE; http://enos.cptec.inpe.br/) como um período com fortes efeitos climáticos de El-Niño, e que, embora Vicens *et al.* (2004) não tenham abordado essa relação, a escassez de chuvas normalmente provocada pelos eventos de El-Niño no sudeste do Brasil foi um fator crucial para o padrão semidecíduo da Floresta de Linhares no período. Corroboram essa ideia as alterações na dinâmica da Floresta de Linhares (aumento da mortalidade de árvores e declínio de biomassa) que já foram registradas por estudos realizados durante períodos com secas severas atribuídas ao El-Niño (Rolim *et al.*, 1999; Rolim *et al.*, 2005).

Diante das evidências de semideciduidade na Floresta de Linhares, Rizzini & Garay (2004) analisaram parâmetros físicos e químicos das folhas de árvores da Floresta de Linhares e descobriram que, na verdade, algumas espécies conseguem se manter como sempre-verdes porque adotam a esclerofilia como mecanismo adaptativo frente ao estresse hídrico. Por outro lado, espécies semidecíduas, notadamente mais abundantes, podem controlar a proporção de queda de folhas segundo a severidade da seca. Tais constatações reafirmam as informações de Jordy Filho (1987) sobre a ocorrência de atributos estruturais típicos de resistência à seca em algumas espécies arbóreas dominantes na Floresta de Linhares, e também fornecem evidências de que tal floresta pode responder de forma diferenciada à variação interanual de precipitação e severidade da seca.

Certamente por conta da contradição entre alguns dos autores citados, ainda encontramos estudos que optaram por descrever a Floresta de Linhares como floresta ombrófila densa ou *dense rain forest* (por exemplo, de Paula & Soares 2011; Buso Junior *et al.*, 2013; Magnago *et al.*, 2014), ou que apenas relatam o uso controverso de duas denominações (por exemplo, Rizzini *et al.*, 1997; Engel & Martins 2005; Garay *et al.*, 2008).

Fato é que essa controvérsia semântica se deve a estudos que não se apoiaram em observações periódicas do comportamento da floresta ou que não consideraram informações sobre a distribuição sazonal de chuvas na região. Mas também há de se compreender a dura tarefa de classificação da vegetação com base em fatores que flutuam ao sabor de um clima naturalmente dinâmico. Com isso, queremos dizer que a adoção das denominações “floresta ombrófila densa”, “floresta pluvial” ou *dense rain forest* pode ter sido encorajada pela observação da floresta em anos mais úmidos, quando a fisionomia semidecídua certamente não foi tão evidente.

Por outro lado, temos que assumir o caráter muitas vezes arbitrário das classificações de vegetação. Nesse sentido, o uso da denominação "floresta estacional perenifólia" pode estar correto de acordo com critérios de Longman & Jeník (1987), mas não encontra suporte na classificação de Veloso *et al.* (1991), devido à falta de flexibilidade desse último sistema para a construção do termo "floresta estacional densa" (se é que esse poderia ser mesmo um sinônimo dos termos "floresta estacional perenifólia" ou "floresta estacional sempre-verde"). Tomando ainda por base a classificação das fitofisionomias da América do Sul cisandina tropical e subtropical proposta por Oliveira-Filho (2009), o termo "floresta estacional perenifólia" seria possível, mas não descreveria a real condição da Floresta de Linhares. Segundo o autor, florestas estacionais perenifólias são atribuídas a fundos de vales onde a estação seca é compensada por reservas de água no solo.

Curiosamente, a recente revisão do Manual Técnico da Vegetação Brasileira (IBGE 2012), um produto derivado da classificação de Veloso *et al.* (1991), inclui o termo "floresta estacional sempre-verde" (ou "floresta estacional perenifólia") dentre suas tipologias de vegetação com o claro objetivo de contemplar as florestas sempre-verdes ocorrendo sob clima sazonalmente seco na borda sul da Amazônia, em Mato Grosso. Nessa região, as florestas estacionais perenifólias típicas ocorrem sobre latossolos profundos fora dos vales úmidos, os quais, por sinal, são ocupados por uma fisionomia ombrófila floristicamente distinta (IBGE 2012). Há, entretanto, uma real preocupação de IBGE (2012) em informar que a perenidade das florestas da borda sul da Amazônia foi confirmada pela análise de um índice de vegetação (NDVI) no período 1982-1999 (esse mesmo índice foi utilizado por Vicens *et al.*, 2004, para confirmar a semideciduidade da Floresta de Linhares no ano de 1997). Segundo Ivanauskas *et al.* (2008) tal perenidade seria resultado da presença de inúmeros cursos de água em relevo plano e da suposta capacidade das árvores amazônicas em absorver água em profundidade (provavelmente até 6 metros) no período seco.

No caso da Floresta de Linhares, entretanto, faltam estudos que indiquem a profundidade atingida pelas raízes de suas árvores. De qualquer forma, podemos acrescentar que seus solos podzólicos são mais fortemente drenados que os latossolos da borda sul da Amazônia. Além disso, as médias de precipitação anual na borda sul da Amazônia normalmente alcançam níveis superiores a 1500 mm (Ivanauskas *et al.*, 2008), contra cerca de 1200 mm na Floresta de Linhares (sabemos, inclusive, que anos menos chuvosos são relativamente comuns). Diante dessas informações, não podemos afirmar, em absoluto, que a Floresta de Linhares seria uma "floresta estacional perenifólia" segundo a classificação de IBGE (2012).

Na verdade, considerando apenas as classificações mais atuais e "ditas" brasileiras, talvez fosse mais prudente apoiar o uso das denominações "floresta estacional semidecidual" (*sensu* Veloso *et al.*, 1991; e IBGE 2012) e "floresta estacional semideciduifólia" (*sensu* Oliveira-Filho 2009), tal como fizeram Rolim *et al.* (1999), Rolim & Nascimento (1997), Rizzini & Garay (2004) e Vicens *et al.* (2004). Entretanto, isso também não nos deixa confortáveis, pois é notável a ocorrência de anos mais úmidos (1600-2000 mm/ano) em que estações secas amenas (por vezes sem deficiência hídrica) podem levar à fisionomia sempre-verde ou perenifólia.

Há, portanto, uma real necessidade de considerar a flexibilidade do regime de renovação foliar da Floresta de Linhares em sua própria classificação. Em vez da adoção de uma classificação "engessada", entendemos que seria mais adequado denominá-la duplamente de floresta estacional semidecidual (nos períodos marcados por estações secas pronunciadas) e de floresta estacional perenifólia (nos períodos muito úmidos). Naturalmente, tal proposta poderá causar certa desconfiança em fitogeógrafos acostumados a classificações tradicionais onde as tipologias da vegetação são perfeitamente separadas. Por isso, se um único termo realmente for necessário para descrever a Floresta de Linhares, sugerimos que seja "floresta estacional semidecidual a perenifólia".

As afinidades florísticas com a Hileia Baiana e a Amazônia

Embora tenha sido muitas vezes citada na literatura fitogeográfica, a relação florística entre a Floresta de Linhares e a floresta de terras baixas do sul da Bahia ainda é um tema que carece de maior investigação. A ideia de que a Floresta de Linhares seria parte integrante do que Andrade-Lima (1966) chamou de Domínio da Hileia Baiana (a floresta pluvial costeira da Bahia que apresenta fisionomia semelhante à Floresta Amazônica, ou Hileia Amazônica) encontra suporte nas discussões de Rizzini (1979), Peixoto (1982), Peixoto & Gentry (1990) e Barroso & Peixoto (1991) sobre as similaridades de composição, estrutura e diversidade entre tais regiões. Evidentemente, a Floresta de Linhares está geograficamente próxima da Hileia Baiana e as duas se assemelham no que se refere à elevada diversidade florística e à presença de árvores majestosas de *Lecythis*, *Cariniana* e *Caryocar* emergindo sobre um dossel com cerca de 30 metros de altura.

Entretanto, alguns estudos têm sugerido que, em termos florísticos, a Floresta de Linhares pode não ser mais semelhante à Hileia Baiana do que às outras partes no leste do Brasil. Jesus & Rolim (2005) e Rolim *et al.* (2006), por exemplo, sugeriram que a composição de espécies arbóreas da Floresta de Linhares seria mais similar à do interior do vale do rio Doce do que à do sul da Bahia. Em um trabalho de revisão sobre estudos fitogeográficos no Brasil, Fiaschi & Pirani (2009) indicaram a latitude de 19° S (onde se encontra a Floresta de Linhares) como o limite entre os blocos sul e norte da Floresta Atlântica. Os autores também citaram que as diferenças de composição florística entre esses dois blocos estariam ligadas à influência da flora subtropical-andina sobre o bloco sul e a conexão histórica entre o bloco norte e a Amazônia (ver discussões sobre essa possível conexão em Oliveira-Filho & Ratter 1995; Fernandes 2003; e Santos *et al.*, 2007). Considerando essa hipótese de quebra biogeográfica na latitude de 19° S, Saiter (2015) utilizou dados ambientais e de composição arbórea para modelar a dissimilaridade ecológica ao longo da porção central da Floresta Atlântica. O autor identificou um forte turnover ecológico nas imediações da Floresta de Linhares e sugeriu a maior similaridade florística dessa região com as florestas localizadas entre a bacia do rio Doce e o rio Paraíba do Sul.

Apesar disso, é mesmo marcante o fato de essas duas regiões florísticas compartilharem casos de endemismo. Thomas *et al*. (1998) encontrou que entre 25 e 30% das espécies vasculares de duas florestas próximas à cidade baiana de Ilhéus (Serra Grande e Reserva Biológica de Una) são endêmicas do sul da Bahia e norte do Espírito Santo. Saiter (2015) citou algumas espécies arbóreas com esse padrão: *Beilschmiedia linharensis* Sa. Nishida & van der Werff, *Cariniana parvifolia* S. A. Mori, Prance & Menandro, *Hydrogaster trinervis* Kulhm., *Kielmeyera occhioniana* Saddi, *Mollinedia marqueteana* Peixoto, *Plinia stictophylla* G.M. Barroso & Peixoto, *Riodocea pulcherrima* Delpetre, *Simira grazielae* Peixoto e *Trattinnickia mensalis* Daly. Elementos tipicamente amazônicos também ocorrem em ambas, conforme já salientado por Ruschi (1950), Rizzini (1979) e Fernandes (2003). Alguns exemplos de taxa com esse padrão são os gêneros *Glycydendron*, *Melicoccus*, *Rinorea*, *Senefeldera* e *Symphonia*, e espécies como *Erythroxylum macrophyllum* Cav., *Caraipa densifolia* Mart., *Macoubea guianensis* Aubl., *Parkia* pe*ndula* (Willd.) Walp., *Pagamea guianensis* Aubl. e *Pseudima frutescens* (Aubl.) Radlk.

Recentemente, Buso Junior *et al*. (2013) se basearam no pólen encontrado em sedimentos lacustres de Linhares para apresentar uma rica discussão sobre o paleoambiente dessa região. Segundo os autores, alguns gêneros de árvores e lianas típicos da Amazônia já estavam presentes na Floresta de Linhares há 7.500 anos, indicando que a ligação entre os blocos florestais Amazônico e Atlântico esteve em curso antes desse período. Buso Junior *et al*. (2013) também indicaram que a região apresentou um clima mais úmido durante o Holoceno Médio (cerca de 7000-4000 anos atrás), e que o estabelecimento do atual clima sazonal se deu há cerca de 4.000

anos. O clima mais úmido do Holoceno Médio permitiu a ocorrência de uma floresta pluvial marcada pela abundância de palmeiras e fetos arborescentes (Buso Junior *et al*., 2013).

Acrescentando às constatações de Buso Junior *et al.* (2013) a afirmação de Carnaval & Moritz (2008) sobre a estabilidade de um clima úmido e da cobertura florestal na região costeira entre os rios Doce e São Francisco durante o Pleistoceno, somos levados a pensar que, no passado, a Floresta de Linhares teve ligação florística mais forte com a floresta pluvial da costa da Bahia, talvez como um bloco florístico único. Então, o surgimento de um clima sazonal na Floresta de Linhares teria levado a mudanças na composição florística, com efeitos negativos sobre a vigorante influência da flora "pluvial" baiana. Como herança dessa antiga ligação, entretanto, permaneceram na Floresta de Linhares espécies endêmicas e elementos tipicamente amazônicos compartilhados com a costa da Bahia, tal como descrito anteriormente.

De fato, essa é uma interessante hipótese que poderá ser confirmada se explicações plausíveis para a permanência dessa "herança pluvial" forem comprovadas. É possível que espécies com requerimentos fisiológicos incompatíveis com um clima sazonal tenham sobrevivido sobretudo em trechos onde solos podem se manter úmidos ao longo de todo o ano, tal como às margens de cursos hídricos. Ou que a permanência na Floresta de Linhares esteja ligada a uma capacidade de resistir a curtos períodos de seca de algumas espécies pluviais. Por outro lado, o tempo transcorrido desde que o clima passou a ser mais seco pode não ter sido ainda suficiente para a extinção local de tais espécies.

As afinidades florísticas com o Médio Vale do rio Doce e a Falha de Campos dos Goytacazes

Como mencionado anteriormente, existem estudos que sugerem uma forte ligação florística da Floresta de Linhares com florestas do Médio Vale do rio Doce. Na verdade, isso foi mostrado primeiramente por Jesus & Rolim (2005) utilizando dados florísticos conjugados de Lombardi & Gonçalves (2000) e Lopes *et al.* (2002) para a região do Parque Estadual do Rio Doce e Estação Ecológica de Caratinga, ambos localizados no leste de Minas Gerais. Essa é uma região de embasamento Pré-Cambriano caracterizada por fundos de vales e colinas entre 250-600 metros de altitude e clima estacional marcado por um período seco que se estende de maio a setembro e gera déficit hídrico durante 4-5 meses (Cupolillo *et al.* 2008). No Médio Vale do rio Doce desenvolve-se uma floresta estacional semidecidual submontana de acordo com a classificação de Veloso *et al.* (1991).

Saiter *et al.* (2015), entretanto, relataram a importância de diferenças climáticas decorrentes do aumento da distância do oceano sobre a variação florística ao longo da bacia do rio Doce. Segundo os autores, o clima na parte costeira da bacia é menos sazonal do que no seu interior. Esse contexto acaba alimentando dúvidas sobre qual diferença florística seria a mais forte, a existente entre a Floresta de Linhares e a Hileia Baiana, ou aquela entre a Floresta de Linhares e o Médio Vale do rio Doce. Esperamos esclarecer tal questão mais à frente, no tópico sobre índices de similaridade.

Antes, porém, é pertinente retomar o que já mencionamos sobre o estudo de Saiter (2015). Tal estudo descobriu um forte turnover de espécies arbóreas na latitude 19º S, o que sugere maiores afinidades florístico-ecológicas da Floresta de Linhares com florestas semidecíduas do Médio Vale do rio Doce e do sul do Espírito Santo e norte do Rio de Janeiro, nesse último caso uma região denominada de Falha de Campos dos Goytacazes por Oliveira-Filho & Fontes (2000). Vale ressaltar que, embora Oliveira-Filho & Fontes (2000) tenham caracterizado a Falha de Campos dos Goytacazes como uma região costeira onde a sazonalidade climática provoca a interrupção de florestas ombrófilas, análises posteriores realizadas por Oliveira-Filho *et al.* (2005) indicaram não haver uma forte interrupção na distribuição de espécies arbóreas na região, uma vez que variações florísticas acompanhavam o aumento gradual de umidade no sentido norte.

De fato, Silva & Nascimento (2001) já haviam constatado a semelhança florística da Floresta de Linhares com a Estação Ecológica Estadual de Guaxindiba (Mata do Carvão), uma floresta semidecídua sobre tabuleiros localizada no município de São Francisco do Itabapoana, norte do Rio de Janeiro. Segundo esses autores, é marcante a presença de *Paratecoma peroba* (Record) Kuhlm. na Estação Ecológica Estadual de Guaxindiba, uma espécie arbórea decídua típica da Floresta de Linhares e do vale do rio Doce (ver Figura 4). Acrescentamos que estudos também já confirmaram a ocorrência nas florestas semidecíduas do sul do Espírito Santo (por vezes até do norte do Rio de Janeiro) de outras espécies outrora consideradas endêmicas da Floresta de Linhares (Silva & Nascimento 2001; Nascimento & Lima 2008; Dan *et al.*, 2010; Curto 2011; Archanjo *et al.*, 2012; Abreu *et al.*, 2014), como *Campomanesia espiritosantensis* Landrum., *Crepidospermum atlanticum* Daly, *Glycydendron espiritosantense* Kuhlm., *Handroanthus arianeae* (A.H.Gentry) S.Grose, *Swartzia linharensis* Mansano e *Trigoniodendron spiritusanctense* E.F.Guimaraes & J.R.Miguel.

Índices de similaridade e a alta diversidade florística da Floresta de Linhares

Estamos diante de um conjunto de características que nos encoraja a encerrar esse capítulo com alguma abordagem analítica sobre as relações florísticas da Floresta de Linhares. Um forma simples que encontramos para atingir esse objetivo foi calcular índices de similaridade entre as regiões de interesse. A Quadro 1 apresenta a riqueza de espécies arbóreas por região e as similaridades segundo o índice de Sørensen (*S*). As regiões consideradas foram: Floresta de Linhares, Hileia Baiana, Médio Vale do rio Doce e Falha de Campos dos Goytacazes.

Para tanto, extraímos da base de dados NeoTropTree (http://www.icb.ufmg.br/treeatlan/;

Oliveira-Filho 2014) dados de ocorrência de espécies arbóreas em sítios relativamente bem coletados em cada região. A base de dados NeoTropTree compreende listas de espécies arbóreas e dados geoclimáticos para sítios previamente selecionados dentro da região Neotropical. As listas florísticas são obtidas a partir de três fontes primárias de dados: (a) Inventários florísticos e fitossociológicos publicados; (b) Estudos taxonômicos; (c) Registros de herbários disponíveis no Herbário Vitual da flora e dos fungos – INCT (http://inct.splink.org.br/), dentre os quais são priorizados aqueles sob determinação de taxonomistas. Depois agrupamos os dados dos sítios com o claro objetivo de potencializar as similaridades em um contexto regional, diminuindo assim o efeito de esforços de coleta sobre a composição de cada sítio. Então, obtivemos uma matriz binária composta por quatro regiões (linhas), 1744 espécies (colunas) e 3641 registros de ocorrência. A relação de sítios agrupados por região também está disponível no Quadro 1.

De maneira complementar, utilizamos a mesma matriz binária para também realizar uma clássica análise de agrupamento por meio da técnica UPGMA (*Unweighted Pair Group Method*) e utilizando o mesmo índice de similaridade. O resultado dessa análise está na dendrograma da Figura 2. Utilizamos para todas as análises o pacote estatístico PAST 2.15 (Hammer *et al*., 2001). Uma rápida inspeção nos resultados do Quadro 1 foi suficiente para despertar algumas conclusões. A Floresta de Linhares é tão similar à Hileia Baiana quanto à Falha de Campos de Goytacazes. Proporcionalmente, a similaridade em relação ao Médio Vale do rio Doce também é alta. Embora o dendrograma tenha apresentado a separação da Hileia Baiana em relação ao grupo composto pelas outras três regiões, o coeficiente de correlação cofenética foi baixo (0,61). Segundo Rodrigues & Diniz-Filho (1998), coeficientes menores que 0,80 podem indicar inconsistência entre as matrizes de valores cofenéticos e de valores de similaridade originais, isto é, uma falsa hierarquia entre grupos.

Isso significa que, para a Floresta de Linhares, as relações florísticas estabelecidas por estudos prévios devem ser interpretadas com certo cuidado. Não há como apoiar claramente uma maior ou menor relação florística da Floresta de Linhares com uma ou outra região, ainda que, no presente caso, a similaridade com a Falha de Campos dos Goytacazes tenha sido ligeiramente maior.

Estamos, na verdade, motivados a afirmar que a flora da Floresta de Linhares corresponde a uma “grande mistura” de espécies com diferentes requerimentos fisiológicos relacionados à disponibilidade de água no ambiente. Usamos a palavra “grande” com o verdadeiro intuito de expressar a alta diversidade ali encontrada, e a palavra “mistura” no sentido de reportar a equilibrada inter-relação que existe tanto com as florestas megadiversas da Hileia Baiana, quanto com as florestas naturalmente mais pobres em espécies do Médio Vale do rio Doce e da Falha de Campos dos Goytacazes. Entretanto, isso não deve ser entendido como uma recusa da quebra biogeográfica entre os blocos sul e norte da Floresta Atlântica em plena Floresta de Linhares (já discutida nesse capítulo), pois, de fato, não há dúvidas de que várias espécies têm essa região como seu limite latitudinal de distribuição geográfica. Além disso, é notório que a composição florística da Hileia Baiana tem menor relação com a flora do Médio Vale do rio Doce (S = 0,480) e da Falha de Campos dos Goytacazes (S = 0,504).

Tal abordagem apenas reforça a importância da Floresta de Linhares para a riqueza fitogeográfica do leste do Brasil e a necessidade de conservação de seus remanescentes. Apesar de existir um grande bloco florestal protegido por meio de reservas públicas e privadas (cerca de 48.000 ha), todo o resto da Floresta de Linhares já foi destruído ou permanece na forma de fragmentos muito pequenos que estão isolados por uma matriz agropecuária e experimentam os mais diversos tipos de impactos. Nesse cenário, esperamos que nossas discussões possam estimular futuros estudos sobre a elevada diversidade florística ali encontrada e, quem sabe, projetos destinados à sua conservação.

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Figura 1. Fisionomia semidecídua da Floresta de Linhares. Fotografias obtidas no limite oeste da Reserva Biológica de Sooretama em outubro de 2010 (A, ao fundo) e outubro de 2014 (B). O intervalo entre a segunda metade de setembro e o final de novembro é considerado um período de transição seco-úmido. Fotografias de Gilberto Terra (A) e Geovane S. Siqueira (B).

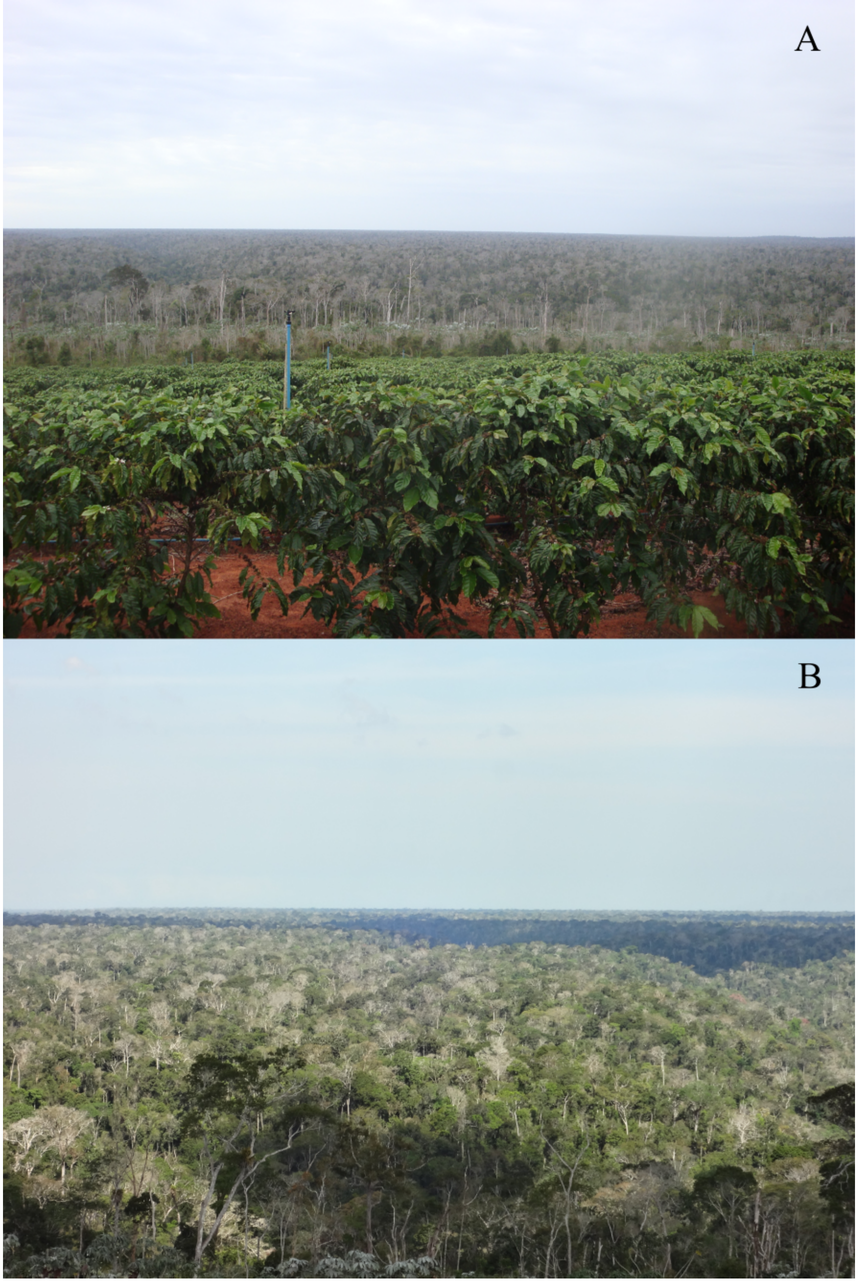


Figura 2. Mapa fitogeográfico do Estado do Espírito Santo segundo Ruschi (1950). Reprodução autorizada pelo Arquivo do Instituto Nacional da Mata Atlântica.

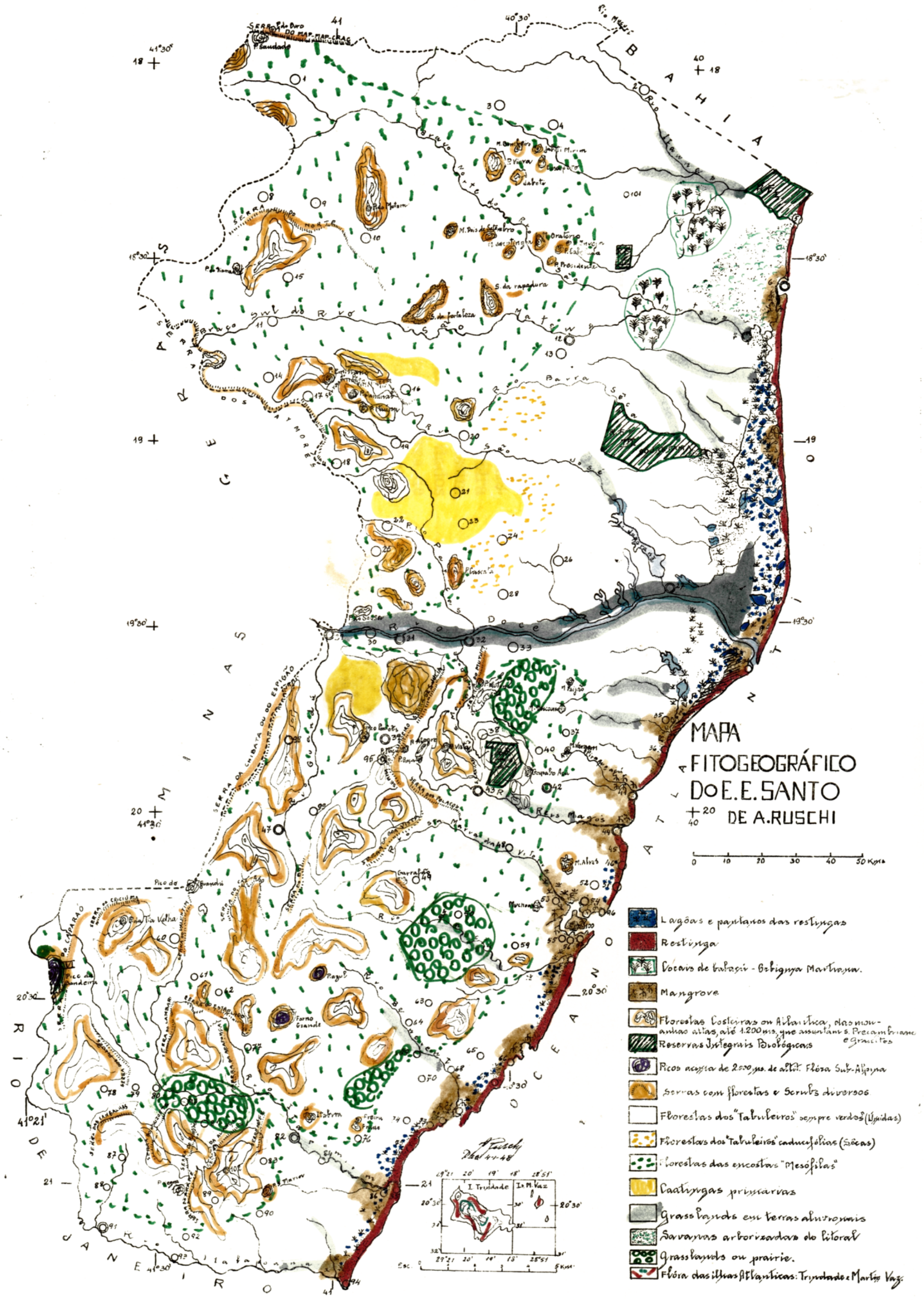


Figura 3. Mapa fitogeográfico do Estado do Espírito Santo segundo Ruschi (1969). Reprodução autorizada pelo Arquivo do Instituto Nacional da Mata Atlântica.

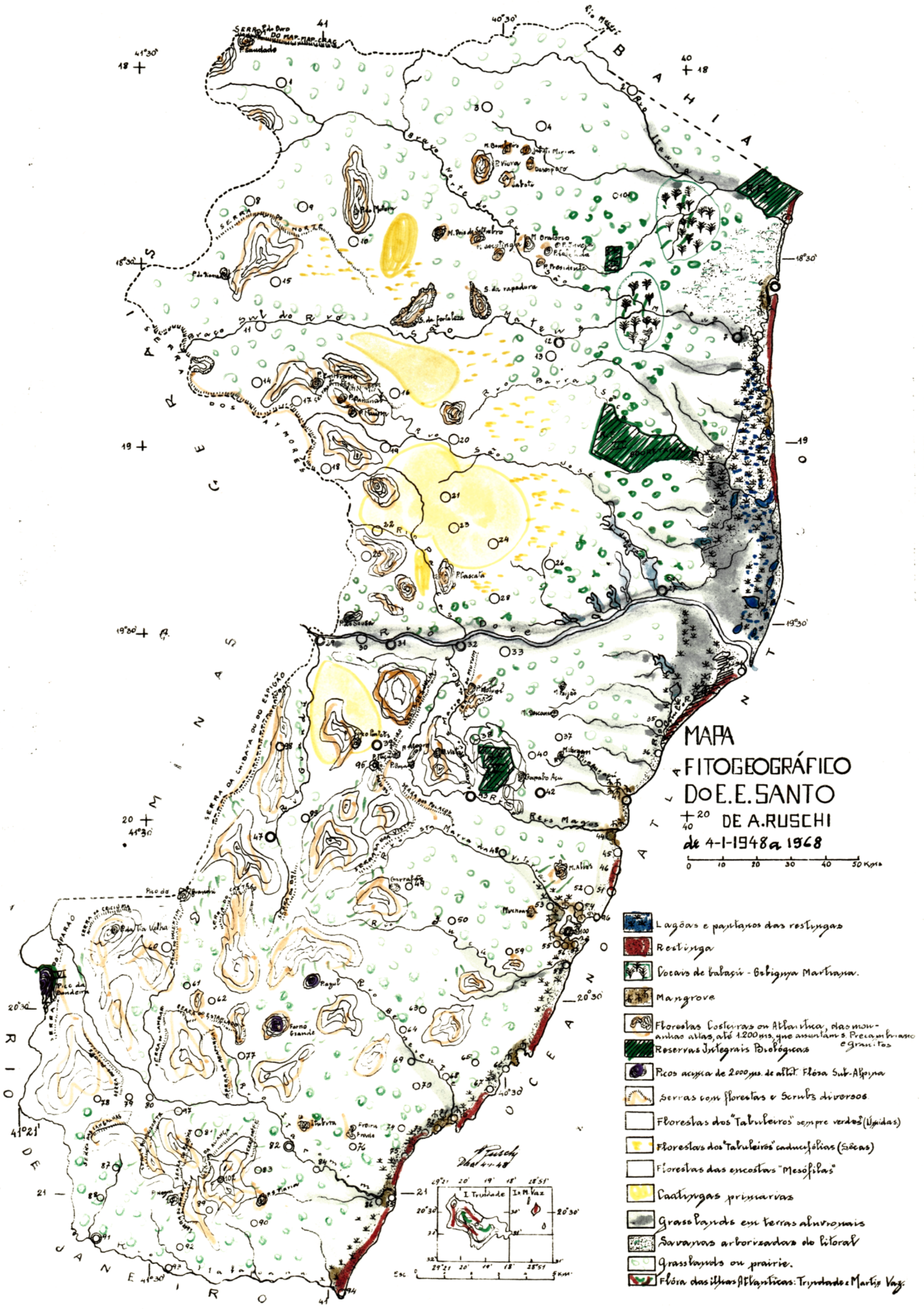
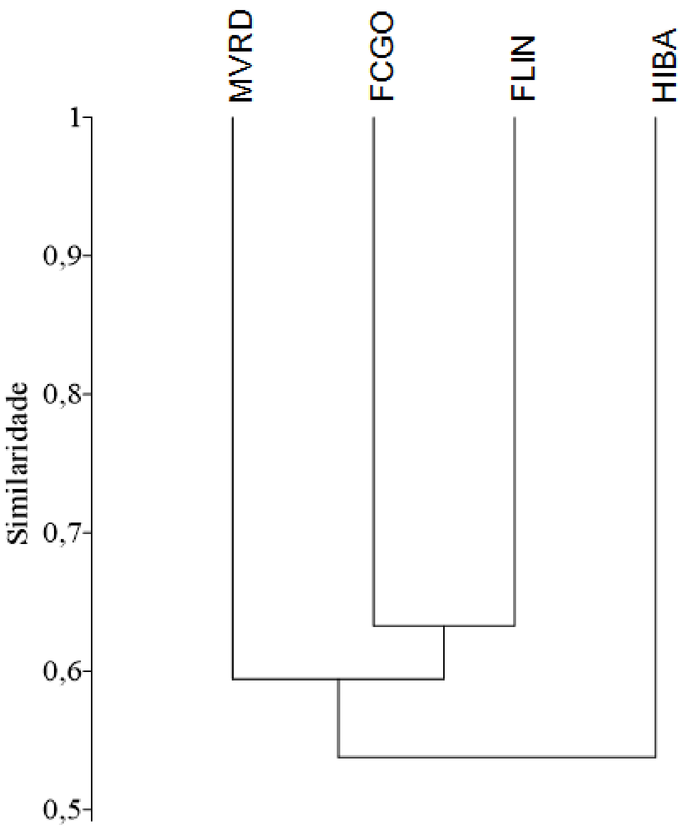


Figura 1

Figura 4. Indivíduo de *Paratecoma peroba* (Record) Kuhlm. em São João de Petrópolis, município de Santa Teresa, Espírito Santo. Uma espécie decídua típica da Floresta de Linhares e do vale do rio Doce, mas que também pode ser encontra em florestas estacionais semideciduais do sul do Espírito Santo e norte do Rio de Janeiro. Fotografia de Felipe Z. Saiter.

Figura 5. Dendrograma obtido por análise de agrupamento (UPGMA) a partir de listas florísticas de quatro regiões da Floresta Atlântica no leste do Brasil. Coeficiente de correlação cofenética = 0,61. FLIN, Floresta de Linhares; HIBA, Hileia Baiana; MVRD, Médio Vale do rio Doce; FCGO, Falha de Campos dos Goytacazes.



Quadro 1. Riqueza de espécies arbóreas e similaridades florísticas de quatro regiões do leste do Brasil.

Riqueza de espécies arbóreas				
Floresta de Linhares (FLIN)				931
Hileia Baiana (HIBA)				1037
Médio Vale do rio Doce (MVRD)				852
Falha de Campos dos Goytacazes (FCGO)				821
Similaridade Florítica – Índice de Sørensen				
	FLIN	HIBA	MVRD	FCGO
FLIN	1			
HIBA	0,629	1		
MVRD	0,571	0,480	1	
FCGO	0,633	0,504	0,617	1
Sítios agrupados em cada região				
FLIN: Floresta Nacional de Goytacazes, Reserva Biológica de Sooretama e Reserva Natural Vale.				
HIBA: Ilhéus, Itacaré, Porto Seguro, Reserva Biológica de Una e Serra Grande.				
MVRD: Antônio Dias, Estação Ecológica de Caratinga, Ipaba, Ipanema e Parque Estadual do Rio Doce.				
FCGO: Castelo, Fazenda do Ouvidor, Floresta Nacional de Pacotuba, Mata Bom Jesus, Mata do Carvão, Reserva Particular do Patrimônio Natural Cafundó e São José de Ubá.				

Considerações Finais

Os resultados apresentados nesta tese me permitem concluir que a variação florística na região central do Domínio Atlântico brasileiro é influenciada por gradientes ambientais e pela distância geográfica entre sítios. Destaco, entretanto, que o determinismo ambiental foi mais importante do que a distância geográfica para explicação dos padrões fitogeográficos regionais e sub-regionais. Apesar de fatores históricos serem de difícil mensuração, devo também indicar que as evidências existentes na literatura sobre mudanças climáticas pretéritas oferecem interessantes justificativas para os padrões fitogeográficos em escala mais ampla.

Tal como informei na Introdução Geral, a integração entre os capítulos se deu no contexto da conservação de florestas na região central do Domínio Atlântico. Percebo que isso foi um reflexo da grande complexidade fitogeográfica que encontrei na região central do Domínio Atlântico. Essa complexidade é certamente fruto da grande heterogeneidade ambiental e florística dessa região que é reconhecida pelos seus elevados níveis de diversidade e endemismo de plantas.

Diante disso, devo ressaltar aqui a necessidade de se considerar as especificidades florístico-ecológicas em diferentes escalas durante o planejamento de ações conservacionistas na região central do Domínio Atlântico. Isso significa que as características de diferentes ambientes e florestas devem ser consideradas em ações locais ou sub-regionais destinadas, por exemplo, à restauração de áreas degradadas. Quero dizer que, no caso de recursos bióticos usados na restauração, cuidados devem ser tomados para que espécies típicas de um determinado tipo florestal ou sub-região não sejam incorporadas em projetos executados em ambientes ecologicamente distintos. Isso garantirá não só a economia e o sucesso de tais projetos, como também uma ordem mais natural dos processos ecológicos. De outro modo, exemplificando uma possível abordagem de gestão em macroescala, as florestas do Espírito Santo (ao menos grande parte delas) e do leste da Bahia não devem ser tratadas em um mesmo contexto de identificação de áreas prioritárias para conservação. Não faz muito sentido, pelo menos floristicamente, priorizar uma área do leste da Bahia, e não uma do Espírito Santo, sob o argumento de que ambas pertencem a florestas similares dentro do chamado “Corredor Central da Mata Atlântica”. Fica bastante claro que, a natureza sempre oferecerá subsídios para as tomadas de decisão relacionadas à conservação da biodiversidade. Cabe a nós, encontrar tais subsídios por meio das ferramentas científicas disponíveis, ainda que elas possam ser um tanto quanto limitadas.