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ORIGINAL ARTICLE

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

Felipe Zamborlini Saiter[1,2]*, Jason L. Brown[3], William Wayt Thomas[4], Ary T. de Oliveira-Filho[2] and Ana Carolina Carnaval[3]

[1]*Instituto Federal do Espírito Santo, Santa Teresa, ES 29650-000, Brazil,* [2]*Departamento de Botânica, Universidade Federal de Minas Gerais, Belo Horizonte, MG 31270-901, Brazil,* [3]*Department of Biology, City College of New York and the Graduate Center of CUNY, New York, NY 10031, USA,* [4]*The New York Botanical Garden, Bronx, NY 10458-5126, USA*

*Correspondence: Felipe Z. Saiter, Instituto Federal do Espírito Santo, Santa Teresa, ES 29650-000, Brazil.
E-mail: fsaiter@ifes.edu.br

ABSTRACT

Aim Using a comprehensive floristic database (2616 species, 36,004 occurrence records from 128 unique localities), we model species turnover along the central region of the Atlantic Forest hotspot to (1) test whether local rivers, particularly the Rio Doce, are associated with marked biogeographical breaks, and (2) investigate how regional compositional changes correlate with geo-climatic variables.

Location The central region 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 of turnover in species composition occurred around latitudes 18°–19° S, *c.* 50–100 km north of the Rio Doce, and concurred with shifts in availability of both humidity and energy. We identified three major floristic regions in the central region of the Atlantic Forest, which we called Bahia Interior Forests, Bahia Coastal Forests, and the Krenák-Waitaká Forests – each of them divided into two to four subregions.

Main conclusions Our results suggest that local climatic conditions, not riverine barriers, drive biogeographical shifts in this region – a finding that supports studies of current and historical determinants of the composition of the Atlantic Forest biota. Floristic composition at higher elevations (> 600 m) is clearly distinct from those in lower elevations, likely as a result of physiological constraints 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.

Keywords

biogeographical break, conservation planning, Doce River, floristic turnover, GDMs, regionalization, Rio Doce, tree species

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

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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 data sets for model training and validation (Ferrier *et al.*, 2002). Turnover of plant species is known to be influenced by both topographical 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 phytogeographical 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 *et al.*, 2006; Lírio *et al.*, 2015; but see Gascon *et al.*, 2000; Dexter *et al.*, 2012; and Souza *et al.*, 2013). 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, 2003; Hayes & Sewlal, 2004; Haffer, 2008; Ribas *et al.*, 2012).

On the other hand, large-scale studies based on reliable floristic data sets of well-known tropical forest plant groups (e.g. trees) and climatic data provided by interpolated databases such as WorldClim (Hijmans *et al.*, 2005) and CliMond (Kriticos *et al.*, 2012) demonstrate strong correlations between floristic composition and climatic shifts (e.g. Toledo *et al.*, 2012; Qian, 2013; Rezende *et al.*, 2015; Saiter *et al.*, 2015). Such a pattern is based on the physiological requirements of species, especially those related to the availability of both water and energy (Hawkins *et al.*, 2003). Water scarcity may limit the ranges of plant species due to negative effects on mineral absorption by the roots, sap transportation and leaf metabolism (Grubb, 1977; Pausas & Austin, 2001). In turn, low temperature and low radiation (both energy-related variables) influence the plant species distribution by affecting leaf metabolism and reproduction (Grubb, 1977; Pausas & Austin, 2001).

We investigate the roles of environmental and landscape shifts on plant turnover in the biodiverse Atlantic Forest of eastern Brazil. Biogeographical studies of multiple animals and plants support the existence of a biogeographical break around the Rio Doce (*c.* 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; Lírio *et al.*, 2015). 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; Lírio *et al.*, 2015), recent analyses suggest that climatic shifts may be responsible for this pattern (Ribeiro *et al.*, 2011; Carnaval *et al.*, 2014). Irrespectively of the underlying mechanisms, the pervasiveness of the biogeographical break leads 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 (2616 species, 36,004 occurrence records) and environmental information from 128 unique localities, here we modelled turnover in the floristic composition of the central region 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 phytogeographical patterns are better explained by shifts in key environmental determinants (i.e. climate or geographical 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 region of the Atlantic Forest in eastern Brazil (Fig. 1a,d), extending between the Recôncavo in the state of Bahia (*c.* 12° S latitude) and the Rio Paraíba do Sul in the state of Rio de Janeiro (*c.* 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 savanna in central Brazil), the Campos Rupestres (highland savannas), and the Caatinga (semi-arid steppe in north-east Brazil).

Occurrence and geo-climatic data

We used a binary matrix of tree species occurrences for 128 sites (Fig. 1a) extracted from NeoTropTree, a database containing checklists of tree species for sites distributed across the Neotropics (Oliveira-Filho, 2014; data downloaded from http://prof.icb.ufmg.br/treeatlan/ on 20 June 2014). NeoTrop-tree checklists were gathered from occurrence records from three basic sources: [a] published floristic and quantitative surveys; [b] taxonomic monographs; and [c] herbarium records available in the Herbário Vitual da Flora e dos Fungos (INCT; http://inct.splink.org.br/). The data were verified and filtered according to information reliability, expert opinion, and the taxonomic literature. As the density of floristic and quantitative surveys for certain localities can be very high, NeoTropTree merges all information available within a locality into a single checklist, excepting when the

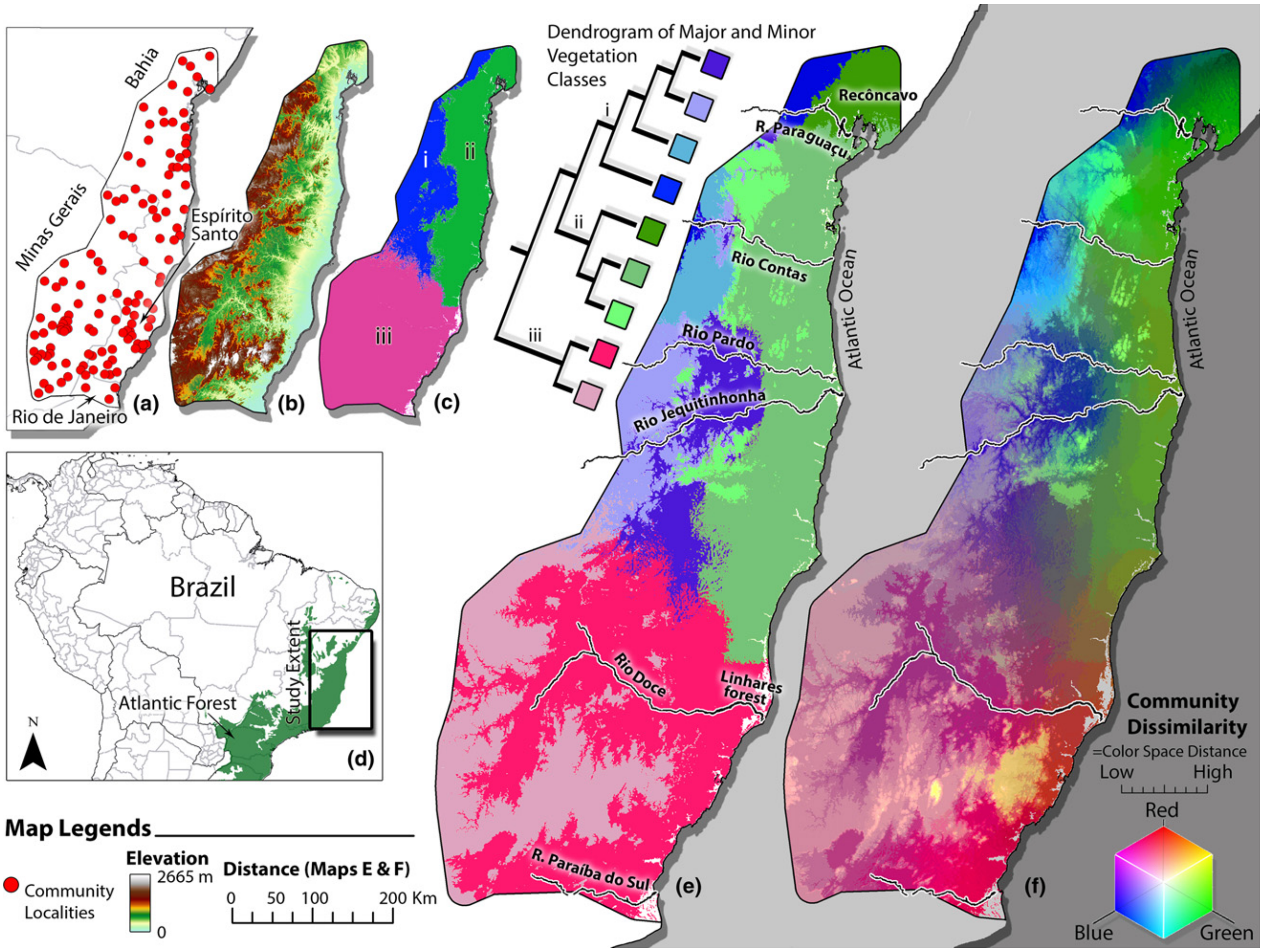

Figure 1 Prediction of turnover patterns in tree species composition in the central region of the Atlantic Forest, eastern Brazil. (a, d) Atlantic Forest domain, study extent, and 128 localities which provided data for a generalized dissimilarity model – GDM; (b) elevation map; (c) major floristic regions classified from GDM: i, Bahia Interior Forests, ii, Bahia Coastal Forests, and iii, Krenák-Waitaká Forests; (e) floristic subregions and their interrelationships; (f) continuous GDM framework.

vegetation type does not remain constant across a maximum radius of 5 km. In this case, each vegetation type is represented by a distinct checklist.

As a result, a total of 2616 species and 36,004 presence records were included in the analyses. From this total, only 12 species are broadly distributed, that is, occur in more than 90 sites. This indicates that our study is mainly based on the distribution of both intermediate-ranged and more endemic species, which are, we argue, more useful in determining spatial patterns of turnover in community composition across a highly biodiverse region.

Present-day climate data consist of Hijmans *et al.*'s (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).

To directly evaluate the role of rivers as elements structuring plant turnover, we created two categorical variables to be included, along with the climatic layers, as predictors in a dissimilarity model. The first depicts all major watersheds present in the region; the second depicts all inter-riverine areas (see Appendix S2).

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 (e.g. Ferrier *et al.*, 2002; Brown *et al.*, 2014; Lasram *et al.*, 2015). A common use of GDM is to predict spatial patterns of turnover in community composition across large areas (Brown *et al.*, 2014). 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 geographical information system software, each axis is assigned a separate RGB colour (red, green or blue).

To match the resolution of the community composition data obtained from NeoTropTree, we upscaled the environmental data to 5 km^2 by averaging the higher resolution (30 arc-second) data. Both data sets (species presence and environmental data) were input into a GDM 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 with 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 reduced 39 initial predictor variables 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 two to four subregions. The numbers of regions and subregions were based on two-step cluster analyses in SPSS 21.0 (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 region of the Atlantic Forest. This is a considerable proportion, as statistical noise and unexplained variation are usually very high in analyses based on species occurrence data (ter Braak, 1987). The unexplained fraction of turnover likely results from unmeasured biotic interactions (e.g. competition and natural enemies), false absences in the checklists (e.g. misidentification of species and mismatching in sample effort among sites), unmeasured anthropogenic effects on forest composition, and stochastic variation.

The continuous GDM framework (Fig. 1f) can be split into three major floristic regions (hereafter referred to Bahia Interior Forests, Bahia Coastal Forests and Krenák-Waitaká Forests; Fig. 1c). The Bahia Interior Forests encompassed moist and dry forests of north-eastern Minas Gerais and inland Bahia, and is further divided into four subregions (Fig. 1e). The Bahia Coastal Forests include the wet forests north of 18–19° S, which can be further separated into three subregions (Fig. 1e). In turn, the Krenák-Waitaká forest region encompasses two sub-regions of moist forest south of 18–19° S (Fig. 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 subregions that are distributed along distinct elevational belts: forests at low and mid-elevation (up to 500–600 m) are compositionally different from those at higher elevations (>600 m; see correspondence between Fig. 1b,e). In the Bahia Coastal Forests, we further identify two subregions 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 subregions 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 dendrogram in Fig. 1 for relationships among regions and subregions).

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 north-eastern Minas Gerais (Fig. 1).

Instead, the GDM identifies 12 significant predictors of species composition turnover; none of them is a river variable (Fig. 2). In fact, the final model is no different from a GDM built with no river information (not shown). The top five predictors of species turnover, in relative contribution, are radiation of wettest quarter (Bio 24), mean moisture index of warmest quarter (Bio 34), elevation, mean temperature of warmest quarter (Bio 10), and precipitation of driest month (Bio 14). This attests 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 region of the Atlantic Forest.

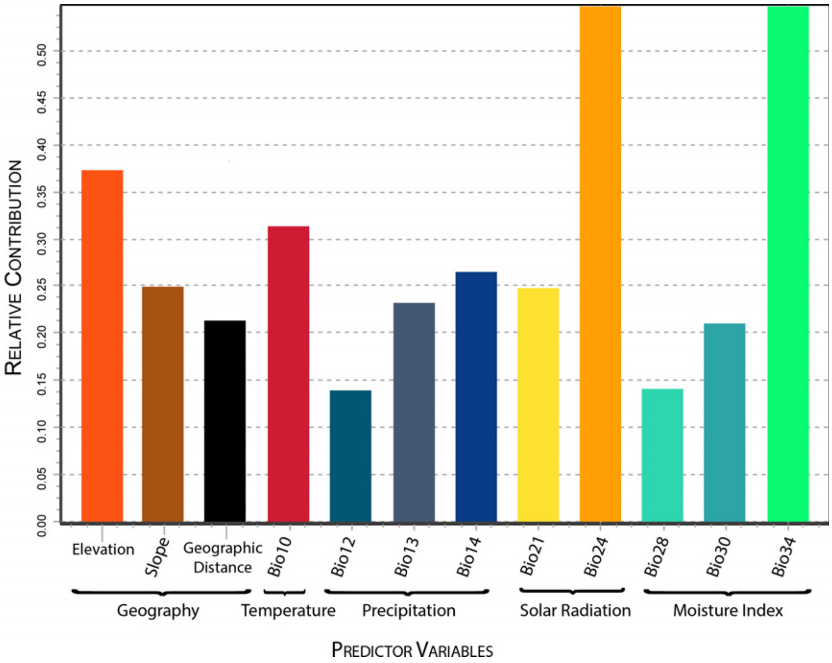

Figure 2 Twelve significant geo-climatic predictors of tree species composition in the central region of the Atlantic Forest, eastern Brazil.

Instead of being caused by a riverine barrier, the phytogeographical break near the Rio Doce seems to have a climatic basis.

Because the role of rivers as effective barriers to dispersal is tied to river width, river dynamics and specific modes of dispersal (Gascon *et al.*, 2000), we expected the Rio Doce not to impose a strong barrier effect to tree species. First, the Rio Doce is not as large as the main Amazonian rivers postulated as effective barriers to plants and animals (Mori, 1990; Costa, 2003; Hayes & Sewlal, 2004; Haffer, 2008; Ribas *et al.*, 2012). As the river is no more than 1 km wide, even at its mouth, we expect it to restrict the dispersal of only a few species whose fruits are unable to float (barochoric trees). In the case of animal-dispersed (zoochoric) plant species, especially when seeds are carried by non-volant animals, dispersion may occur in the headwaters, where the river is narrower (see Gascon *et al.*, 2000; Souza *et al.*, 2013 for studies in the Amazon). In addition, channel migration through shifts in sedimentation dynamics over time (e.g. meander cut-offs) can physically transfer land blocks and their biota from one margin to another, promoting species dispersal (Gascon *et al.*, 2000). In the Rio Doce, this hypothesis is supported by geomorphological evidence of river channel migration (i.e. palaeochannels) in middle and lower valleys (Mello *et al.*, 1999; Cohen *et al.*, 2014; Polizel & Rossetti, 2014).

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 south-eastern 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 the 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 north-eastern Minas Gerais, has indeed been described as seasonal subhumid 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; Duarte *et al.*, 2014; Oliveira-Filho *et al.*, 2015). We can still recognize these influences in our analysis. Subtropical taxa such as *Araucaria angustifolia* and *Mimosa scabrella*, as well as many species of Lauraceae, Melastomataceae, Monimiaceae, Myrtaceae and tree ferns (Behling & Pillar, 2007; Duarte *et al.*, 2014; Lírio *et al.*, 2015) are solely observed in part of the Krenák-Waitaká Forests (the Mantiqueira Range, around the 20° 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, *c.* 48–18 ka (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*, *Caraipa densifolia*, *Erythroxylum macrophyllum*, *Macoubea guianensis*, *Parkia pendula* and *Pagamea guianensis*. This pattern is predicted by hypotheses of a historical bridge between Amazonia and the Atlantic Forest through the gallery forests within the north-east—south-west corridor of open vegetation formations of central Brazil, through the Caatinga and the Cerrado (Oliveira-Filho & Ratter, 1995; Costa, 2003; Oliveira-Filho *et al.*, 2015).

Historical climatic conditions may also provide an explanation for the number of endemic species shared between wet southern Bahia (e.g. *Beilschmiedia linharensis*, *Cariniana parvifolia*, *Hydrogaster trinervis*, *Kielmeyera occhioniana*, *Mollinedia marqueteana*, *Plinia stictophylla*, *Riodocea pulcherrima*, *Simira grazielae* and *Trattinnickia mensalis*) 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 centre of plant diversity (Thomas *et al.*, 1998), and it has been hypothesized that rain forest coverage has remained stable in this region for a long time (Carnaval & Moritz, 2008). Further, palaeoclimate studies suggest that coastal Bahia was as wet in the mid-Holocene (roughly 6 ka) 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 subregion identification process implemented by our approach clearly distinguishes the higher elevation forests of the central region 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 subregions is remarkable because some species commonly found in the Atlantic Forest-Caatinga transition (e.g. *Acrocomia intumescens*, *Myrcia rosangelae*, *Duguetia moricandiana* and *Gochnatia oligocephala*) 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 palaeoclimate 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 world-wide (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. This approach, we argue, may likewise be useful in other biomes world-wide: all ecoregions identified by Olson *et al.*'s (2001) were based on general landscape or vegetation maps, and may be improved through the incorporation of plant species occurrence data. For North America, for instance, Olson *et al.*'s (2001) ecoregion map is based on a modified version of Omernik's (1995) work, which comprises a classification of landscapes according to geology, physiography, vegetation, climate, hydrology, soils and geographical range of a limited number of animal species. In the Afrotropics, White's (1983) vegetation map was used for ecoregion definition (Olson *et al.*'s, 2001).

Our results reinforce the importance of employing robust and verified data sets of occurrence records across different taxa and at finer scales, in lieu of on maps of environment and vegetation, to delimit biogeographical 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 phytogeographical 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 Geo-climatic variables.
Appendix S2 Major watersheds and inter-riverine areas.

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 < 11% of its historical range, yet its fragments harbour 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. analysed the data; A.C.C., F.Z.S. and J.L.B. led the writing.

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