Correlation of variations in species abundance of Atlantic forests regenerating on abandoned pastures with different environmental and spatial variables

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Introduction

Two billion hectares of degraded forests and savannas have been indicated as potential areas for restoration on the planet (Laestadius et al. 2012). In Brazil, it is estimated that there are approximately 177 282 km² of potential area for forest restoration (Laestadius et al. 2011). These areas are highly fragmented and usually have reduced agricultural potential due to soil degradation and compaction caused by livestock (Rodrigues et al. 2009). Nevertheless, they have great potential as carbon sinks and for biodiversity recovery (Lima et al. 2020).

The recovery of rainforests on abandoned pastures occurs gradually, following processes of species colonisation and increasing complexity of vegetation composition and structure (Chazdon 2014; Scervino and Torezan 2015). It usually begins with small patches composed of dominant and light-demanding species, which often are dispersed by the wind and occasionally by animals. These include ferns, shrubs and fast-growing tree/shrub species. These species, in turn, provide favourable conditions for the establishment of long-lived shade-tolerant species (Scervino and Torezan 2015). Abiotic factors have an important role in the establishment of woody species in open areas (Chazdon 2014; Reid et al. 2015). Heterogeneity of physical-chemical properties of the soil, luminosity and canopy openness, for instance, were found to be related to the composition of regenerating subtropical forests (Higuchi et al. 2015; Silva et al. 2016). Distance from forest fragments was also suggested as a factor influencing the species composition of regenerating forests on abandoned pastures. As the distance from the nearest forest edge increases, the number of species tends to decrease (Crouzeilles et al. 2016; Uriarte and Chazdon 2016).

Besides the portion of variation in species composition that is solely related to the environment, there is a fraction of variation that can be spatially structured. This suggests the occurrence of neutral processes, such as dispersal limitation, stochastic spatial distribution, and random speciation (Hubbell 2001; Gotelli 2008; Lewis et al. 2014; Guo et al. 2017). In addition, a fraction of the variation in species composition could be correlated with spatially-structured environmental features. This suggests the effects of niche-based processes mediated by environmental characteristics, which, in turn,
are spatially structured, or dispersal-based spatial processes that are actually interpreted as measured but irrelevant environmental gradients (Tuomisto et al. 2012; Arellano et al. 2016). Studies investigating the effects of environmental variables and spatial structures on species composition are important for understanding processes of forest regeneration in open areas. Such studies could guide the adoption of appropriate methods of forest restoration, thus avoiding wasted time and resources (Hiers et al. 2016).

In this study, we evaluate whether environmental and spatial variables are related to the variation in woody species abundance of regenerating forests on abandoned pastures in the subtropical Atlantic Forest. We intend to answer two questions:

(i) Which environmental variables are related to the abundance of woody species growing in regenerating subtropical Atlantic forests? We expect to find effects of soil (physical and chemical properties), relief (slope and elevation) and distance from forest fragments on species composition, as these variables appear to be strong drivers of floristic variation in the Atlantic Forest (Narvaez et al. 2014; Higuchi et al. 2015; Schaefer et al. 2015; Guo et al. 2017).

(ii) Is the spatial structure of the vegetation and of the environmental variables related to the variation in species abundance of regenerating subtropical Atlantic forests? We expect to find a significant effect of these components, because recent studies have indicated that spatially-autocorrelated environmental variables and spatial structuring of communities driven by biotic processes are related to species abundance variation in the Atlantic Forest (Gasper et al. 2015; Neves et al. 2015; Saiter et al. 2015; Maçaneiro et al. 2016a; Loebens et al. 2018).

Materials and methods

Study area

The study area (27°05’S–49°11’W; 27°07’S–49°13’W) is located in the Serra do Itajaí National Park, state of Santa Catarina, southern Brazil (Figure 1). The study area has a total area of ~250 ha, with an altitude varying from 700 to 1 039 m a.s.l. The predominant vegetation in the study area is the subtropical upperhill broadleaved evergreen rainforest (Oliveira-Filho 2015), hereafter referred to as evergreen rainforest (ERF); the ERF is part of the Atlantic Forest (Gasper et al. 2015; Neves et al. 2015; Saiter et al. 2017). Each area was on a slope with the same land use history (intensive cattle raising) (Figure 2).

We systematically distributed 15 sample plots of 10 × 20 m (0.02 ha) in each area. We arranged the sample plots in three transects starting at the base of the slope and finishing at the top, aiming to capture the environmental variation in each area (Figure 1). We placed the sample plots approximately 15 m apart with 20 m between transects. In each plot we sampled the canopy (UL), i.e., woody individuals with diameter at breast height (DBH) ≥ 5.0 cm. On each sample plot we placed a 10 × 10 m (0.01 ha) subplot to sample the understory (LL), i.e., woody individuals with height ≥ 50 cm and DBH < 5.0 cm. The following variables were measured for each individual in the UL: perimeter at breast height (PAP) measured at 1.3 m from the ground level; total plant height, which was predicted visually; and species identification. For the individuals in the LL, only the total height of each plant was measured.

We identified the botanic material through comparisons with vouchers deposited at Herbarium Dr Roberto Miguel Klein–FURB and by consulting taxonomic literature and different experts. We used the family and species classification system proposed by the APG IV (2016) in accordance with the Flora do Brasil (2020) database.

Considering that the spatial structure of the vegetation may be associated with seed dispersal processes (Gotelli 2008; Lewis et al. 2014; Guo et al. 2017), we classified the species according to their dispersal syndrome according to Van der Pijl’s (1982) morphological criteria: wind dispersal (anemochorous), spontaneous explosion dispersal (autochorous), and animal dispersal (zoochorous). To perform this classification, we analysed seed morphology of the woody species observed in the study area. On each sample plot, we collected a 500 g sample of top soil (0–20 cm), as suggested by Santos et al. (2013).
soil sample consisted of four samples collected within each sample plot. The samples were placed in plastic bags, labelled, and sent to the Instituto Brasileiro de Análises (IBRA/ São Paulo) where 32 chemical variables (see supplementary material) and three physical variables, namely, proportions of silt, sand and clay, were measured. The slope of each sample plot was recorded using a Bosch GLM 80 laser measure, and the soil penetration resistance (SPR) was determined using a FieldScout SC 900 penetrometer (Teixeira et al. 2017). The distance (in meters) of each plot to the nearest forest fragment (FF) was calculated, and the elevation of each plot was obtained from a regional digital elevation model using ArcGIS 10.1 (ESRI 2012).

Data analysis

We modelled the association of environmental and spatial variables with species abundance matrices for the UL and LL using transformation-based redundancy analysis (tb-RDA; Borcard et al. 2011). Two tb-RDA models were fitted for each abandoned pasture, one for the UL and another for the LL. To identify collinear environmental variables and prevent their inclusion in the models, we conducted a Principal Component Analysis (PCA) including all the variables described above as per Eisenlohr’s (2014) recommendations. From 39 variables, we considered 29 in the analysis (Table S1). We applied the Hellinger transformation to the species matrices aiming to avoid meaningless results generated by the application of methods using the Euclidean distance in matrices with double zeros (Legendre and Legendre 2012). Subsequently, we standardised the scale of the environmental variables to circumvent differences in units of measurement (Zar 2010).

The geographical coordinates (latitude and longitude) of the sample plots were used to create spatial variables known as Moran’s Eigenvector Maps (MEMs), that is, orthogonal vectors that maximize spatial autocorrelation (Moran’s I.

Figure 1: (a, b) Location of the study areas in Faxinal do Bepe and distribution of the sample plots along the three gradients: (c) Area 1; (d) Area 2; and (e) Area 3.
index) between points, which are used to represent the spatial relationship among sets of points (Dray et al. 2006). This was carried out using the Delaunay triangulation with the aid of the ‘spacemakerR’ R package.

For each area, 14 MEMs (n–1) were generated and these variables were used as predictor variables in the respective tb-RDA model. We selected statistically significant MEMs in the tb-RDA model (α = 0.05) through forward selection (Blanchet et al. 2008) using the ‘adespatial’ R package. We fitted an additional tb-RDA and applied the same procedure to select significant environmental variables. Finally, we fitted a final tb-RDA embedding the previously selected MEMs and environmental variables as predictors of the abundance of species in each area. The global significance of the models was assessed at α = 0.05 through ANOVA based on 999 permutations (Legendre and Legendre 2012).

Variance partition (Dray et al. 2012; Legendre et al. 2012) was applied to each area in order to assess the variability in species abundance in different fractions as follows: [a] – amount of variation that is correlated with environmental variables, but is not spatially structured; [b] – amount of variation that is correlated with environmental variables and is spatially structured; [c] – amount of variation that is spatially structured and is not correlated with environmental variables; [d] – amount of variation that remained unexplained, i.e., the model residuals. Analysis to determine if fractions [a] and [c] were significant at α = 0.05 was carried out using ANOVA based on 999 permutations (Legendre and Legendre 2012).

Results

Considering all areas, we sampled 1 334 individuals (UL = 637; LL = 697), identifying 51 species within 24 families (Table 1). The family with the greatest number of individuals and species was Asteraceae (nine species and 872 individuals). More than 65% of the observed species have zoochorous dispersal, while 70% of the sampled individuals have anemochorous dispersal. The UL contained 10 species with zoochorous dispersal, while 32 zoochorous species were present in the LL (Table 1). Area 1 had the greatest species richness (UL = 12 spp.; LL = 34 spp.), followed by Area 2 (UL = 15 spp.; LL = 28 spp.) and Area 3 (UL = 7 spp.; LL = 23 spp.). Area 1 also had the greatest number of individual plants (UL = 272 ind.; LL = 266 ind.), followed by Area 3 (UL = 203 ind.; LL = 286 ind.) and Area 2 (UL = 162 ind.; LL = 145 ind.).

All the tb-RDA models we built were significant at α = 0.05 (Table 2). Considering the UL, we found that the two first axes of the tb-RDAs identified gradients of species abundance in all areas. In Area 1, variation in species abundance was correlated with slope, MEM 2, FF, Zn, and Cu (Figure 3); in Area 2, it was correlated with clay and Zn (Figure 3); and in Area 3, species abundance was correlated with MEM 1 and elevation (Figure 3). Similarly, we also observed a gradient of species abundance in the LL. In Area 1, variation in species abundance was correlated with MEM 2 and slope (Figure 3); in Area 2, it was correlated with MEM 2, clay, Cu, and Zn (Figure 3); and in Area 3, it was correlated with MEM 1, elevation, and H + Al in CEC (Figure 3).

The variance partitioning indicated distinct patterns in each area and layer (Figure 4). Fraction [a] was significant in the UL for Area 1 (F = 4.17, p = 0.001) and in the LL for all areas (Area 1: F = 1.87, p = 0.04; Area 2: F = 2.48, p = 0.01; Area 3: F = 1.49, p = 0.04). Fraction [c], was significant only for the LL in Area 1 (F = 1.79, p = 0.04).

Discussion

We found that the variation in species abundance of regenerating forests on abandoned pastures is driven mostly by different sets of environmental filters and marginally by
spatially-structured biotic processes, even in areas close to each other. Our first hypothesis was confirmed, as soil variables were selected in all models, except in the model for the UL of Area 3. Variables related to topography (i.e., slope and elevation), which function as proxies of soil characteristics (Ferreira-Júnior et al. 2007; Baldeck et al. 2013), were selected in four of the six models. Distance from fragments, on the other hand, appeared in only one model (canopy Area 1).

According to our findings, environmental variation, fraction $a$, accounted for most of the variation in species abundance in both canopy and understory (UL: 32–51%; LL: 6–28%), suggesting that niche-based processes act as the most important drivers of variation in species abundance in...
regenerating abandoned pastures in our study region. This indicates that these canopy communities may be past the early strong influence of neutral processes in structuring the assemblages (Chase 2014). These results are in accordance with the findings of Baldeck et al. (2013) that habitat filtering occurs during early stages of forest development.

Studies on ecological gradients conducted across wider spatial scales have suggested that the composition of woody vegetation is strongly related to climatic variables, including rainfall seasonality, distance from the ocean, and annual temperature range, among others (Eisenlohr and Oliveira-Filho 2015; Oliveira-Filho et al. 2015). At the local level, however, relief and soil properties may be more relevant. On a slope, for example, changes in topography may create abrupt shifts in physical/chemical properties of the soil that could influence distribution patterns of woody species (Narvaez et al. 2014; Maçaneiro et al. 2016a; Silva et al. 2016). Fraction [a] is a conservative estimate of niche-based processes influenced by environmental filters because relevant variables may not have been measured (Arellano et al. 2016). Important variables which may affect community structure, such as soil water holding capacity, microclimate, photosynthetic radiation and canopy cover, have not been considered in this study.

Our second hypothesis in this study was also supported, as spatially-structured environmental factors, fraction [b], and spatial structuring of communities, fraction [c], were found to be correlated with species abundance variation. Spatial structure [c] – which can be interpreted as an overestimate of the importance of dispersal-based processes on community structure, as important spatially-structured environmental variables may have not been measured (Legendre et al. 2009; Baldeck et al. 2013; Arellano et al. 2016) – accounted for only a modest portion of the variation in species abundance in the LL (1–5%), but none of the variation in the UL. This marginal influence of dispersal-based processes in the understory is expected since niche processes are supposed to strongly drive composition in this layer (Gilbert and Lechowicz 2004; Hu et al. 2013).

Further, wind dispersal of propagules appears to drive the structuring of communities with a more homogeneous spatial distribution, as seeds are randomly carried for longer distances. Animal dispersal, in turn, may drive the structuring of communities with greater spatial heterogeneity depending on the scale, as some animals occasionally deposit seeds in microenvironments that are more favourable to germination (Beckman and Rogers 2013; Maçaneiro et al. 2018). Three times more species with zoocchorous dispersal mechanisms were found in the LL than in the UL, and this appears to be related to the stronger relationship of dispersal-based processes with the variation in species abundance in the LL.

Fraction [b], the variation correlated with the spatially structured environment, is challenging to interpret because it can represent the effect of niche-based processes mediated by environmental characteristics that are spatially structured, or dispersal-based spatial processes that are actually interpreted as measured (but irrelevant) environmental gradients (Tuomisto et al. 2012; Arellano et al. 2016). It appears that the first interpretation is the most reasonable for regenerating forests, as the gradients we found consisted mainly of variations in slope, elevation, clay and nutrient content. These factors are known to be related to the structuring of woody communities in the subtropical Atlantic Forest (Gomes et al. 2020). Slope and elevation can be related to soil depth and organic matter content, and clay to soil moisture retention capacity and nutrient availability (Sarkar et al. 2018). Elevation and organic matter content were positively correlated in our data ($r = 0.43$, $p < 0.01$), whereas elevation and soil penetration resistance were negatively correlated ($r = -0.30$, $p < 0.05$). This could be related to the fact that cattle preferred to move over the less elevated portions of the study area because of the gentler slopes. With a lighter cattle trampling intensity, soil compaction tends to be less, thus favouring plant recruitment (Stern et al. 2002). Variations in species abundance throughout local elevation gradients can also be detected in more mature subtropical Atlantic forests: lower portions of hills tend to harbour species with a greater affinity to higher soil moisture contents, whilst higher regions of hills tend to shelter species which are adapted to drier and shallower soils (Klein 1980; Maçaneiro et al. 2016b).

Table 2: Summary of the fitted tb-RDA models. The p-values were generated by permutation-based ANOVAs testing model global significance

| tb-RDA output | Upper Layer | Lower Layer |
|---------------|-------------|-------------|
|               | Area 1      | Area 2      | Area 3 |
| $R^2_{w}$     | 0.58        | 0.32        | 0.18   |
| $p$-value     | 0.001       | 0.004       | 0.015  |
| Explained var. Axis 1 | 37.2% | 26.5% | 27.2% |
| Explained var. Axis 2 | 17.0% | 14.8% | 2.2% |
| Selected variables | MEM 2, Slope, Cu, Zn, Mg/K, FF | Zn, Clay | MEM 1, Elevation |
|               | Area 1      | Area 2      | Area 3 |
|               | 0.14        | 0.37        | 0.16   |
|               | 0.002       | 0.001       | 0.003  |
| Explained var. Axis 1 | 16.2% | 29.9% | 17.9% |
| Explained var. Axis 2 | 9.7%  | 12.3%       | 11.3%  |
| Selected variables | Slope, MEM 2 | MEM 2, Cu, K, CEC, Zn, Clay | MEM 1, Elevation, H+AI CEC |
Figure 3: Ordination diagrams for the fitted tb-RDA models using data on species abundance, and environmental and spatial variables for the upper and lower layers of regenerating forests on abandoned pastures in southern Brazil. MEM: Moran’s Eigenvector Map; Zn: zinc; Cu: copper; FF: distance to nearest forest fragment; CEC: cationic exchange capacity; Mg/K: magnesium/potassium; K CEC: potassium in cationic exchange capacity; H+Al CEC: hydrogen + aluminum in cationic exchange capacity.
note that different experimental designs may be needed to
disentangle niche- from dispersal-based processes inherent
to fraction [b], as stressed by Arellano et al. (2016).

Further studies on abandoned pastures could include
data on soil moisture, microclimate, photosynthetic radiation,
canopy cover, and biotic processes (for example, dispersion,
dynamics, competition, and natural enemies) with the aim
of increasing the amount of explained variance. In addition,
regenerating Atlantic forests that have undergone a different
land use before abandonment should also be included
in further studies investigating environmental and spatial
drivers. This is of importance because community structuring
may also respond to variations in factors such as seed bank,
seed inputs, seedling herbivory, and soil moisture, among
others (Feldpausch et al. 2007).

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Figure 4: Amount of variance explained by the different predictors, namely, fraction [a], the pure environmental variation; fraction [b], the spatially structured environmental variation; fraction [c], the pure spatial variation; and fraction [d], unexplained variation; in Area 1 (a, b), Area 2 (c, d), and Area 3 (e, f).
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