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Spatial variability of tree species diversity in a mixed tropical forest in Southern Brazil

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ABSTRACT

Floristic surveys and diversity indices are often applied to measure tree species diversity in mixed tropical forest remnants. However, these analyses are frequently limited to the overall results and do not allow to evaluate the spatial variability distributions of tree diversity, leading to develop additional tools. This study aimed to estimate the spatial variability of tree diversity and map their spatial patterns in a Brazilian mixed tropical forest conservation area. We used indices to measure the tree species diversity ($dbh \geq 10$ cm) in 400 sampling units (25 m x 25 m) from a continuous forest inventory. Semivariograms were fitted to estimate spatial dependences and punctual kriging was applied to compose maps. Mean diversity values were constant in the continuous inventories, indicating a forest remnant in an advanced stage of ecological succession. On the other hand, tree diversity presented spatial patterns identified by geostatistics, in which the dynamics were composed of heterogeneous mosaics spatially influenced by tree species with different ecological features and densities, gap dynamics, advancement of forest succession, mortality, and *Araucaria angustilofia*'s cohorts.

Key words: *Araucaria angustilofia*, Atlantic Forest biome, diversity indices, geostatistics.

INTRODUCTION

Over the past century, intensive human exploitation has caused severe logging and biodiversity loss in native mixed tropical forests in the Southern region of Brazil (Behling and Pillar 2007). Located at the transition between tropical forests in the North and temperate fields in the South, Brazilian mixed tropical forest remnants are currently susceptible to monoculture activities (Arnold and Fonseca 2011) and the impacts of climate change (Colombo and Joly 2010), which cause degradation in forest fragments and deforestation in protected natural areas.

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Floristic surveys and diversity indices are the most widely used tools to evaluate the conservation status of these mixed tropical forest remnants (Sonego et al. 2007, Ribeiro et al. 2013, Polisel et al. 2014). These measures are fundamental for the evaluation of forest landscapes, such as: Shannon's index (1948), which assumes individuals are randomly sampled and all species are represented in a sample; Simpson's index (1949), a robust measure that considers the probability of any two individuals belonging to the same species; and Margalef's index (1958), which indicates species diversity as the ratio between the number of species and the logarithm of the total number of individuals in a sample.

However, these analyses have often been limited to the overall results of floristic compositions, whose approaches do not allow us to evaluate the spatial variability of tree diversity. This context leads, therefore, to a search for additional tools for modeling spatial patterns, such as geostatistical analyses based on the theory of regionalized variables, in which a spatial function is applied to measure a spatial phenomenon (Webster and Oliver 2007), aiming to compose maps, sampling procedures, and local interventions.

Nowadays, geostatistical methods and their interpolation techniques show potential for modeling and mapping spatial dependence in native forests (Ahmed and Ewers 2012, Akhavan et al. 2015, Barni et al. 2016, Benítez et al. 2016, Hernandez-Stefanoni and Ponce-Hernandez 2006, Roveda et al. 2016, Sales et al. 2007, Scolforo et al. 2016, Zawadzki et al. 2005). However, the lack of research for modeling the spatial variability of tree species diversity in mixed tropical forests represents a significant gap in ecological knowledge, especially in light of the influence of current climate changes on native forest conservation.

Thus, this study aimed to estimate the spatial variability of tree diversity and map their spatial patterns in a mixed tropical forest conservation area in the Southern region of Brazil, to provide indicators of ecological stages of succession and impacts on tree diversity. As the main hypotheses, we consider that the tree diversity indices show spatial dependence and the use of geostatistical modeling makes it possible to obtain accurate tree diversity maps, leading to inferences related to forest conservation and climate change vulnerability.

MATERIALS AND METHODS

STUDY AREA

This study was carried out in a mixed tropical forest remnant with an absence of anthropic disturbance of the vegetation for around 60 years, located in the National Forest of Irati (NFI), in the Southern region of Brazil (Figure 1) at the coordinates 25° 01' S, 25° 40' S, 51° 11' W, and 51° 15' W. The region's climate is classified as temperate oceanic (Cfb - Köppen), with cold summers, without a dry season, and with average temperature and annual rainfall of 17 °C and 1,400 mm, respectively (Alvares et al. 2013).

TREE SPECIES DIVERSITY MEASURES

We identified and classified, according to APG III (The Angiosperm Phylogenygroup 2009), trees with a diameter at 1.30 m above the ground (dbh) $\geq$ 10 cm in 400 plots of 25 m × 25 m (Figure 1) allocated in 40 ha of a mixed tropical forest remnant in a continuous forest inventory carried out in 2002, 2008, and 2014. Then, diversity indices were applied to measure tree species diversity in each plot, such as: Shannon's index (1), in which the highest value represents high diversity; Simpson's index (2), where the uppermost value indicates high species dominance and therefore low diversity; and Margalef's index (3), in which the highest diversity is represented by a high value (Magurran 2003):

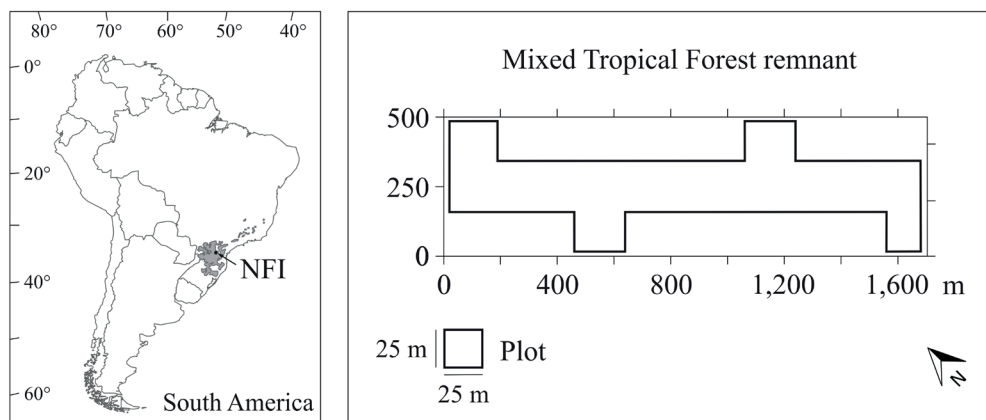$$H' = -\sum_{i=1}^{S} p_i \ln\left(p_i\right) \tag{1}$$

Figure 1 - Mixed tropical forest natural distribution and National Forest of Irati (NFI) in the Southern region of Brazil, South America.

$$D = \Sigma \left[\frac{n_i (n_i - 1)}{N(N-1)} \right] \quad (2)$$

$$D_{Mg} = \frac{(S-1)}{\ln(N)} \quad (3)$$

where: H' is the Shannon's index, D is the Simpson's index, D_{Mg} is the Margalef's index, $p_i = \frac{n_i}{N}$, N the is total number of trees in the sample, n_i is the number of trees in the ith tree species, and S is the total number of tree species in the sample.

SPATIAL ANALYSES

Initially, descriptive statistics and Kolmogorov-Smirnov's test (*K-S*), at 95% probability level (Feldman and Valdez-Flores 2010), were applied to the database, in which the transformations $\ln(x_i)$, $\ln(x_i + 1)$ and $\sqrt{x_i}$ were evaluated for non-normal data distributions (Webster and Oliver 2007, Robertson 2008). Afterward, geostatistics was used to estimate spatial diversity patterns through semivariance measures (4) determined between equidistant plots in the spatial directions: 0°, 45°, 90°, and 135°, and obtaining the mean semivariances between equivalent lag distances (*h*):

$$\gamma(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} \left[Z(x_i) - Z(x_i + h) \right]^2 \quad (4)$$

where: $\gamma(h)$ is the semivariance of $Z(xi)$, h is the lag distance, and $N(h)$ is the number of pairs of measured plots $Z(x_i)$ and $Z(x_i + h)$ separated by a distance h.

Confirming the absence of anisotropy, the isotropic Exponential, Gaussian, and Spherical semivariogram models (Webster and Oliver 2007) were fitted to estimate the diversity indices at any distance between the plots using the weighted least squares method for minimizing the sum of squares of semivariance deviations weighted by the number of pairs of plots in each lag distance (Reilly and Gelman 2007). Also, models were evaluated in accordance with Pelissari et al. (2017), considering smallest weighted sum of squared deviations (*WSSD*), highest coefficient of determination (R^2), and validation statistics, such as lowest values of mean absolute error (*MAE*) and root mean square error (*RMSE*), and highest index of agreement (*d*).

Punctual kriging was applied to interpolate the diversity indices using the GS+ software (Robertson 2008), in which estimates were made using the weighted sum of the known values of neighboring plots around the unknown places. Thus, using the selected semivariogram models, weights (λ_i) were assigned through Lagrange multipliers to estimate unknown values (Chaudhry et al. 2013). Subsequently, diversity maps were produced with

five relative classes, in which spatial patterns and their features were evaluated.

In addition, in the absence of spatial dependence structures, we applied inverse distance weighting (*IDW*) deterministic interpolation to map cohort formations and tree mortality rates, aiming to relate their spatial patterns to the diversity maps. For this, each weight was measured as the inverse of the distance between a non-sampled location and its neighboring sampled plots (Lu and Wong 2008), considering a weighting power equal to two (Lloyd 2005).

RESULTS

In a mixed tropical forest remnant, 131 tree species from 44 families were identified in 2014, in which Myrtaceae was the richest family (19 species), followed by Lauraceae (15 species), and Fabaceae (11 species). We highlight *Araucaria angustifolia* (Bertol.) Kuntze as a species with high density (7.2%) and greatest dominance (26.5%); followed by *Ocotea odorifera* Rohwer, with highest density (9.2%) and high dominance (5.5%); and *Ilex paraguariensis* A. St.-Hil., with similar density (9.2%) and dominance (5.0%).

Applying diversity indices, mean values equal to 2.56 and coefficients of variation (*cv*) between 11 and 13% were observed for Shannon's index (Table I), while lowest mean values (0.9) and *cv* between 4.6 and 7.5% were obtained by Simpson's index, although highest $\overline{x}$ (4.55 to 4.75) were identified for Margalef's index, with *cv* close to 20%. Also, minimum values decreased on the occasions of the forest inventory, while mean and maximum values showed a stable tendency, with normality (*K-S*) only for Margalef's index, due to its simplified formula for measuring diversity using the ratio between total numbers of species and trees in the sample.

Data transformations $\ln(x_i)$, $\ln(x_i+1)$, and $\sqrt{x_i}$ were evaluated for Shannon's and Simpson's indices that showed negatively-skewed distributions. However, these transformations did not provide the appropriate normality condition and, therefore, the original data were used (Table II), since normal distribution is not an assumption required for applying geostatistical analysis, in which it is recommended to avoid the biased influence of a few high values on the kriging interpolator in positively-skewed data distributions.

Spherical model showed the best fits for Shannon's and Margalef's indices, and Gaussian model was the most accurate for Simpson's index (Table II). In these fits, increasing semivariances from the nugget effect until the range were verified in the isotropic semivariograms (Figure 2), in

TABLE I

Descriptive statistics of diversity indices in a mixed tropical forest remnant in the Southern region of Brazil.

Diversity index	Year	x_{min}	$\overline{x}$	x_{max}	S_x	cv	K-S
	2002	1.39	2.56	3.18	0.28	11.0%	0.077*
Shannon	2008	1.04	2.56	3.17	0.32	12.3%	0.094*
	2014	0.85	2.56	3.20	0.33	12.9%	0.118*
	2002	0.62	0.90	0.95	0.04	4.6%	0.169*
Simpson	2008	0.58	0.89	0.95	0.05	5.7%	0.222*
	2014	0.36	0.89	0.95	0.07	7.5%	0.283*
	2002	2.09	4.55	7.45	0.88	19.4%	0.038[ns]
Margalef	2008	1.44	4.56	6.93	0.92	20.5%	0.049[ns]
	2014	1.34	4.75	7.03	0.97	20.4%	0.051[ns]

x_{min} = minimum value; $\overline{x}$ = mean value; x_{max} = maximum value; S_x = standard deviation; *cv* = coefficient of variation; *K-S* = Kolmogorov-Smirnov's test; ns = normal distribution; * = non-normal distribution at 95% probability level.

TABLE II
Semivariogram parameters and validation statistics of diversity indices in a mixed tropical forest remnant.

Index	2002					2008					2014				
	Model	C_0	C_0+C	a		Model	C_0	C_0+C	a		Model	C_0	C_0+C	A	
Semivariogram parameters															
Shannon	Sph.	0.036	0.082	224		Sph.	0.039	0.101	224		Sph.	0.026	0.112	224	
Simpson	Gaus.	0.977	1.912	256		Gaus.	1.374	2.887	285		Gaus.	1.527	4.488	223	
Margalef	Sph.	0.448	0.789	202		Sph.	0.440	0.877	200		Sph.	0.402	0.954	216	
Validation statistics															
Index	Model	MAE	$RMSE$	d		Model	MAE	$RMSE$	d		Model	MAE	$RMSE$	D	
Shannon	Sph.	0.18	0.23	0.73		Sph.	0.19	0.24	0.77		Sph.	0.19	0.24	0.82	
Simpson	Gaus.	0.02	0.03	0.71		Gaus.	0.03	0.04	0.72		Gaus.	0.03	0.05	0.78	
Margalef	Sph.	0.63	0.76	0.66		Sph.	0.63	0.77	0.71		Sph.	0.63	0.78	0.74	

C_0 = nugget effect; $C_0 + C$ = sill; a = range (m); Sph. = Spherical model; Gaus. = Gaussian model; MAE = mean absolute error; $RMSE$ = root mean square error; d = index of agreement.

which we obtained the smallest weighted sum of squared deviations (*WSSD*), and coefficients of determination (R^2) greater than 0.86 for Shannon's index (Figures 2a-c), 0.760 to 0.925 for Simpson's index (Figures 2d-f), and 0.849 to 0.888 for Margalef's index (Figures 2g-i).

Multimodal diameter distributions for *Araucaria angustifolia* species (Figures 3) were identified in the mixed tropical forest, with cohorts at the diameter classes equal to 10-30 cm and 40-60 cm. These tree cohorts showed there are some correlations in smallest scale, which cannot be observed in the semivariograms (Figures 2j-l), as well as to the annual tree mortality rates per plot between 2002 and 2008 (Figure 2m) and 2008 and 2014 (Figure 2n), in which high annual tree mortality was related to the species *Ilex paraguariensis* (42 and 21 trees ha^{-1}), *Casearia decandra* Jacq. (21 and 17 trees ha^{-1}), and *Myrsine umbellata* Mart. (20 and 19 trees ha^{-1}).

Diversity index maps showed different spatial patterns, with increasing diversity for Shannon's (Figures 4a-c) and Margalef's indices (Figures 4g-i), as well as spatial homogeneity for Simpson's index, with increasing values in the lowest Shannon and Margalef areas at the X-coordinate 0-200 m (Figures 4d-f). *IDW* was applied to *Araucaria angustifolia* basal area (Figures 4j-l), in which increasing values were observed in areas with expanding diversity according to Shannon's and Margalef's indices, especially at the X-coordinate 0-800 m. *IDW* was also applied to annual tree mortality rates (Figures 4m-n), in which highest mortality was observed mainly at the Y-coordinate 250-500 m and X-coordinate 0-200 m, where we identified the lowest diversity in the index maps.

DISCUSSION

As a consequence of human pressure over the years, mixed tropical forest is one of the most vulnerable Brazilian forest ecosystems (Carlucci et al. 2011). The conservation of these forest remnants has become a key challenge, since the efforts made by official agencies and non-governmental institutions have not been able to maintain the integral preservation of the forest fragments (Sanqueta et al. 2002, Vibrans et al. 2008). Nevertheless, mixed tropical forest remnants are important sources for scientific research, mainly for understanding their species diversity dynamics.

In this paper, mean diversity index values ($\bar{x}$) were similar to those of other studies in mixed tropical forests (Rondon Neto et al. 2002, Narvaes et al. 2005, Sonego et al. 2007), showing
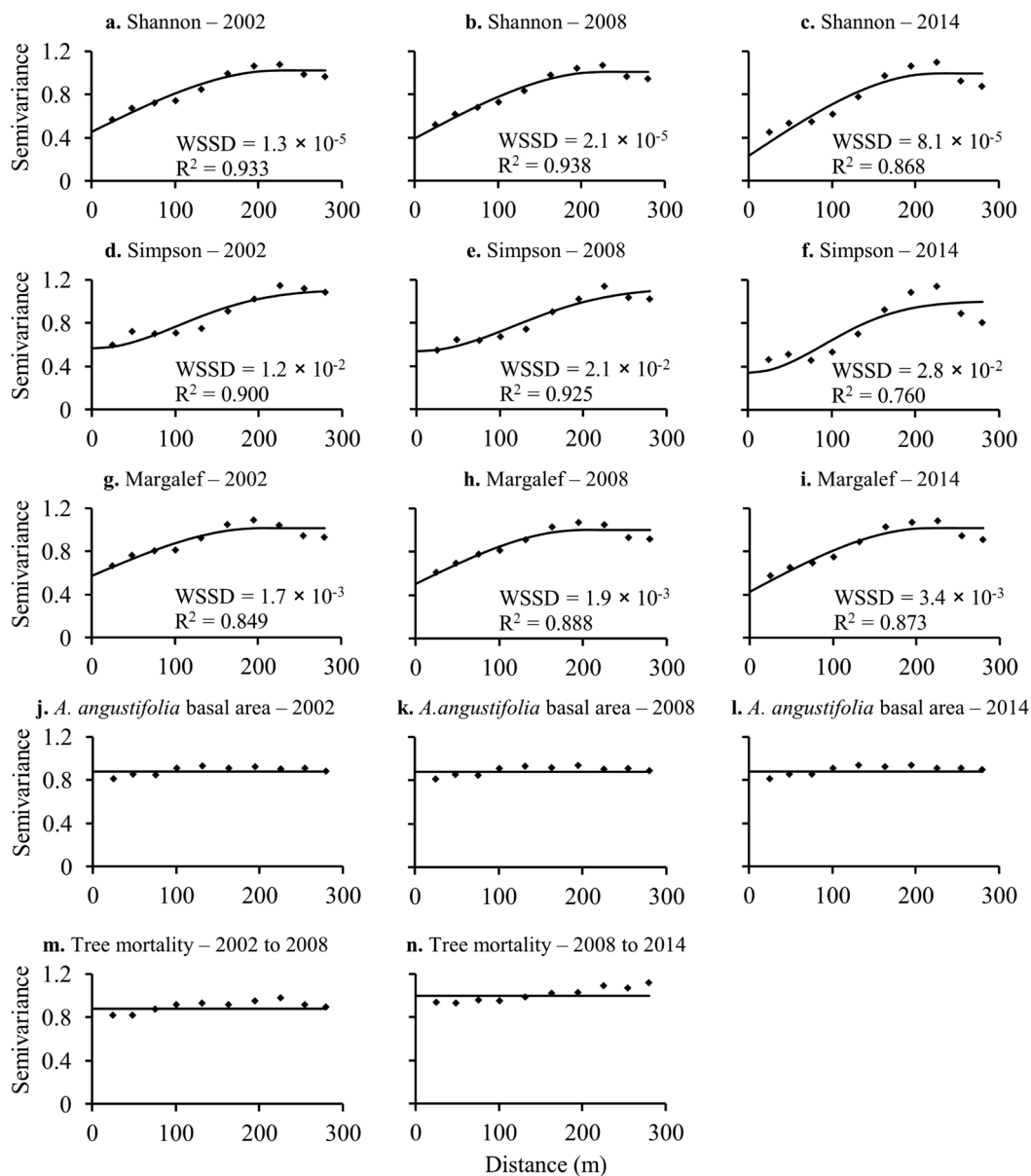
Figure 2 - Scaled semivariograms of Shannon's index (**a** to **c**), Simpson's index (**d** to **f**), Margalef's index (**g** to **i**), and pure nugget semivariograms for Araucaria angustifolia basal area per plot (**j** to **l**) and annual tree mortality rates per plot (**m**, **n**) in a mixed tropical forest.
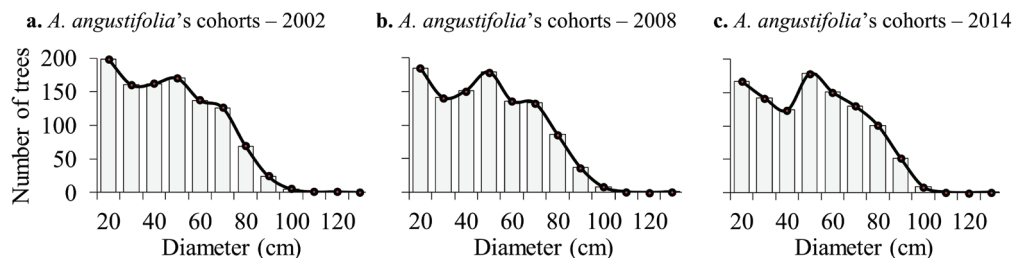

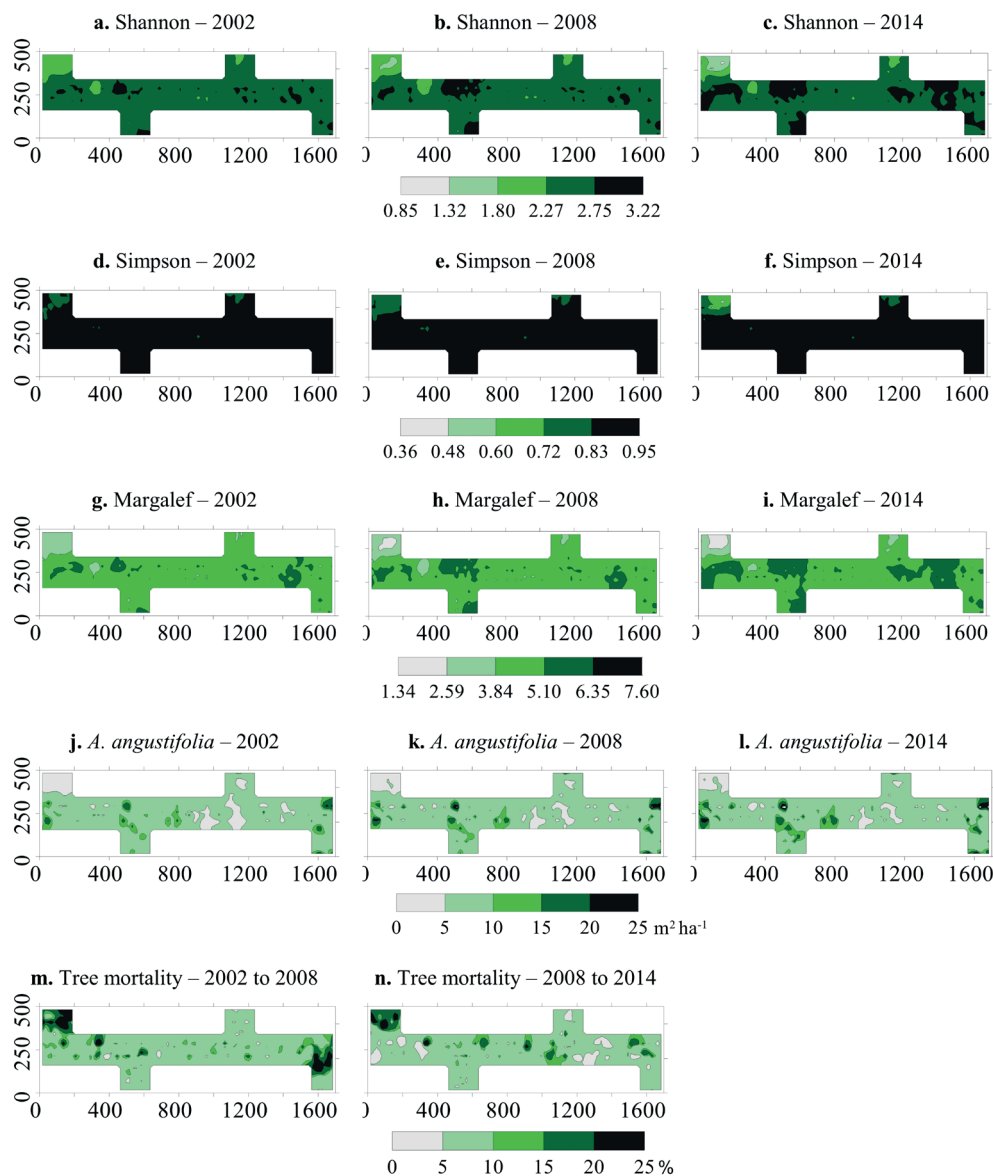**Figure 3** - Multimodal diameter distributions for Araucaria angustifolia in a mixed tropical forest remnant.

Figure 4 - Maps of Shannon's index (**a** to **c**), Simpson's index (**d** to **f**), Margalef's index (**g** to **i**), Araucaria angustifolia basal area per plot (**j** to **l**), and annual tree mortality rates per plot (**m**, **n**) in a mixed tropical forest remnant.

a constant tendency at the forest inventory times (Table I). These results indicate a behavior of temporal stability of tree diversity, associated with a forest remnant in an advanced stage of ecological succession, in which small changes in coefficients of variation (*cv*) are related to tree mortality and recruitment in the forest.

In the geostatistics fits (Table II), nugget effect values (C_0) represent the diversity variability in short scale, while range values (*a*) equal to or greater

than 200 m indicated the highest distance between plots in which tree diversity spatial correlation is identified. In addition, accuracy was confirmed by the lowest values of mean absolute error (*MAE*) and root mean square error (*RMSE*), and an index of agreement (*d*) greater than 0.7 for Simpson's and Shannon's indices; while the higher variability of Margalef's index influenced the values for *MAE*, *RMSE*, and *d*.

Thus, hypotheses were supported, in which diversity indices present spatial dependence in the mixed tropical forest remnant, and geostatistical modeling allowed us to observe the spatial dynamics composed for heterogeneous patterns (Figure 4). This spatial dependence was confirmed by the increasing semivariance and its stabilization behavior (Figure 2a-i), as well as through the stable values of mean absolute errors (*MAE*) and root mean square errors (*RMSE*) and increasing index of agreement (*d*) in the forest inventory (Table II).

Thus, commonly used mean values did not make it possible to measure changes in spatial diversity, in which the spatial patterns were related to the floristic variabilities through the recruitment of trees into the threshold diameter (*dbh* ≥ 10 cm) from 85 tree species in areas with increasing diversity, especially *Coussarea contracta* (Walp.) Müll. Arg., *Ilex paraguariensis,* and *Myrciaria floribunda* (H. West ex Willd.) O. Berg. This behavior was most apparent in the Shannon (Figures 4a-c) and Margalef maps (Figures 4g-i) and is attributed to log transformation in their formulas, which makes the smallest spatial changes more evident. On the other hand, Simpson's index, which uses a linear scale, resulted in the highest spatial variability homogeneity (Figures 4d-f), indicating the influence of *Araucaria angustifolia* as the most dominant species in the sample (Orellana et al. 2016).

Spatial diversity dynamics can be related to cohorts in communities with a high density, and are representative of species with a long-life cycle (Ogden and Stewart 1995), such as *Araucaria angustifolia*, and established after disturbance events that increase light conditions and favor natural regeneration (Claessens et al. 2006). Thus, in the multimodal diameter distributions (Figure 3), the first cohort is represented by the 40-60 cm class, while the second is identified by the 10-30 cm class, with a higher number of trees than the first cohort due to the lower influence of tree senescence (Ebling and Péllico Netto 2015).

Natural disturbances affect spatial diversity distributions, benefiting specific forest communities (Coomes et al. 2005), increasing tree dominance, and, consequently, reducing species diversity, in which current climate effects can increase changes in forest structure (Dale et al. 2000). Thus, lower diversity index values in the top-left part of the maps, between the Y-coordinate 250-500 m and X-coordinate 0-200 m (Figure 4), were caused by the higher dominance of pioneer species, especially *Mimosa scabrella* Benth. (Silva et al. 2016), resulting in local diversity reductions for Shannon's and Margalef's indices and increasing dominance for Simpson's index.

A reduction in spatial diversity may result from environmental factors, such as the formation of gaps that increase the dominance of pioneer and secondary species in the successional dynamics (Hartshorn 1978, Whitmore 1989, Guariguata and Ostertag 2001). Subsequently, tree mortality will increase via competition with shade-intolerant species (Whitmore 1989, Luo and Chen 2015), resulting in a more random spatial distribution (Figures 3m-n). These results show the need for understanding the tropical forest succession mechanisms (Wright 2005, Quesada et al. 2009), especially considering current climate changes and loss of global biodiversity.

Our results also showed that tree mortality affects spatial diversity dynamics and is directly responsible for spatial changes in the forest inventory. Thus, climate changes tend to increase tree mortality in native forests through the intensification of extreme weather events (Parks and Bernier 2010, Luo and Chen 2015, Chen et al. 2016), such as successive droughts and global temperature increases (Allen et al. 2010, Feldpausch et al. 2016), in which tree longevity makes rapid adaptation to environmental changes impossible (Lindner et al. 2010), especially among hardwood species, which are physiologically more susceptible (Mahareli et al. 2004), as are the mixed tropical species.

CONCLUSIONS

Mean values of mixed tropical forest diversity indices were stable in the continuous inventories,

indicating a forest remnant in an advanced stage of ecological succession. On the other hand, tree species diversity presents spatial patterns identified by geostatistical analyses, in which the spatial dynamics were composed of heterogeneous mosaics spatially influenced by tree species with different ecological features and densities, gap dynamics, advancement of forest succession, mortality, and *Araucaria angustilofia*'s cohort formation.

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