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ORIGINAL PAPER

Modelling changes in forest attributes driven by human activities at different spatial scales in the subtropical Atlantic Forest

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Abstract

Human activities are the main drivers of biotic homogenization, thus affecting ecosystem functions. In this study, we aimed to investigate the relationship among anthropogenic disturbances and forest attributes. Moreover, we sought to identify direct and indirect effects of topographic heterogeneity (TH), more specifically of standard deviation of altitude, on anthropogenic disturbances and forest attributes, respectively, through a path analysis. We used data gathered on 186 systematically distributed sample plots located in the Brazilian subtropical Evergreen Rainforest. We selected 14 predictor variables related to anthropogenic disturbances aiming to model seven forest attributes related to species diversity, composition, and structure. The aboveground biomass, rarefied species richness, proportion of standing dead trees, and proportion of individuals of pioneer species in the regeneration layer were better predicted by global linear regression models. The proportions of individuals of pioneer species in the canopy layer and of threatened species in the canopy and regeneration layers were better explained by local geographically weighted regression models. Human activities at different spatial scales may lead to disturbances (e.g., edge effects and habitat fragmentation), thus driving changes in forest attributes. The land use amidst forest remnants was related to biomass production and biotic homogenization. Logging and road networks may imperil the maintenance of threatened species. The path analysis showed that TH indirectly affects species richness via pasture area. Furthermore, topography appeared to act as a barrier for the expansion of certain human activities over the landscape. Our findings evoked the need for implementation of adaptative conservation strategies.

Keywords Edge effects · Biotic homogenization · Second-growth forest · Landscape matrix · Topographic heterogeneity

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Introduction

Biodiversity conservation is grounded in the maintenance of ecosystem functions, which, in turn, generate essential ecosystem services (Brockerhoff et al. 2017). Humans are innate users of such services but are, nevertheless, recognized as the main drivers of current biodiversity losses (Ceballos et al. 2015). It is known that as losses increase, the rate of change in ecosystem functions also increases (Cardinale et al. 2012). Therefore, biodiversity losses in forest ecosystems can jeopardize important services delivered by them, like protection of water resources and carbon sink. Tropical forests, for example, store more than half of the world's forest carbon stocks, whereas 56% of this carbon is stored in aboveground biomass (Pan et al. 2011). Indeed, studies have shown that primary productivity and biomass stocks are positively related to species richness (Poorter et al. 2015; Liang et al. 2016).

Several anthropogenic disturbances threaten forest ecosystems, such as edge effect (Laurance et al. 2006; Broadbent et al. 2008), defaunation (Bello et al. 2015; Peres et al. 2016), land use change (Jakovac et al. 2015), logging (Huth and Ditzer 2001), habitat loss (Flynn et al. 2009), and climate change (Allen et al. 2010). The variety of human disturbances may generate synergetic forces leading to biodiversity losses and uncertain pathways of forest succession (Laurance et al. 2014; Arroyo-Rodríguez et al. 2017). Biotic homogenization is another threat to biodiversity driven by anthropogenic disturbances (Olden 2006; Lôbo et al. 2011); it is characterized by an increase in species composition similarity among sites. Another issue in this complex scheme is that humans imprint a topographic signature on landscapes: forests on low-altitude and flat terrains may be more exposed to land use changes and cover losses (Freitas et al. 2010; Sandel and Svenning 2013). Sloped terrains, in contrast, may harbor more forest remnants and promote the increase in forest cover. Thus, topography could be related to human activities, which, in turn, may affect forest attributes such as aboveground biomass (Méndez-Toribio et al. 2016).

Most remaining forest patches in the Atlantic Forest phytogeographic domain are a result of disturbances with different frequencies and intensities. Historical and ongoing deforestation reduced its forest area to ~ 12% of its original cover (Fundação SOS Mata Atlântica 2018), and most of the remaining stands consist of young secondary forests (Ribeiro et al. 2009). Moreover, less than 25% of the existing forest land is fully satisfying current demands for ecosystem services (Ferraz et al. 2014). Some stands were selectively logged (Carola 2010), while others regenerated naturally on abandoned agricultural lands (Rezende et al. 2015). Thus, old-growth forests are scarce and even large remnants may present signs of recent human disturbance (Chazdon 2014; Ferraz et al. 2014). Therefore, stands resembling the structural and compositional features of old-growth forests are scant in the Atlantic Forest.

Inasmuch as anthropogenic disturbances are acknowledged as drivers of ongoing biodiversity losses, little is known about their effects on subtropical forest ecosystems in highly fragmented landscapes. These facts motivated us to investigate the effects of anthropogenic disturbances on forest attributes related to structure, diversity, and composition. More specifically, we aimed to answer the following questions: (1) Which anthropogenic disturbances are the main drivers of changes in species composition, ecological guilds and structural features, and in which degree they are related to these attributes? (2) Is topography related to landscape structure and local anthropogenic disturbances? (3) If yes, is it possible to identify an indirect effect of topography on forest attributes through anthropogenic disturbances? To address these questions, we used data gathered on 186 sample plots of a systematic sampling inventory conducted in the Brazilian subtropical Atlantic Forest. The spatially unbiased data allowed us to portray a realistic picture of the conservation status of a large number of subtropical Atlantic Forest sites.

Methods

Study area

We defined the study area as the Evergreen Rainforest (ERF) of the state of Santa Catarina, southern Brazil. It originally represented 33% of the state's ~ 96,000 km^2 territory (Fig. 1), and currently ~ 40% of the original ERF cover remains (Vibrans et al. 2013). Most remnants consist of less than 70 years old secondary forests (Baptista and Rudel 2006). Forest cover reduction and overall degradation were driven by intensive logging of several species with increased economic importance and by the conversion of forestland into pastures and agriculture (Vibrans et al. 2020). Coal mining also contributed to forest degradation in the south of the study area (Colonetti et al. 2009).

The ERF is the most biodiverse forest type within the Atlantic Forest domain. It is featured by a canopy layer dominated by Lauraceae, Myrtaceae and Fabaceae species, and by an abundance of epiphytes, ferns, and palms (Oliveira-Filho and Fontes 2000; Gasper et al. 2014). Tropical climatic conditions prevail in the study area,

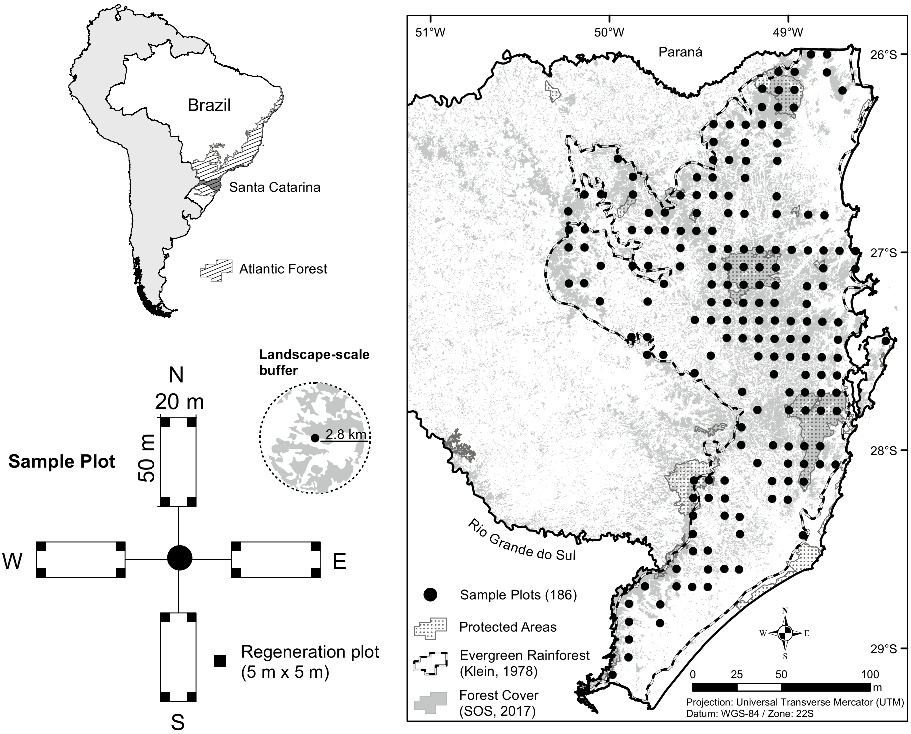

Fig. 1 Location of the 186 sample plots over the Evergreen Rainforest in Santa Catarina state, southern Brazil, and the layout of the buffer built around the center of each sample plot to calculate landscape metrics

such as average annual temperatures above 18 °C and rainfall ranging from 1500 to 2000 mm year^{-1}. According to the Köppen climate classification, the study area is influenced by the Cfa climate type (Alvares et al. 2013).

Data collection

We used data collected by the Forest and Floristic Inventory of Santa Catarina (IFFSC) between 2008 and 2010 on 186 sample plots. The sample plots were systematically distributed at the intersections of a 10 km × 10 km grid. The IFFSC sample plot is composed of four 20 m × 50 m subplots located at 30 m from the sample plot center and oriented toward the four cardinal directions, adding up to 0.4 ha (Fig. 1). All living trees with diameter at breast height (dbh) $\geq$ 10 cm on the subplots were measured; total tree height was visually estimated after reference measurements of up to eight trees per sample plot were taken using a hypsometer.

Individuals with dbh < 10 cm and height $\geq$ 1.50 m were recorded on four 5 m × 5 m plots located at the edges of each 20 m × 50 m subplot to assess the regeneration layer. The sample plots' altitude above sea level ranged from 34 to 1195 m. At least 90% of the sample plots were located in secondary forests.

Forest attributes

We selected as response variables seven attributes related to species diversity, composition, and structure (Table 1). We described community diversity through the rarefied species richness of the canopy layer (SRCL) using individual-based rarefaction curves (Gotelli and Colwell 2001); we extracted the SRCL using a standard sample of 95 individuals. In turn, we described community composition through the proportion of individuals belonging to pioneer species in the canopy layer (PPCL) and in the regeneration layer (PPRL); and the proportion of individuals of threatened species in the canopy layer (PTCL) and in the regeneration layer (PTRL). We classified species as pioneer (i.e., light demanding) according to Flora Ilustrada Catarinense (Reitz 1965). We defined threatened species according to the Brazilian list of endangered species (MMA 2014).

Forest structure was described by the aboveground biomass stock (AGB; Mg ha^{-1}) and proportion of standing dead trees in the canopy layer (PDCL). We estimated the AGB at the individual level using the pantropical model $\text{AGB} = 0.0673\ (\rho \cdot \text{dbh}^2 \cdot \text{h})^{0.976} + \varepsilon$ (Chave et al. 2014), where AGB is the aboveground biomass (kg), ρ is the species' wood density (g cm^{-3}), h is the total tree height (m), and ε is the random residual. We gathered ρ data from the Global Wood Density database (Zanne et al. 2009); when ρ for a given species was lacking, we calculated the mean ρ of its genus, as suggested by Chave et al. (2006). We applied specific AGB models to *Cecropia glaziovii*, Cyatheaceae species (Uller et al. in review), and *Syagrus romanzoffiana* (Moreira-Burger et al. 2010). The palm *Euterpe edulis* and the tree fern *Dicksonia sellowiana* were not included in the estimates due to the lack of specific AGB models to generate reliable estimates at the individual level.

Table 1 List of response and predictor variables used in this study

Category	Scale	Data source	Variable	Unit
Response variables				
Diversity and composition	Sample plot	Forest inventory	Rarefied species richness in the canopy layer (SRCL)	Number of species with a sample size of 95 ind
	Sample plot	Forest inventory	Proportion of individuals of pioneer species in the canopy layer (PPCL)	%
	Sample plot	Forest inventory	Proportion of individuals of threatened species in the canopy layer (PTCL)	%
	Sample plot	Forest inventory	Proportion of individuals of pioneer species in the regeneration layer (PPRL)	%
	Sample plot	Forest inventory	Proportion of individuals of threatened species in the regeneration layer (PTRL)	%
Structure	Sample plot	Forest inventory	Proportion of standing dead trees in the canopy layer (PDCL)	%
	Sample plot	Forest inventory	Aboveground biomass in the canopy layer (AGB)	Mg ha^{-1}
Predictor variables				
Edge effect	Landscape	Buffers	Edge density	m ha^{-1}
	Landscape	Buffers	Mean shape index (McGarigal and Marks 1995)	–
	Forest patch	Buffers	Patch perimeter-area ratio	m m^{-2}
	Forest patch		Distance from the sample plot center to the patch edge	m
Forest connectivity	Landscape	Buffers	Total forest area	m^2
	Landscape	Buffers	Mean proximity among patches	m
Human accessibility	Landscape	Buffers	Total road length	m
	Sample plot	Field observation	Inner pathways	Presence/absence
Land use	Landscape	Buffers	Agriculture area	m^2
	Landscape	Buffers	Forest plantation area	m^2
	Landscape	Buffers	Pasture area	m^2
Local disturbances	Sample plot	Field observation	Clearcutting	Presence/absence
	Sample plot	Field observation	Selective logging	Presence/absence
	Sample plot	Field observation	Cattle grazing	Presence/absence
Topographic heterogeneity	Landscape	Buffers	Standard deviation of altitude	m

Predictor variables

We selected 14 predictor variables related to anthropogenic disturbances at the landscape, forest patch, and sample plot scales (Table 1). We gathered data on landscape and forest patch-scale variables from a land use map of Santa Catarina (Geoambiente 2008) within buffers of 2.8 km radius built around the center of each sample plot (Fig. 1). Additionally, we employed data from OpenStreetMap (Geofabrik 2018) to compute the total length of roads within the buffers. We performed these procedures in ArcGIS 10 (ESRI 2012), and most of the variables were calculated using V-LATE 2.0 beta (Vector-based Landscape Analysis Tools Extension). At the sample plot scale, the presence or absence of human activities was recorded by the IFFSC (Table 1).

We assigned the predictor variables to five categories representing independent types of human disturbances on forest communities (Table 1). In this way, we aimed to assess the effect of each category, as well as the combined effects of the categories on the response variables. Moreover, we aimed to identify which predictor variable in each disturbance category presented the largest contribution in explaining the variation in the response variables.

We assessed the relationships among topography heterogeneity (TH) and human disturbances, as well as indirect effects of the former on forest attributes. We used the standard deviation of altitude within the buffers as an indicator of TH (Table 1). Altitude data were derived from the digital elevation model calibrated by Valeriano and Rossetti (2012).

Data analysis

We fitted linear multiple regression models through ordinary least squares (OLS) using the 'base' R package aiming to illustrate the global relationships among each forest attribute and the anthropogenic disturbances. All possible combinations of the 14 predictors within the five categories of disturbances were considered, such that each model had only one predictor variable per category. We admitted a single variable in each category aiming to build parsimonious models and to avoid strong collinearity within the categories. The models may generally be written as

$$\mathrm{Y} = \alpha + \beta_1 \cdot \mathrm{EE} + \beta_2 \cdot \mathrm{CN} + \beta_3 \cdot \mathrm{LU} + \beta_4 \cdot \mathrm{HA} + \beta_5 \cdot \mathrm{LD} + \varepsilon$$

where Y is a forest attribute; EE is an edge effect descriptor; CN is a forest connectivity descriptor; LU is a land use descriptor; HA is a human accessibility descriptor; LD is a local disturbance descriptor; α and β_k ($k = 1, 2, \ldots, 5$) are regression parameters to be estimated; and ε is the random residual.

We used the Akaike Information Criterion (AIC) to select the best models among the 144 candidates for each forest attribute. The predictor variables embedded in all selected models yielded a variance inflation factor ($\mathrm{VIF} < 4$). We also fitted null models (intercept-only models) to compare their performance with the best OLS model for each response variable.

In addition, we fitted Geographically Weighted Regression models (GWR; Fotheringham et al. 2002) to search for effects of predictor variables on forest attributes at the local level. We employed the adaptive Gaussian kernel function for geographical weighting to allow for variations in bandwidths as a function of sample plot density (Fotheringham et al. 2002). We fitted the GWR models using the 'spgwr' R package. We searched for evidence that the GWR models were more suitable to explain the relationships among the variables than the global OLS models. For this, we tested, using ANOVA and $\alpha = 0.05$, the null hypothesis that the GWR models did not significantly reduce the sum of squared errors in comparison to the global OLS models.

We applied different transformations in the response variables aiming to fulfill the assumptions of homoscedastic and normally distributed residuals. The AGB, PDCL, PPCL and PTCL were $\log_{10}$ transformed, and the PPRL and PTRL were square-root transformed. The SRCL did not require any transformation to fulfill the aforementioned assumptions. The estimated regression coefficients of the OLS and GWR models were standardized (denoted as $\widehat{\beta}*$), with exception of the coefficients associated with presence-absence (dummy) variables because of their direct relationship with the models' intercept. Standardized coefficients can be interpreted as standardized effect sizes (Neter et al. 1996).

We performed two analyzes to assess the influence of topography on forest attributes and anthropogenic disturbance patterns. We first calculated Pearson's correlation coefficient between topographic heterogeneity and all anthropogenic disturbances. Subsequently, we performed a path analysis (Grace 2006) to evaluate the indirect effects of topography on forest attributes. Our conceptual model assumed that topographic heterogeneity is directly related to the intensity of anthropogenic disturbances and is indirectly related to forest attributes. In the path model for each forest attribute, we used the anthropogenic disturbance variables embedded in the respective best OLS model. Every relation among the variables was expressed by a hypothetical causal path. We calculated standardized coefficients of partial regression for each causal path, also known as path coefficients (Grace 2006). Path coefficients measure the direct effects of one variable on another; in turn, the indirect effect is given by the multiplication of the path coefficients on a path linking two variables (Grace 2006). Because we could not assume that all variables were normally distributed and most of them presented increased kurtosis, we validated the models through the Bollen-Stine bootstrap method for structural equation modelling (Bollen and Stine 1992). These procedures were conducted using the 'lavaan' R package.

Results

The OLS models outperformed the GWR models regarding the prediction of AGB, SRCL and PPRL (Table 2). The AGB presented a stronger positive association with forest cover and agriculture area. In the OLS model for the SRCL, the significant predictors were pasture area, mean shape index (both with a negative effect), and mean proximity (positive effect). The PPRL was, in turn, positively associated with perimeter-area ratio and forest cover (Table 2). The OLS models with $\Delta AIC < 2$ for each forest attribute are found in the Supplementary Materials, except for the PDCL, whose null model performed equivalently to full models. This indicates that the predictors we considered may not be related to tree mortality.

The PPCL, PTCL and PTRL were better predicted by GWR models. The GWR model for the PPCL performed better in the extreme south of the study area ($0.26 \le R^2 \le 0.28$), where pasture area ($0.24 \le \widehat{\beta}* \le 0.40$) and clearcutting ($0.52 \le \widehat{\beta} \le 0.66$) presented the greatest effect (Fig. 2). In the central-southern region (dark grey and black points in Fig. 2), edge density ($-0.36 \le \widehat{\beta}* \le -0.26$) and pasture area ($0.36 \le \widehat{\beta}* \le 0.44$) were related to PPCL (Fig. 2). The PTCL was better predicted at the central portion of the study area ($0.25 \le R^2 \le 0.34$; black points in Fig. 3), where the perimeter-area

Table 2 Summary of the best OLS models

Response variable	Predictor variable	$\hat{\beta}$	$\hat{\beta}*$	p value
Aboveground biomass (AGB)	Intercept	1.67	–	**< 0.001**
$R^2 = 0.17$	Distance from the edge	6.63×10^{-5}	0.14	**0.04**
AIC = −65.8	Forest cover	1.63×10^{-8}	0.35	**< 0.001**
AIC (null model) = −42.4	Agriculture area	2.16×10^{-8}	0.29	**0.001**
	Inner pathways	-6.97×10^{-2}	–	**0.02**
	Selective logging	6.78	–	0.07
Rarefied species richness (SRCL)	Intercept	40.653	–	**< 0.001**
$R^2 = 0.17$	Mean shape index	−1.185	−0.181	**0.009**
AIC = 1218.1	Mean proximity	4.05×10^{-4}	0.195	**0.005**
AIC (null model) = 1241.4	Pasture area	-5.42×10^{-7}	−0.243	**< 0.001**
	Road length	-2.38×10^{-5}	−0.102	0.146
	Selective logging	2.020	–	0.077
Proportion of individuals of pioneer species in the regeneration layer (PPRL)	Intercept	2.41	–	**< 0.001**
$R^2 = 0.09$	Perimeter/area	123.3	0.358	**0.003**
AIC = 564.2	Forest cover	6.48×10^{-8}	0.303	**0.012**
AIC (null model) = 570.2	Forest plantation area	-7.33×10^{-8}	−0.094	0.205
	Inner pathways	2.46×10^{-1}	–	0.126
	Clearcutting	3.22×10^{-1}	–	0.102

Statistical significance ($p \leq 0.05$) is indicated in bold text. $\hat{\beta}$ = estimated regression coefficient; $\hat{\beta}*$ = estimated standardized regression coefficient

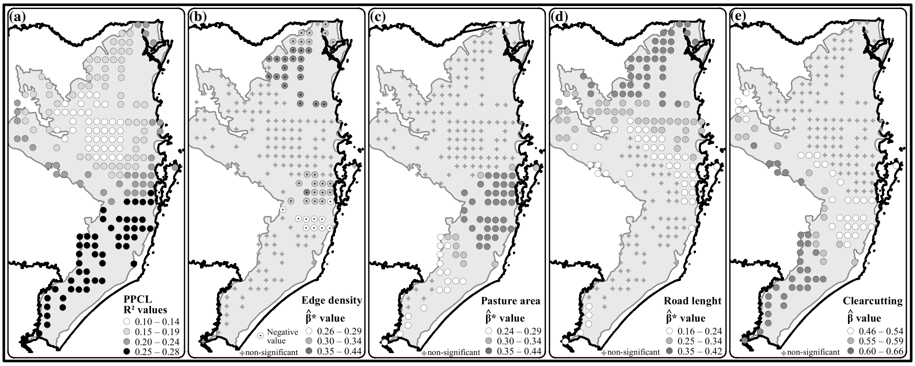

Fig. 2 Local R^2 (**a**) and significant ($\alpha = 0.05$) local regression coefficients of the predictor variables (**b**–**e**) embedded in the GWR model fitted to the proportion of individuals of pioneer species in the canopy layer (PPCL)

ratio ($-0.46 \leq \hat{\beta}* \leq -0.36$) and clearcutting ($0.53 \leq \hat{\beta} \leq 0.70$) yielded the largest effects (Fig. 3). In the regeneration layer, the PTRL presented a stronger relationship with road length ($0.22 \leq \hat{\beta}* \leq 0.69$) and selective logging ($0.63 \leq \hat{\beta} \leq 0.93$) in the extreme north

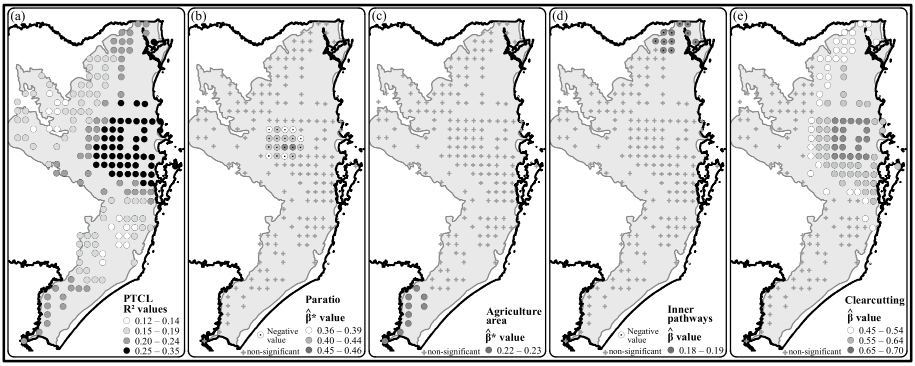

Fig. 3 Local R^2 (**a**) and significant ($\alpha = 0.05$) local regression coefficients of the predictor variables (**b**–**e**) embedded in the GWR model fitted to the proportion of individuals of threatened species in the canopy layer (PTCL)

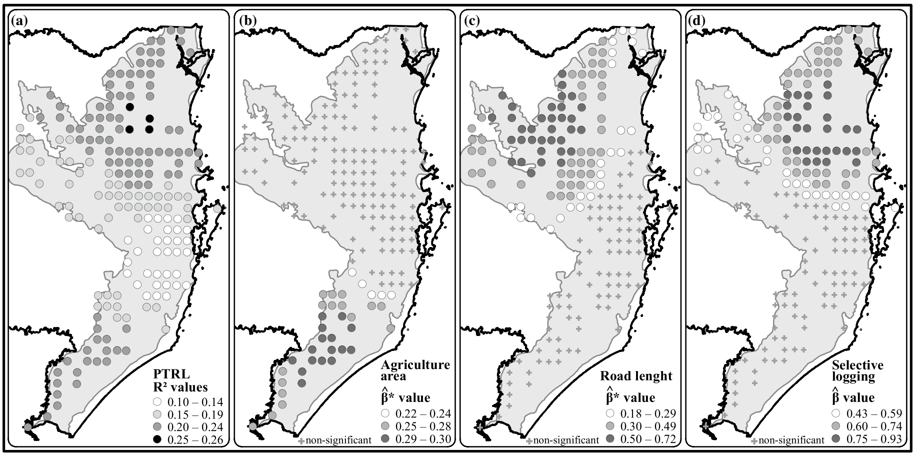

Fig. 4 Local R^2 (**a**) and significant ($\alpha = 0.05$) local regression coefficients of the predictor variables (**b**–**d**) embedded in the GWR model fitted to the proportion of individual of threatened species in the regeneration layer (PTRL)

($0.22 \leq R^2 \leq 0.26$; Fig. 4), whilst agriculture area ($0.28 \leq \hat{\beta}^* \leq 0.30$) yielded a greater effect in the extreme south ($R^2 = 0.22$; Fig. 4).

TH was significantly ($p < 0.05$) correlated with most of the landscape metrics. Forest cover was positively correlated with TH ($r = 0.48$), while edge density ($r = -0.48$), perimeter-area ratio ($r = -0.43$), agriculture area ($r = -0.29$), road length ($r = -0.20$), forest plantation ($r = -0.19$) and pasture area ($r = -0.03$) were negatively correlated with TH, as expected.

The path analysis revealed that our conceptual model was valid only for the SRCL (Fig. 5). TH had negative effects on pasture area, which, in turn, yielded negative effects

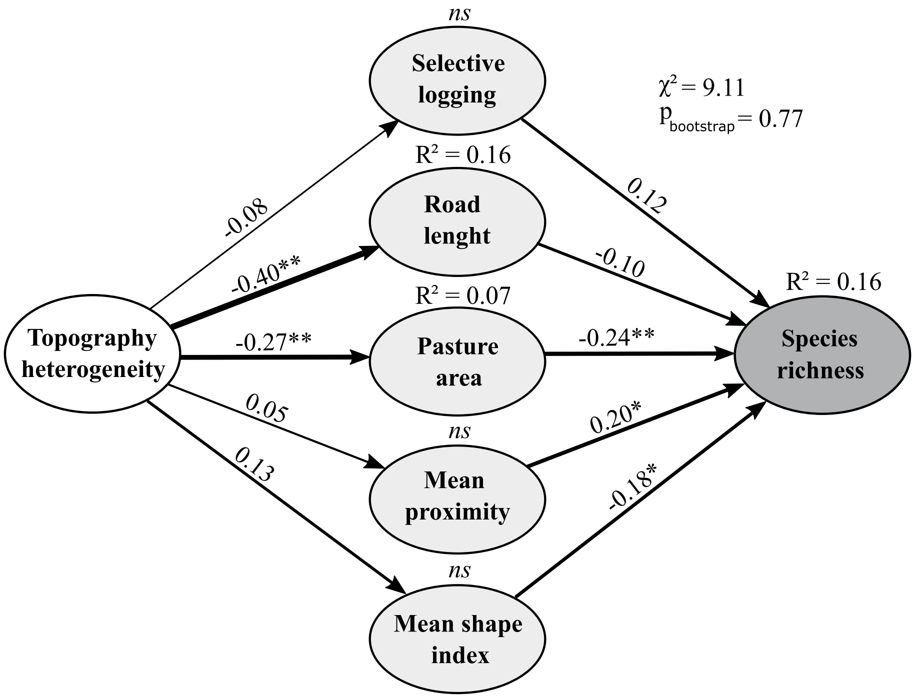

Fig. 5 Structural model for the SRCL. The path coefficients linking TH to anthropogenic disturbances are Pearson correlations, and the paths between anthropogenic disturbances and the SRCL are coefficients of partial regressions. The paths linking TH (exogenous variable) to SRCL (response variable) via each anthropogenic disturbance (endogenous variables) represent the indirect effects of TH on species richness. $*p < 0.05$; $**p < 0.01$; *ns* non-significant

on the SRCL. From these relationships, TH affects indirectly the SRCL via pasture area, with a positive effect of 0.079 standard deviations.

Discussion

Effects of human activities on AGB

We identified the main human activities driving changes in forest attributes related to composition, diversity and structure. Some of these activities may be perceived as threats to forest and biodiversity conservation. Greater forest connectivity and distance between sample plots and forest edges were related to stands with more AGB, as shown also by Paula et al. (2011) and Haddad et al. (2015). Less fragmented Atlantic forests may have been less disturbed by logging and thus still shelter some large trees, which accumulate most of a stand's AGB (Lutz et al. 2018). In our study area, less fragmented forests are usually found near or within protected areas (Fig. 1). These areas have an important role in protecting large trees in the subtropical Atlantic Forest, as shown by Scipioni et al. (2019). On the other hand, the presence of inner pathways was related to stands with less AGB.

Pathways may lead to the proliferation of soft-wooded species due to increased light availability (Silva et al. 2017) and may augment soil compaction, which can limit tree growth.

The presence of selective logging and larger agriculture area within the landscape buffers presented a positive relationship with AGB, although it would not be expected. A possible explanation for this relationship is that selective logging in the ERF has been carried out in stands with greater AGB, where trees with larger diameters may still be found. Regardless of our results, Gatti et al. (2015) showed that intense regimes of selective logging may significantly reduce the AGB of tropical forests and its effects may last for several decades. The lack of historical data on the frequency and intensity of selective logging in the Atlantic Forest may hinder the detection of its influence on AGB reduction.

The positive effect of agriculture area on AGB could be understood as a synergy with the forest cover effect. When forest cover alone is regressed on AGB, it renders an $R^2 = 3\%$, while agriculture area regressed on AGB does not explain any of its variation. In turn, when both variables are regressed on AGB, the model yields an $R^2 \approx 12\%$. This synergetic effect may be explained in a few ways. First, fertilizers applied in agriculture areas might increase biomass production of nearby forests (Vitousek et al. 1997; Schlesinger 2009). Second, agriculture is usually implemented in sites with better physical and chemical soil properties; hence, forests near these sites are naturally more productive. Third, when agriculture is conducted over complex landscapes, it could deliver more food resources for animals and thus the connectivity among forests patches may intensify the mobility of seed dispersion. This interaction may, in the long run, drive the increment of forest biomass by the increase in species diversity and/or tree density (Tscharntke et al. 2005). Fourth, all the above may occur simultaneously.

Aside from these issues, according to Brazil's Forest Code, landowners are obligated to designate a Legal Reserve (LR), that is a forest area corresponding to 20% of the total area of a property within the Atlantic Forest domain; this area should provide the minimum conditions for maintenance of biodiversity (Brasil 2012). The importance of LRs for biodiversity conservation in Brazil is widely acknowledged (Metzger et al. 2019). Other policies, nonetheless, such as payment for carbon sequestration and management of secondary forests, could be implemented to encourage landowners to maintain other forest areas than LRs, thus harmonizing forest conservation with agricultural and economic development.

Human disturbances may affect species richness and composition

The SRCL was related to forest connectivity, mean shape index, and pasture area. Landscapes with more pasture area and with more isolated forests with irregular shape (non-circular) tend to present less tree species. It is known that fragmentation has negative effects on species diversity. Edge effects may accelerate the death of individuals belonging to species that do not tolerate intense desiccation and wind turbulence, thereby leading to changes in species diversity patterns (Laurance 2000; Tabarelli et al. 2004). Furthermore, the landscape matrix may affect tree species richness because colonization processes depend both on the resilience and on the distance among forests (Prevedello and Vieira 2010; Leithead et al. 2012). The connectivity among forest patches could also be influenced by the land use amidst them. Pastures, for instance, could be regarded as barriers for seed dispersers (de la Pena Domene et al. 2018), as potential dispersers may avoid open areas due to greater likelihood of predation.

The proportion of individuals of threatened species was related to disturbances at the local level, as revealed by the GWR models. All threatened species in our dataset are shade tolerant and consequently are more susceptible to the increase of light exposure prompted by forest edges (Laurance et al. 2002). Against our expectations, selective logging and road length yielded positive effects on the PTRL. A possible explanation is that although these endangered species had been logged (Martinelli and Moraes 2013), it did not completely inhibit the maintenance of seedling banks over time. For example, threatened species corresponded to more than 30% of the trees on a sample plot at the northern region of the study area. The original tree density of threatened species like *Ocotea catharinensis* may have been so great that many individuals were not felled due to their inferior stem quality or small size. Indeed, Reitz et al. (1979) asserted that individuals of *O. catharinensis* added up to one third of the wood volume in one hectare at the northern region of the study area. Other threatened species, such as *Euterpe edulis* and *Cedrela fissilis*, are still among the most abundant in southern Santa Catarina (Colonetti et al. 2009), despite the expansion of agriculture.

The maintenance of populations of threatened species was favored by Brazil's Federal Decree 750 and Atlantic Forest law, which prohibited deforestation of primary and secondary forests (with exception of early successional forests) (Brasil 1993, 2006). Nevertheless, threatened species are still being illegally logged in the study area, and it may imperil the conservation of these species, especially of their genetic diversity (Montagna et al. 2018). Possible actions that would prevent this illegal activity, at least partially, would be the reinforcement of supervision and the implementation of sustainable forest management programs that would be economically attractive to landowners.

Impacts on species guilds patterns

The PPCL presented a stronger association with the evaluated disturbances in the extreme southern region of the study area (Fig. 2), where pasture areas and presence of clearcutting were related to PPCL. Clearcutting is often conducted to expand pasture areas, or even to facilitate the access of cattle into stands. Unfenced pastures permit cattle to enter forests for thermal comfort and alimentation. They also transit within permanent preservation areas along rivers and streams for water consumption. Several studies have shown that cattle trampling and grazing disturb the natural regeneration of Atlantic forests (e.g., Rosa et al. 2016; Vefago et al. 2019). Facing these issues, more sustainable cattle ranching methods, like silvopastoral systems, are highly encouraged. Such win–win approaches would provide shade and forage for livestock, whilst the natural regeneration of adjacent forest stands would be spared. In addition, other benefits would be attained regarding multiple environmental services and diversification of income for landowners.

Early succession species may proliferate in forest fragments adjacent to open habitats due to the increase in light availability (Laurance et al. 2006). The dispersion of such species may also be driven by tree mortality, which may be more pronounced in forest edges bordered by pastures than in edges bordered by vegetation in early stages of succession (Mesquita et al. 1999). Nonetheless, we did not find evidence that the PDCL is related to the PPCL on the evaluated sample plots. Remarkably, we also did not identify a relationship among PDCL and the anthropogenic disturbances. Tree mortality did not appear to be strongly related to edge effects generated from surrounding land use (e.g., pasture), nor from human disturbances in our study area. Mortality is most likely related to natural species turnover processes of secondary succession.

The massive colonization of pioneer species may lead to biotic homogenization and may delay species turnover in secondary forests (Tabarelli et al. 2012; Silva et al. 2017).

Anemochoric species in pastures adjacent to forest fragments may produce an increased amount of seeds that may retard successional processes, although little is known about how far these species may penetrate stands (Laurance et al. 2006). The PPRL was not related to pasture area (Table 1). The predominance and maintenance of such species in the natural regeneration layer may, however, be influenced by greater intensities of edge effects, as evidenced by the positive association between the PPRL and perimeter-area ratio.

Relationships among topography and human disturbances

Greater TH was shown to be associated with greater forest cover, smaller edge density, and less anthropism. Steeper terrains usually shelter less fragmented forests than plain terrains because of the restricted accessibility and limited conditions for tree felling and agriculture mechanization (Rezende et al. 2015). Such conditions also appear to limit land use changes and urbanization. We observed less agriculture, pasture and forest plantation areas, as well as sparser road networks, in landscapes with greater TH.

The path analysis indicated that TH has negative effects on pasture area, thus it has positive indirect effects on species richness. Areas where TH limits forest degradation may have augmented conservation value not only due to the preservation of larger forest patches, but also for protecting different pools of tree species (Everson and Boucher 1998). On the other hand, our results indicate that areas with less TH are more vulnerable to forest degradation. This is specially relevant for conservation purposes because coastal plains, for instance, shelter several rare tree species but are, nevertheless, under pressure due to real estate development (Oliveira et al. 2019) and have a few protected areas (Fig. 1).

Conclusions

Our study supported evidences that human activities at different spatial scales lead to disturbances such as edge effects and habitat fragmentation/isolation. These disturbances are related to ongoing changes in the structure and composition of secondary Atlantic forests and might even imperil biodiversity conservation. Land use amidst forest remnants is a relevant factor for forest conservation. Agriculture and pastures can affect forest attributes in different ways. The former was related to stands with more AGB in landscapes with large forest remnants, while the latter was related to stands with less species diversity. Pasture areas appeared to be related to the intensity of pioneer species colonization in nearby forests and may stand as a driver of biotic homogenization, thus delaying species turnover. In addition, the proportion of threatened species was positively related to long road networks and selective logging. Therefore, monitoring forest regeneration throughout time is essential to evaluate the eventual impacts of anthropogenic disturbances on this seminal component.

TH limits certain human activities, thus promoting the preservation of forests with greater species diversity. Conversely, coastal plains are more exposed to human activities, and therefore, by necessity, conservation strategies should be aimed at these environments. We could only validate our conceptual path model embedding indirect effects of TH on the SRCL. Therefore, new conceptual models could be proposed and tested.

Our study provided insights on issues related to the conservation of a threatened phytogeographic domain, the Atlantic Forest. Understanding these challenges are necessary for comprehensive decision-making regarding forest conservation and management. Nevertheless, for the planning of strategies related to the definition of priority areas for conservation and ecological corridors, other components, such as environmental features and socioeconomic aspects, should be considered along with biodiversity and structural aspects.

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