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Pathways affect vegetation structure and composition in the Atlantic Forest in southeastern Brazil

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ABSTRACT

Although impacts generated by gaps can affect vegetation, few studies have addressed these impacts in the Atlantic Forest. Our aim was to investigate the effects of pathways of varying widths on vegetation structure and composition, considering dispersal syndromes, diversity, life forms, successional categories and threatened and exotic species occurrence in the Atlantic Forest. We studied three pathways with widths of 2, 10 and 20 m, intersecting a protected area in southeastern Brazil. To assess edge effects, plots were established adjacent to paths (edge) and 35 m from the edge (neighborhood), and in a control area without pathways. Wider pathways (10 and 20 m) exhibited reduced tree height and diameter, high liana density, exotic species, and a high proportion of pioneer and anemochorous species. In conclusion, our results indicate that the vegetation structure of narrow pathways (2 m) is similar to the control area, and that wide linear gaps cause negative effects on vegetation and extend to a distance of at least 35 m into the forest interior. Considering that linear gaps generate permanent effects to vegetation and may affect other organisms, we suggest that these effects must be considered for successful management of protected areas, including planning and impact mitigation.

Keywords: Carlos Botelho State Park, conservation, linear gaps, plants, roads, trails

Introduction

Pathway construction amidst forests creates gaps that increase habitat fragmentation, one of the main threats to tropical forests (Gascon *et al.* 2000). Unlike natural forest gaps, anthropic linear gaps are practically immutable due to maintenance activities, imposing persistent effects on the conditions and resources of the forest nearby (Laurance *et al.* 2009). The effects of pathways relate to topography (e.g. earthmoving), soil conditions, microclimatic conditions, light exposure, which create distinct environments compared to the forest interior (Tabarelli *et al.* 1999; Webb *et al.* 1999;

Laurance *et al.* 2009), affecting habitat structure and species composition (Mantovani 2001; Enoki *et al.* 2012).

Tall trees and shade tolerant species usually inhabit old-growth tropical forest interiors (Liebsch *et al.* 2008). Environments with increased light availability create conditions for the colonization of early-successional species, normally wind-dispersed (Tabarelli *et al.* 1999; Laurance *et al.* 2009). The maintenance of these conditions over time and space allows the permanence of species associated with disturbed environments (Murcia 1995). Consequently, a permanent shift in plant community structure and composition might occur (Mantovani 2001).

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Several studies addressed the changes in vegetation structure and composition at the edges of linear forest gaps (Demir 2007; Enoki *et al.* 2012; Otto *et al.* 2013; Li *et al.* 2014) and just a few conducted in tropical forests focused on linear gaps caused by roads, gas pipelines and power lines (Reznik *et al.* 2012; Prieto *et al.* 2014; Couto-Santos *et al.* 2015), or pastures (Ribeiro *et al.* 2009a). In those studies, linear gaps affected the phenodynamics of animal dispersed plants (Reznik *et al.* 2012), tree species structure and richness (Ribeiro *et al.* 2009a; Couto-Santos *et al.* 2015), and proportion of pioneer species (Prieto *et al.* 2014). However, the extent to which the pathway width affects those forest attributes has never been properly assessed and understood.

The largest remaining portion of the Atlantic Forest, one of the biodiversity hotspots, lies in the Southeastern Brazil (Myers *et al.* 2000; Ribeiro *et al.* 2009b; Ribeiro *et al.* 2011a). Ecosystems within the Atlantic forest are being continuously degraded by illegal (e.g. poaching, selective logging), and legal (e.g. infrastructure installations such as roads, power lines, natural gas pipelines) impact vectors (Terborgh & Schaik 2002; Ribeiro *et al.* 2011a). On the other hand, roads and pathways are part of the necessary infrastructures that allow the management and surveillance of any park, which are also sometimes used for educational, ecotourism and research purposes. Therefore, research on the impacts of gaps generated by pathways and their associated influence on vegetation integrity is a promising approach to guide a more critical discussion on the two sides of the conservation issue (effective management x effective protection), contributing for decisions on the landscape changes and management strategies along the Atlantic forest continuum.

In this study we investigate the impacts of pathways of varying widths on the vegetation structure and species composition in an Atlantic forest protected area in southeastern Brazil, through the assessment of different life forms, successional categories, threatened and exotic species and the predominance of dispersal syndromes. We hypothesize that impacts in the wider pathway are more pronounced than in areas where pathways are narrow or absent. These impacts differentially affect the vegetation structure and composition among pathways, with wider ones characterized by plants with low height and small diameter, a high proportion of pioneer and wind dispersed species, and the occurrence of exotic species.

Materials and methods

Study site

We conducted this study at Carlos Botelho State Park (CBSP), a 37,644.36 ha protected area, part of the Atlantic Forest continuum, located between 24°06'55" -

24°14'41"S and 47°47'18" - 48°07'17"W, in the São Paulo state, southeastern Brazil (Fig. 1A). Altitudinal amplitude within the CBSP ranges from 20 to 1000 m. The climate is tropical, with mean annual temperature of 18 °C, and annual precipitation between 1500 - 2200 mm (Ferraz & Varjabedian 1999). The predominant vegetation type is Dense Ombrophilous Forest, which is divided into the following categories along the altitudinal gradient (Kronka *et al.* 2005): Lowland Dense Ombrophilous Forest (0 - 50 m), Submontane Dense Ombrophilous Forest (51 - 500 m) and Montane Dense Ombrophilous Forest (501 - 1500 m).

Pathways selected for sampling are located at an average altitude of 800 m, in the Montane Dense Ombrophilous Forest (Fig. 1B). Several ecological aspects for plant communities (e.g. density, richness, diversity and species composition) are more affected in the first 35 m from forest edges (Rodrigues 1998). Thus, to include edge effects, we sampled at the pathways edge and 35 m from the edge (neighborhood) (Fig. 1C). We selected a single path per pathway type because in the same forest continuum and elevation there are no replicas for the pathway types. We collected data on the following pathway types: main road, secondary road and trail (Fig. 1B). In addition, we established a control area, reputedly close to a reference state of conservation (Fig. 1B) (SMA 2008). All sampled plots are distributed within the same forest matrix, climate, altitude, and are spatially close (minimum distance between plots within the same pathway = 200 m and between pathways = 600 m). The control area is at least 1000 m away from the forest edge. Given the small spatial scale of the study, it is possible to assume that differences between plots are more related to direct effects of the pathways instead of purely spatial effects. The topography distribution of the plots encompassed mostly slopes, with some at hilltops and stream valleys, a similar pattern across all survey pathways.

Types of pathway

The main road within the CBSP is a dirt road of 112 km long (named SP-139) and about 20 m wide that intersects a total of 33 km of the state park area, with a completely open canopy (Fig. 2A). The secondary road is a dirt road approximately 12 km long and mostly 10 m wide, with the canopy covered at some points (Fig. 2B). The trail is approximately 4.5 km, 2.0 m wide, with the canopy covered along its total extension (Fig. 2C). The control area is representative of the mature forest occurring in most of the park (Fig. 2D), without apparent anthropic influence (SMA 2008).

Sampling Design

In each pathway we a priori selected a stretch of 1400 m along its total extension that was parallel to the pathway. We disregarded the first 500 m of each pathway in order



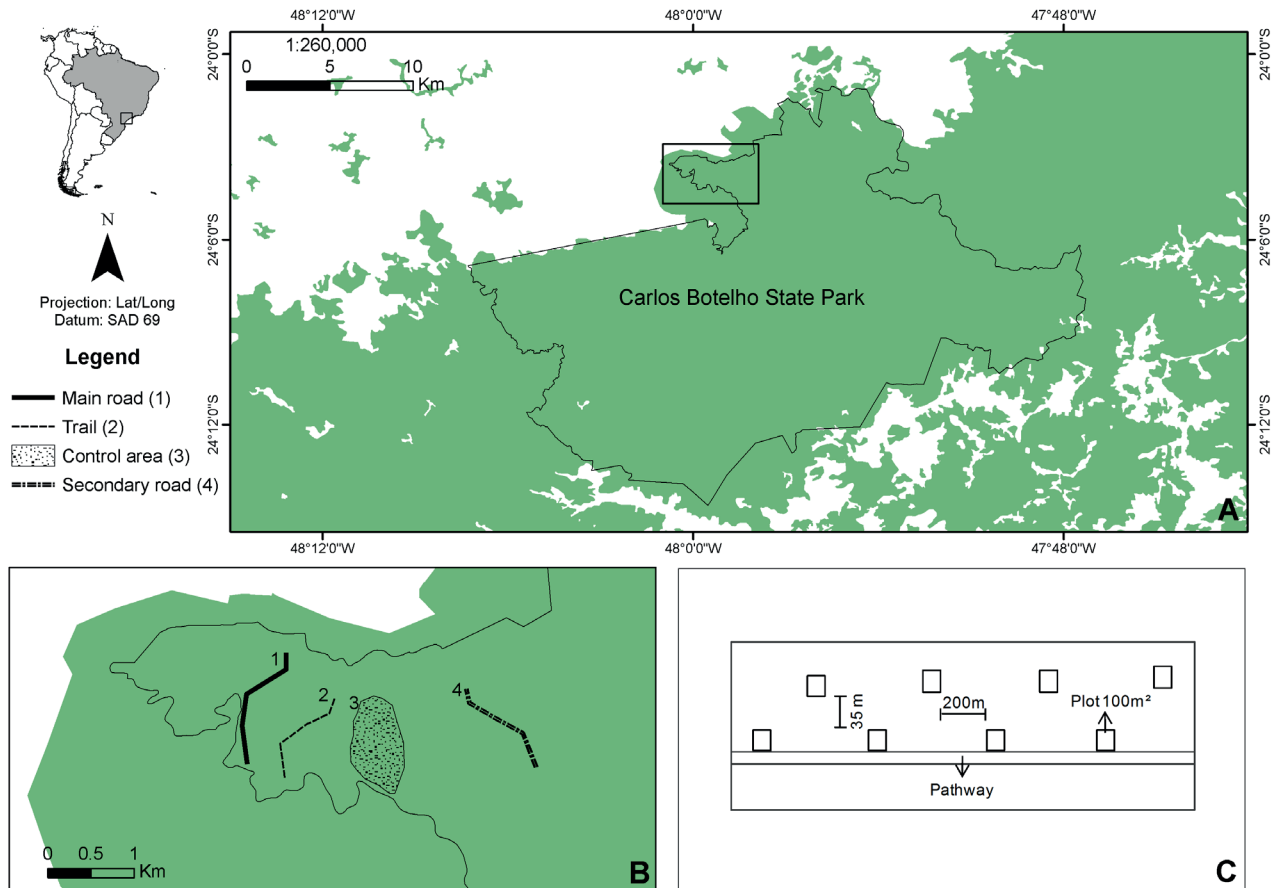


Figure 1. A. Location of Carlos Botelho State Park, SE Brazil. B. Situation of the pathways and control area sampled – 1: main road, 2: trail, 3: control area, 4: secondary road. C. Distribution of plots along the pathway (four adjacent to the pathway - edge - and four 35 m towards the forest interior - neighborhood).

to minimize forest edge effects, and only achieve pathway edge effects. Along each selected stretch eight 10 x 10 m sampling plots were alternately set: four adjacent to the path (edge) and four 35 m from the edge (neighborhood) (Fig. 1B). Plots were separated at least by 200 m of each other along the path to secure the independence of sampling units (Dias & Couto 2005; Lenza *et al.* 2011) (Fig. 1B). At the control area we set the eight plots in the same manner, except that there was no pathway. We used the pathways width (2, 10 and 20 m), named here as “type of pathway”, as a proxy of edge effects. In this design, the “type of pathway” (including control area) and “distance to edge” (0 and 35 m) are considered as treatments.

Vegetation survey

Vegetation structure and abundance - We recorded the following variables from individuals with diameter at breast height (DBH) ≥ 3.18 cm: total height, DBH and tree crown diameter (Durigan 2003). Total height (measured from ground) and tree crown diameter (by estimating the canopy radius) were visually estimated using a 3 m stick

as a parameter. The same person made all measurements. Based on total height, individuals were classified into three strata: high understory (1.5 - 5 m), intermediate level (5.1 - 11 m) and canopy (above 11 m). We also measured the low understory density of each plot by counting the number of individuals with 10 - 100 cm in height (DBH was always lower than 3.18 cm), in four sub-plots of 1 x 1 m at sampling points randomly assigned within each 10 x 10 m plot. Subplots were only installed for measuring the understory density, where individuals were counted but not identified. We excluded bamboo species (*Merostachys* sp.) from low understory density surveys, because they were considered as a separate variable (see below).

Abundance of epiphytes, vines (considering the herbaceous or woody) and bamboos (*Merostachys* sp.) in each plot was also recorded and classified in categories according to the percentage of the plot area cover. For epiphytes and vines we considered the categories low (< 20 %), medium (20 - 50 %) and high (> 50 %), and for bamboos we established lower abundance thresholds (10 % - low, 10-30 % - medium and > 30 % - high). We recorded the presence of exotic species inside plots and along the pathways. This

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Figure 2. Sampling areas at Carlos Botelho State Park, São Paulo state, SE Brazil. Different pathways used as treatments – A: main road (20 m of width), B: secondary road (10 m of width), C: trail (2 m of width), D: control area.

methodology was adapted from the Brazilian Ministry of Environment Resolution No. 01/94 (CONAMA 2015).

Canopy openness in each plot was measured using hemispherical photographs (Frazer *et al.* 2001), taken with a Nikon Coolpix 4500 camera with a fish-eye FC-E8 lens. We positioned the camera, with the aid of a tripod, at an approximate 60 cm height, at the centre of each plot. Photographs were taken in cloudy days to avoid over exposure to direct sunlight, which may influence image analysis (Frazer *et al.* 2001). We converted the resulting images in black and white colours in ImageJ software (2015). The canopy openness was estimated based on white pixels, which correspond to the percentage of gaps.

Vegetation composition - We considered the following variables to assess vegetation composition in each plot: life forms, diversity, successional categories, threatened and exotic species occurrence and predominance of dispersal syndromes. We identified and tagged all individuals with $DBH \geq 3.18$ cm. Plant species were identified by collecting

individual reproductive branches under SISBIO (#23627-1) and IBAMA (#4968681) collection permission. Identification was based on the literature and consultation to botanists. Vouchers were deposited at the Universidade Estadual de Campinas herbarium (UEC).

We grouped species according to two general successional categories: *pioneer*, including pioneer and early secondary, and *non-pioneer*, including late secondary and climax species (São Paulo 2008; Ronquim & Torresan 2011; Lingner *et al.* 2013). Dispersal syndromes were identified as zoochorous, anemochorous and autochorous following Pijl (1970). In addition, we considered the species' level of threat, according to the list of threatened flora of São Paulo state (São Paulo 2008), the red book of Brazilian flora (Martinelli & Moraes 2013) and IUCN's list of threatened flora (IUCN 2015). The species list was organized according to the taxonomical arrangement adopted by the Angiosperm Phylogeny Group IV (APG 2016). Species names were cross-checked with the List of Species of the Brazilian Flora (2015).

Data analyses

Vegetation structure and abundance - Plots were considered as independent sampling units. We applied a two-way ANOVAs for tree crown diameter, *DBH* and total height (considering mean values for plots), canopy openness for plot and percentage of individuals per stratum (high understory, intermediate level and canopy) and low understory density as response variables and “type of pathway” and “distance to edge” as predictors. The assumptions of normality and homogeneity of variance were verified using the Shapiro-Wilk test and confirmed visually in graphic analyses. When a significant ANOVA was obtained ($P < 0.01$), a post hoc HSD Tukey test was used to investigate differences between treatments, where $P < 0.05$ was considered significant.

Vegetation composition - We tested the difference in species composition for “type of pathway” and “distance to edge”, considering abundance and richness, using the permutational multivariate analysis of variance (Permanova; Anderson 2001) ($P < 0.01$ was considered significant). We used the “adonis” function of the R vegan package with Bray-Curtis distances and 10,000 permutations. In order to verify general tendencies of variation in vegetation composition, we performed an ordination analysis with non-metric multidimensional scaling (NMDS; Minchin 1987). We adopted this approach to better identify and interpret similarities between treatments. All analyses were performed in the R environment (R Core Team 2015).

We performed a diversity profile analysis, because it enables comparisons, as opposed to description of diversity indices only. With $\alpha = 1$, it is equivalent to Shannon's diversity index (H'), and $\alpha = 2$, it is equivalent to Simpson's diversity index (D); $\alpha = 0$ corresponds to richness values in different pathways. Therefore, we were able to compare treatments according to evenness and richness. These analyses were conducted using PAST (Hammer *et al.* 2001).

To evaluate differences in the proportion of zoochorous and pioneers species between the “type of pathway” and “distance to edge” we used generalized linear models with a binomial distribution. Significance of the factors was assessed by means of a Chi-squared Analysis of Deviance ($P < 0.01$ was considered significant). The analyses were carried out in the R statistical software (R Core Team 2015).

Results

Vegetation structure and abundance

We sampled 1019 individual trees ($DBH \geq 3.18$ cm) and 2302 individuals in the low understory (10 - 100 cm, $DBH < 3.18$ cm). Mean crown diameter, mean *DBH*, mean total height, canopy openness, tree percentage per stratum (except intermediate stratum) and low understory

density were affected by type of pathway (Tab. 1). For those variables, trail and control areas were similar, but they significantly differed from main and secondary roads, which were also similar to each other (Tab. 2). The trail and control area had higher values for *DBH*, tree crown diameter, tree height and number of individuals in the canopy stratum, whereas main and secondary roads had higher values for canopy openness and number of individuals in the high and low understory (Tab. 2).

We found low epiphytes abundance, and low/medium herbaceous vines abundance for main road. In main and secondary roads, abundance of both epiphytes and herbaceous vines ranged from low to high. For trail and control area, epiphytes abundance was medium to high, and abundance of herbaceous vines was low, with predominance of woody vines (i.e. lianas). Bamboo (*Merostachys* sp.) clumps predominated in some points of the main and secondary roads (low, medium and high abundance), while in the control and trail areas bamboo abundance was low. In the main and secondary roads we recorded *Urochloa* sp. (= *Brachiaria* sp.), an exotic species, and the invasive *Pteridium* sp.. Additionally, we observed *Citrus x limon* and *Eucalyptus* sp. present along the main and secondary roads outside the sampled plots.

Vegetation composition

Only the type of pathway influenced plant composition (PERMANOVA; type of pathway: $F_{3,25} = 1.78$, $p < 0.001$), while distance to the edge ($F_{1,25} = 1.12$, $p = 0.283$) and their interaction ($F_{2,25} = 1.08$, $p = 0.995$) were not significant. The ordination analysis (NMDS), final stress: 0.22, was consistent with results generated by PERMANOVA, and plots surveyed in the main road were grouped and separated from plots in the control area and trail, highlighting a marked difference between these areas. There was a distribution of points along axis 1 going from the wider pathways to the control area. However, no pattern was observed along axis 2. Data of the secondary road plots data formed an undefined grouping pattern (Fig. 3).

The control area and secondary road presented equal number of species (84 spp.), followed by trail (80 spp.) and main road (76 spp.). The control area and main road had the highest number of exclusive species (27 spp.), followed by secondary road (24 spp.) and trail (17 spp.). Secondary road and trail shared a high number of species (43 spp.). In contrast, control area and main road had the lowest number of shared species. Only 17 species were sampled in all areas (Tab. S1 in supplementary material). Of the total species (178 spp.), 15 are listed in threatened flora lists (São Paulo 2008; Martinelli & Moraes 2013; IUCN 2015). Six species are listed as vulnerable and five as endangered; four are listed in more than one list of threatened flora (Tab. S1 in supplementary material). Main road was the pathway with the lowest number of threatened species. The diversity



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Table 1. ANOVA results. Variables of vegetation structure considering type of pathway, distance to edge (35 m) and interaction, at Carlos Botelho State Park – SP, Brazil. *DBH* - diameter at breast height. $P < 0.01$ was considered significant.

		<i>Df</i>	<i>F</i>	<i>p</i>
Tree crown diameter*	Type of pathway (TP)	3	18.64	<0.0001
	Distance to edge (DE)	1	0.007	0.934
	TP x DE	2	0.714	0.499
	Residuals	25		
DBH (cm)*	Type of pathway	3	13.09	<0.0001
	Distance to edge	1	0.57	0.457
	TP x DE	2	0.72	0.493
	Residuals	25		
Total height (m)*	Type of pathway	3	29.94	<0.0001
	Distance to edge	1	0.91	0.349
	TP x DE	2	0.57	0.571
	Residuals	25		
Canopy openness	Type of pathway	3	13.34	<0.0001
	Distance to edge	1	1.53	0.227
	TP x DE	2	0.91	0.415
	Residuals	25		
Percentage of trees surveyed on the high-understory (1.5 – 5 m)	Type of pathway	3	23.02	<0.0001
	Distance to edge	1	0.163	0.69
	TP x DE	2	0.527	0.597
	Residuals	25		
Percentage of trees surveyed on the intermediate level (5.1 – 11 m)	Type of pathway	3	2.3	0.101
	Distance to edge	1	0.04	0.835
	TP x DE	2	0.34	0.714
	Residuals	25		
Percentage of trees surveyed on the canopy level (above 11 m)	Type of pathway	3	10.49	0.0001
	Distance to edge	1	0.03	0.859
	TP x DE	2	0.02	0.974
	Residuals	25		
Low-understory (10 cm – 100 cm height)*	Type of pathway	3	6.41	0.002
	Distance to edge	1	0.28	0.596
	TP x DE	2	0.08	0.923
	Residuals	25		

* = Mean values for plot

Table 2. HSD Tukey's test. Variables of vegetation structure among type of pathway at Carlos Botelho State Park – SP, Brazil. *DBH* - diameter at breast height. $P < 0.05$ was considered significant.

	Main road	Secondary road	Trail	Control area
Tree crown diameter*	1.77 ± 0.62 ^a	1.55 ± 0.13 ^a	2.98 ± 0.43 ^b	2.77 ± 0.48 ^b
<i>DBH</i> (cm)*	8.34 ± 0.96 ^a	9.35 ± 1.30 ^a	12.37 ± 1.51 ^b	12.62 ± 2.44 ^b
Total height (m)*	6.04 ± 1.18 ^a	6.61 ± 1.33 ^a	10.69 ± 1.23 ^b	10.58 ± 1.33 ^b
Canopy openness	12.87 ± 1.41 ^a	11.67 ± 1.49 ^a	9.31 ± 1.23 ^b	9.15 ± 1.53 ^b
Percentage of trees surveyed on the high-understory (1.5 – 5 m)	50.96 ^a	43.88 ^a	10.47 ^b	10.33 ^b
Percentage of trees surveyed on the intermediate level (5.1 – 11 m)	40.32 ^a	42.61 ^a	32.19 ^a	53.99 ^a
Percentage of trees surveyed on the canopy level (above 11 m)	8.7 ^a	13.5 ^a	25.13 ^b	36.15 ^b
Low-understory (10 cm – 100 cm height)*	24.43 ± 9.42 ^a	21.17 ± 9.35 ^a	11.37 ± 2.48 ^b	12.25 ± 3.00 ^b
Total number of trees with <i>DBH</i> ≥ 3.18 cm	310	237	259	213

^{a, b} = Variables significantly different according to HSD Tukey test $p < 0.05$

* = Mean values for plot

profile analysis demonstrated that the diversity index is similar among the areas (Fig. 4). However, when assigned more weight to evenness ($\alpha = 2$) main road plots and trail edge plots had the lowest values, and when assigned more

weight to richness secondary road had high values (Fig. 4).

Zoochorous species predominated in all areas, representing more than 70 % of the total species number (Fig. 5A). There was no difference in zoochorous species



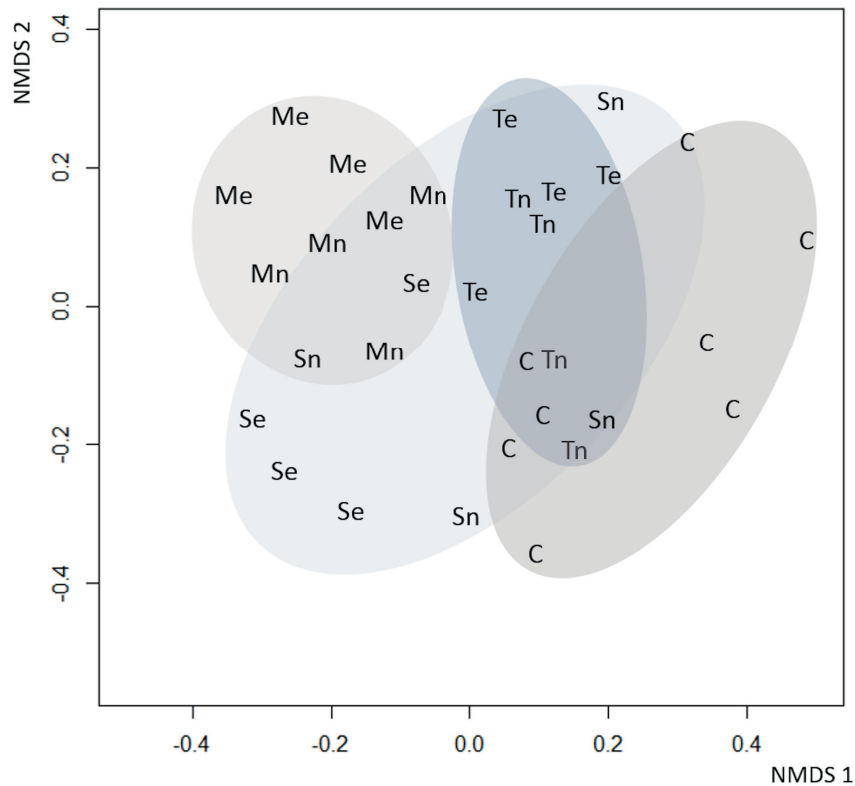


Figure 3. Scaling analysis (nMDS) of plant community among surveyed plots of treatments type of pathway and distance to edge in Carlos Botelho State Park, SP, Brazil. M: main road, S: secondary road, T: trail (e - edge, n - neighborhood), C: control area (nMDS, Final stress: 0.22).

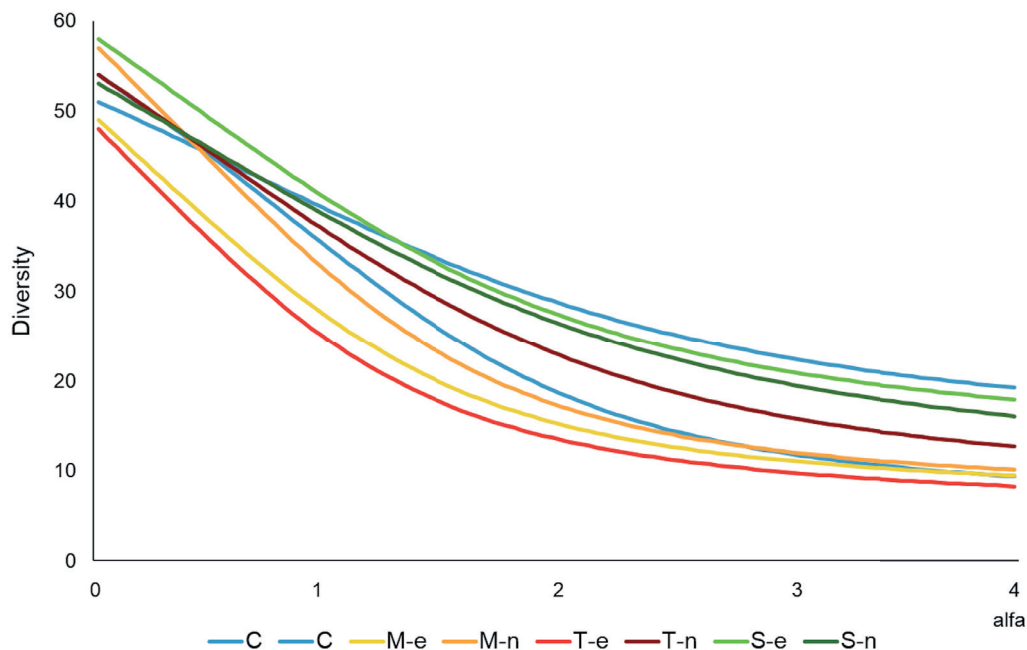


Figure 4. Diversity profile of plant community among pathways at Carlos Botelho State Park, SP, Brazil. M: main road, S: secondary road, T: trail, (e - edge, n - neighborhood), C: control area. $\alpha = 1$, it is equivalent to Shannon's diversity index (H'), and $\alpha = 2$, it is equivalent to Simpson's diversity index (D); $\alpha = 0$ corresponds to richness values. Please see the PDF version for color reference.

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Table 3. Results for generalized linear model for proportion of dispersal syndromes: zoochorous vs. non-zoochorous (anemochorous plus autochorous) species and individuals; and proportion of successional categories: pioneer vs. non-pioneer species and individuals, considering “type of pathway”, “distance to edge” and interaction, at Carlos Botelho State Park – SP, Brazil. $P < 0.01$ was considered significant.

Dispersal syndromes			
Species	Df	Deviance	p
Type of pathway	3	2.855	0.414
Distance to edge	1	2.785	0.095
Type of pathway x Distance to edge	2	0.684	0.71
NULL	31	32.722	
Individuals	Df	Deviance	p
Type of pathway	3	28.505	<0.0001
Distance to edge	1	16.663	<0.0001
Type of pathway x Distance to edge	2	11.532	0.003
NULL	31	111.828	
Successional categories			
Species	Df	Deviance	p
Type of pathway	3	31.158	<0.0001
Distance to edge	1	15.117	0.0001
Type of pathway x Distance to edge	2	0.085	0.958
NULL	31	79.437	
Individuals	Df	Deviance	p
Type of pathway	3	92.778	<0.0001
Distance to edge	1	45.155	<0.0001
Type of pathway x Distance to edge	2	5.500	0.063
NULL	31	192.702	

predominance among types of pathway and distance to edge (Tab. 3, Fig. 5A). The number of individuals, on the other hand, was smaller in the main road edge compared to neighborhood and other pathways and control area (Tab. 3, Fig. 5B).

The proportion of pioneer species and individuals was different for type of pathway and distance to edge (Tab. 3, Fig. 5C, D). Wider pathways presented higher values when compared to the trail and control area (Tab. 3, Fig. 5C, D). The edge plots of wider pathways had the highest values when compared to their own neighborhood plots (Fig. 5C, D).

Discussion

Changes in vegetation were detectable beyond the edges in wider (10 and 20 m) pathways, at least 35 m towards the forest interior. Different widths can determine the degree of microclimatic changes in the edge zone of a pathway (Pohlman *et al.* 2007). Light availability, high temperatures, low relative humidity, variation in soil nutrient availability and sediment runoff are variables that change according to the characteristics of linear gaps (Reid & Dunne 1984; Denslow 1987). Edges of wide pathways are more exposed to those factors when compared to narrow pathways, and can modify both the vegetation structure and the successional process in their vicinities (Goosem 1997). The distribution of plant species in tropical forests reflects different specific tolerances to drought, shade, and nutrient stress (Sterck *et*

al. 2006; Engelbrecht *et al.* 2007; Baltzer & Thomas 2010), implying that species are at least partially separated for different resource niches within a local community (Kraft & Ackerly 2010; Sterck *et al.* 2014).

Species composition differed in pathways with different widths. The control area and the narrow pathway (trail) exhibited similar species composition, but differed from the wider pathway (main road). Plots along the 10 m-width secondary road varied widely in species composition. The secondary road had half the width of the main road and canopy connection occurs in some points along its extension. This characteristic can promote high habitat heterogeneity and contribute to mixed species composition. Shade-tolerant species occurring in secondary road plots (e.g. *Micropholis crassipedicellata*, *Ocotea odorifera* and *Myrcia eugeniopsoides*) were also found in trail and control plots, but pioneer species (e.g. *Tibouchina pulchra* and *Miconia cabucu*) occurred mostly in main road plots. Thus, the high species diversity in the secondary road may be explained by a combination of species with different ecological requirements (Allouche *et al.* 2012), corroborating the intermediate disturbance hypothesis (Connell 1978; Molino & Sabatier 2001). The low diversity in trail can be probably related to the selective logging that occurred during the extractive period (near the 40's) of charcoal production (SMA 2008), as indicated by the presence of some charcoal ovens along the trail (SMA 2008).

A wide linear gap such as the main road (20 m) may disturb microclimate conditions and resource availability for plants, affecting the species distribution and eventually



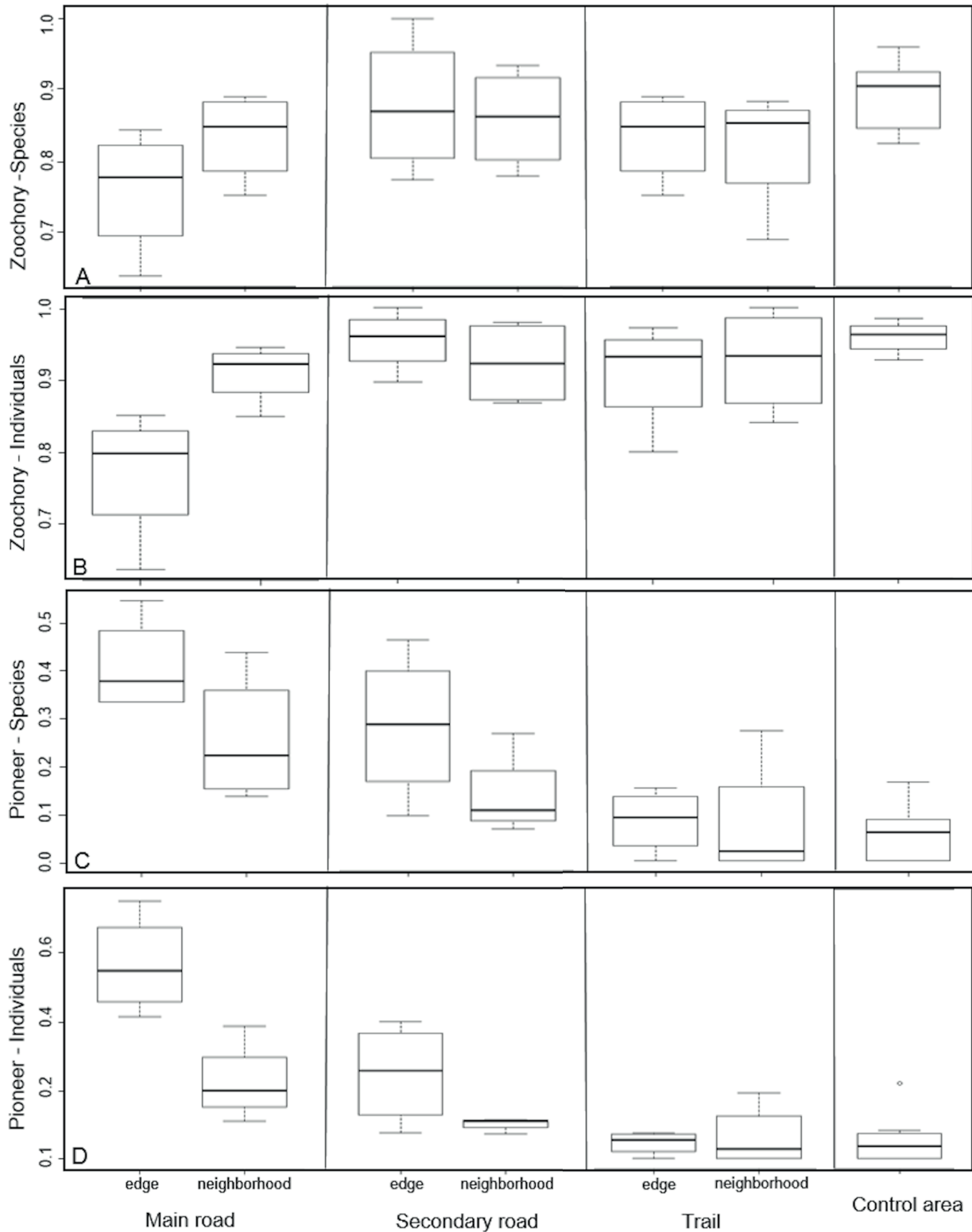


Figure 5. Proportion of dispersal syndromes - zoochorous vs. non-zoochorous (anemochorous plus autochorous) species and individuals; and proportion of successional categories: pioneer vs. non-pioneer species and individuals among “type of pathway” and “distance to edge” at Carlos Botelho State Park, SP, Brazil. The box-plots are displaying the median, the first and third quartile, and the maximum and minimum values of the data sets. A: Zoochorous species, B: Zoochorous individuals, C: Pioneer species, D: Pioneer individuals.

causing differences in the vegetation structure and composition between the edges and their inner adjacent areas (Hartshorn 1980; Sterck *et al.* 2014). Recruitment of generalist species can be facilitated by a wide pathway gap, which would benefit from highly variable ecological conditions found at the edge of the main road (Forman & Alexander 1998), resulting in species dominance (Denslow 1980), as demonstrated by the low evenness found in the main road. An increase in 10 m between the secondary and main road widths can be sufficient to determine differences in species composition, which emphasizes the importance of the gap size in the structuring of local plant communities (Denslow 1980; Zhu *et al.* 2014).

The predominance of species of different successional groups also depends on the gap size and the environmental conditions prevailing at the pathway edges (Denslow 1980), as verified for pioneer species, which have a positive relationship with gap size (Denslow 1980; Laurance *et al.* 2009). Shade intolerant pioneer species usually establish from the seed bank that existed prior to clearing or from subsequent recruitment (Tabarelli & Peres 2002). When a linear gap is established in a forested area, microclimatic conditions are inevitably altered, which allows pioneer species germination and/or seed dispersal (Webb *et al.* 1999). On the other hand, non-pioneer species are much less abundant and are prone to death at edges (Tabarelli & Peres 2002).

Wider pathways benefit anemochorous species because the aerodynamic design of their propagules enable them to be easily wind-transported for long distances in open environments (Howe & Smallwood 1982; Jara-Guerrero *et al.* 2011). Changes in the frequency of dispersal strategies are a result of favorable habitat conditions and disperser activity (wind vs. vertebrate dispersal) coupled with specific life forms (shrubs vs. trees) and the species frequency in these groups through successional stages (Tabarelli & Peres 2002). Accordingly, the wider pathway was characterized by a low frequency of zoochorous and a high density of anemochorous species. Gap size also determines the abundance of shrubs and small trees, since these life forms have greater densities in large rather than in small gaps (Zhu *et al.* 2014), as demonstrated by the higher densities of individuals smaller than 1m height in the wider pathways.

Atlantic Forest threatened species with restricted distributions were also affected by pathway width, with lower numbers occurring in the wider pathway. The exception was *Euterpe edulis*, a dominant palm species in undisturbed areas of the Atlantic forest (Guilherme *et al.* 2004), which, contrary to our expectations, was among the most abundant species in all pathways. Possibly, the high survival rates of juvenile in gaps, compared to areas with dense canopy cover, may explain this unexpected pattern (Nakazono *et al.* 2001; Ribeiro *et al.* 2011b).

Vine abundance is also positively related to increases in linear gaps (Laurance *et al.* 2001; Bataghin *et al.* 2010).

High abundance of vines at forest edges results from their demand for intense light exposure and the presence of slender trees that provide support for their fixation (Putz 1984). On the other hand, epiphytes are more sensitive to microclimate variations (Hietz 1998), require tall trees as substrate, and are therefore negatively related to linear gap width (Gonçalves & Waechter 2002; Wolf 2005). Not surprisingly, we found low abundance of epiphytes in areas intersected by wide pathways.

Intense management and traffic favor dispersal of exotic species along pathways (Dar *et al.* 2015), which is the case in our study, mainly at the main road. Despite the low traffic in the secondary road inside CBSP, exotic species were also recorded for this pathway, suggesting that even light traffic can promote the dispersal of exotic species. Moreover, the traffic-mediated dispersal of exotic species overcome competition with native plants, as many exotic species can withstand extreme conditions, like high light exposure, and succeed in colonising and establishing at the edges of pathways (Dar *et al.* 2015).

Plant communities with high number of individuals with small diameter and height were more frequent in the pathway edges but not in the control area, which indicates a typical initial regeneration phase (Guariguata & Ostertag 2001; Couto-Santos *et al.* 2015). This condition was probably set well before the park creation (between 40's and 70's), with the implantation of the pathways, and remained stable over time due to path maintenance.

In tropical forests, areas adjacent to linear gaps are characterized by low species richness, high proportion of pioneers and anemochorous plants and presence of exotic species, as reported in this study and others (Ribeiro *et al.* 2009a; Reznik *et al.* 2012; Prieto *et al.* 2014). We also found that pathway width influences the nearby vegetation as much as its presence. Therefore, the impacts of pathways on the vegetation and, subsequently, on their associated fauna should be carefully considered for conservation and management purposes (Dewalt *et al.* 2003; Watson *et al.* 2004). Unfortunately, despite under state protection, our study area will probably continue to suffer impacts, because the roads are permanent. Additionally, modifications promoted by linear gaps may change over time according to the adopted management decisions and actions (Pickering *et al.* 2010; Müllerová *et al.* 2011), jeopardizing the status and distribution of several native plant species, as well as the control of the exotic ones, mostly in the wider pathways.

In conclusion, our study highlights that pathways wider than 10 m intersecting native forest areas negatively affect the vegetation structure and species composition, modifying the predominance of life forms and the (distribution/proportion) of dispersal syndromes, with consequences for the successional categories, threatened species, besides increasing the occurrence of exotic species. These changes are permanent, interrupt the process of species turnover in ecological succession, and increase the intensity of



effects according to the pathway width. We expect that changes in the vegetation should also influence the resource availability and habitat use by the fauna (Restrepo *et al.* 1999; Dewalt *et al.* 2003; Watson *et al.* 2004). Our study stresses the importance of assessing the trade-offs between the consequences for conservation and the necessities of management of Atlantic Forest protect areas crossed by different kinds of pathways.

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