Plant diversity in hedgerows amidst Atlantic Forest fragments

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ABSTRACT

Hedgerows are linear structures found in agricultural landscapes that may facilitate dispersal of plants and animals and also serve as habitat. The aim of this study was to investigate the relationships among diversity and ecological traits of woody plants, hedgerow characteristics (size, age, and origin), and the structure of the surrounding Atlantic Forest landscape. Field data were collected from 14 hedgerows, and landscape metrics from 1000-m buffers surrounding hedgerows were recorded from a thematic map. In all sampled hedgerows, arboreal species were predominantly zoochoric and early-succession species, and hedgerow width was an important factor explaining the richness and abundance of this group of species. Connection with forest vegetation did not explain richness and abundance of animal-dispersed species, but richness of non-zoochoric species increased in more connected hedgerows. These results suggest that hedgerows are probably colonized by species arriving from nearby early-succession sites, forest fragment edges, and isolated trees in the matrix. Nonetheless, hedgerows provide resources for frugivorous animals and influence landscape connectivity, highlighting the importance of these elements in the conservation of biodiversity in fragmented and rural landscapes.

Keywords: Atlantic Forest, ecological corridors, forest fragmentation, hedgerows, landscape ecology, rural landscape, seed dispersal, woody plants.

Introduction

In a fragmented landscape, the movement of organisms between habitat patches depends on landscape connectivity, which depends on distances among patches and matrix permeability (Haddad 1999). The presence of some structures in landscapes, such as "stepping stones" and corridors (Eycott *et al.* 2012), can strongly influence connectivity by reducing distances to be crossed through the matrix, thus reducing resistance to ecological flows.

Hedgerows are characteristic elements of rural landscapes that can arise spontaneously or be actively created (e.g., to act as windbreaks), and they are believed to promote the flow of organisms between fragments of natural habitat, serving as both corridors and habitats for forest species that encounter resistance to dispersal on the agricultural matrix (McColling *et al.* 2000). Hedgerow characteristics, such as origin, age, length, and width, can alter its efficiency as a habitat or corridor, and thus, the diversity of species established therein (Forman & Godron 1986). In addition, surrounding landscape structure, such as the presence of forest patches and isolated trees, can promote the arrival of seeds in hedgerows (Harvey 2000).

Hess & Fischer (2001) have suggested that corridors can serve as conduits, barriers, or habitats, among other functions. Propagules of some animal-dispersed species may be deposited in the corridor, indicating that seed dispersal may not reach the ends of long corridors; thus such plant species must establish and reproduce within the corridor to complete dispersal in subsequent generations (Beier & Loe 1992). On the other hand, for wind-dispersed seeds in open spaces, corridors can act as barriers that trap such seeds, which can also result in establishing plants in the corridor.

Nonetheless, the presence of plants established in a corridor can suggest that plant species are dispersed through it (zoochory) or into it (anemochory, and to a lesser extent, autochory), but this approach is biased by the species' abilities to establish in the edge-like microhabitats of the corridors (Hobbs 1992; Fritz & Merriam 1994). A possible surrogate for assessing this ability is successional status; pioneer species, able to endure relatively sunny, warm, and dry conditions, establish more easily, whereas late successional species may be unable to germinate or establish as seedlings because of harsh microclimates (McColling *et al.* 2000). In tropical fragmented landscapes, it is important to determine how hedgerows function for different groups of

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plant species as this has implications for the conservation of both the species themselves and the whole landscape.

In this context, the aim of this study was to investigate the relationships among the characteristics of hedgerows (width, length, age, origin, and connection with forest patches), the structure of the surrounding landscape, and the associated diversity of woody plants. Sampling was performed in hedgerows in a fragmented Atlantic Forest landscape in southern Brazil to test the hypothesis that shorter, older, and spontaneously originating hedgerows, as well as those with greater surrounding forest cover, would be richer in animal-dispersed and late successional woody species.

Material and Methods

The study was conducted in Londrina, north of Paraná state, Brazil between 23°08'47"S–23°55'46" and 50°52'23" –51°19'11"W (please see Fig. 1 in the Supplementary material). The region had a continuous seasonal Atlantic Forest cover until the 1930s, when a rapid change of land use began, favoring agricultural crops and cattle raising, thereby resulting in a landscape with a few forest fragments dispersed throughout a predominantly agricultural matrix (Torezan *et al.* 2005). The climate is subtropical humid (Köppen's Cfa), with hot and rainy summers, but with no definite dry season. Sampling was performed in 14 hedgerows located on rural properties, with no recent maintenance (pruning, cutting, or fire). A hedgerow was defined as a strip of vegetation that served or still serves as the delimitation of rural fields or as windbreaks.

Woody plants were sampled on 100×2 m transects. The number of transects varied from two to four, depending on hedgerow length. The minimum distance between transects was 20 m. Transects were subdivided into 10 m segments. For analysis of the landscape structure surrounding each hedgerow, a thematic map was produced from a set of Landsat-5 Thematic Mapper images, containing 8 classes: water, forest, late secondary succession, early secondary succession, pasture, perennial agriculture, annual agriculture, and urban land. The length and width of the hedgerows were measured in the field. The hedgerows were not uniform in width so measurements were taken at the beginning, middle, and end of each transect with a measuring tape, and the average value was calculated. The age of the hedgerows was obtained from interviews
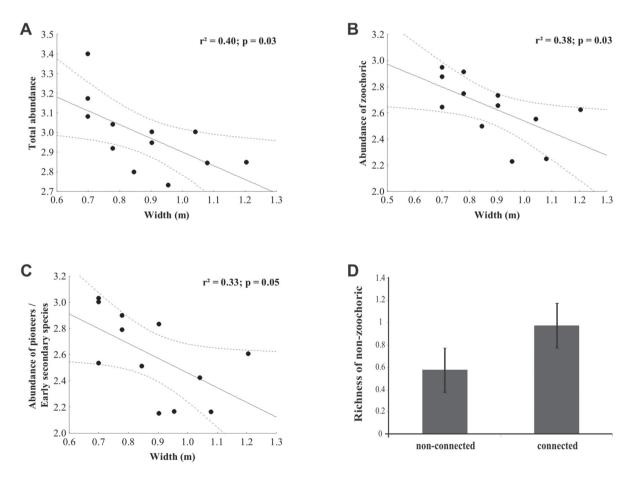

Figure 1. Relationship between hedgerow width and A) total abundance, B) abundance of zoochoric species, and C) abundance of pioneer and early secondary species. D) Richness of non-zoochoric species and connectedness (the bars indicate standard errors).

with landowners, with the aid of aerial photographs and satellite imagery, and was determined from the year that the hedgerow ceased to receive maintenance such as weeding and pruning. Hedgerows that had at least one end attached to a forest structure (with a gap of less than 30 m) were categorized as connected. The hedgerows were also classified as planted (when shrubs or trees are planted in rows, for the protection of property and crops from wind) or spontaneous (when there is natural plant establishment along a common wire fence); in this study, all planted hedgerows were established with only one exotic tree species, including *Pinus* spp., *Eucalyptus* spp., or *Grevill*ea *robusta*. A. Cunn. ex R. Br. All woody plants (trees, shrubs, and lianas) with a height greater than 1 m were recorded. Lianas present but not rooted in the plot were not recorded. Species were identified in the field whenever possible, and specimens were taken to the Londrina University herbarium (FUEL) for confirmation. The sampled tree species were categorized according to successional status (pioneers, early secondary, late secondary, and climax) following Gandolfi *et al.* (1995), Dias *et al.* (1998), and Zangaro *et al.* (2003). To reduce the uncertainty of the classification, pioneer and early secondary tree species were combined into one group (PE) and late secondary and climax species were combined into another (LC). Tree species were also grouped into zoochoric (Z) and non-zoochoric (NZ) (Tab. 1).

Analyses were first performed with all species pooled, and then trees were separated by successional or dispersal species groups. In hedgerows with more than two transects, 20 plots were randomly selected for analysis. Levene's and Shapiro–Wilk tests were used before analyses to verify the assumptions of variance homogeneity and normality, respectively. The differences in species richness and abundance between the connected and non-connected hedgerows, as well as between spontaneous and planted hedgerows, were calculated using the Tukey–Kramer method for unequal sample sizes ($\alpha \leq 0.05$). The relationship between hedgerow age, length, width, and landscape structure with species richness or abundance was verified by simple linear regression ($\alpha \leq 0.05$). Landscape structure was analyzed within 1000-m buffers surrounding each hedgerow. For this analysis, two hedgerows were excluded because of buffer overlap. FRAGSTATS (McGarigal & Marks 1995) was used to generate the landscape diversity index (Shannon diversity index of landscapes) and proximity index (PI). PI is the ratio of the sum of the area of forest fragments included within a particular "search radius" and the sum of the square of the distance, edge to edge, from these fragments to the hedgerow sampled (McGarigal & Marks 1995; Table 1). Spatial autocorrelation was analyzed for all non-categorical variables by means of a Mantel test using SAM software (Rangel *et al.* 2010), and no significant figures were found.

Table 1. Hedgerow structure, landscape structure, and richness and abundance of woody species

Hedgerow	1	2	3	4	5	6	7	8	9*	10	11	12*	13	14
Area (m²)	4320	2725	7800	3300	4160	2160	2250	3000	3000	3500	1500	12000	5850	4800
Width (m)	12	5	6	11	8	8	5	6	6	7	5	8	9	16
Length (m)	360	545	1300	300	520	270	450	500	500	400	300	1500	650	300
Age (years)	10	20	40	20	30	40	10	30	30	10	30	40	30	60
Origin[1]	p	s	s	p	s	p	p	p	s	s	s	s	s	p
Connectedness[1]	nc	c	c	c	c	c	nc	nc		c	c		c	nc
H' Landscape[1]	0.49	0.35	0.63	1.1	0.95	0.66	0.19	0.37		0.98	1.03		0.09	0,02
PI[1]	0.01	0	0.46	436.7	64.32	0.45	0.56	0.02		0.34	4.44		0.09	0
Richness	32	45	62	57	58	48	50	27	50	57	53	58	58	67
Abundance	701	1490	832	1007	886	1009	2514	1099	665	631	1209	1026	539	705
Richness PE[1]	10	16	21	19	19	19	15	6	10	18	23	22	19	27
Abundance PE[1]	146	1073	616	265	142	681	343	792	277	326	1006	1245	147	406
Richness LC[1]	7	10	8	14	9	8	8	3	5	2	11	5	12	8
Abundance LC[1]	111	119	147	132	346	34	104	28	51	53	303	199	105	112
Richness Z[1]	13	17	19	26	22	18	20	9	13	11	25	14	24	26
Abundance Z[1]	177	885	560	357	454	542	442	820	304	316	754	1037	169	421
Richness NZ[1]	5	10	11	9	7	10	4	1	3	11	10	14	8	10
Abundance NZ[1]	81	308	231	42	35	174	6	1	25	71	556	408	84	98

*excluded in some analysis to due to 1000 m - neighborhood overlap with another hedgerow site
[1]p= planted, s= spontaneous, c= connected, nc= non-connected, H' Landscape=Shannon diversity index of landscape, PI= proximity index, PE=pioneer and early secondary species, LC=late secondary and climax species, Z=zoochoric species, NZ=non-zoochoric species

Results

A total of 17,020 individuals (2.6 individuals/m²) were identified, distributed among 198 species and 51 families (please see complete species list in the Tab. 1 in the Supplementary material). The most common life form was arboreal (57% of species and 80% of total individuals), followed by lianas (23% of species and 17% of total individuals), and shrubs (20% of species and 3% of total individuals). Among the arboreal species, 19% were exotics. The native tree species were represented by 70% of pioneers (PE) and 63% by zoochoric species (Z). Average species richness in the hedgerows was 51 species, with averages of eight late succession species and 18 zoochoric species.

Negative relationships between hedgerow width and total abundance ($r^2 = 0.40$; $b = -0.63$; $p = 0.03$), PE abundance ($r^2 = 0.33$; $b = -0.57$; $p = 0.05$), and zoochoric abundance ($r^2 = 0.38$; $b = -0.61$; $p = 0.03$) (Fig. 1) were observed. No relationship was observed between the other hedgerow features and abundance or richness. Connection with forest patches led to an increase in richness ($p = 0.038$; $M_{UC} = 0.57$; $M_C = 0.97$) of non-zoochoric species only (Fig. 1). All other landscape variables did not show any relationship with abundance or species richness in hedgerows.

Discussion

Most of the species in the hedgerows were pioneer trees, suggesting that neighboring forest edges, early succession sites, and tree clumps scattered through the matrix are probably the seed sources for those structures. In addition, edge effects occur on both sides of hedgerows (Fritz & Merriam 1994), contributing to this predominance of pioneers and the scarcity of LC species, whose establishment depends on the existence of forest microclimates (Hernandéz-Stefanoni & Dupuy 2008). Nonetheless, the limited late successional species recruitment suggests that succession is arrested in hedgerows (Perkulis *et al.* 1997) and that hedgerows function poorly as dispersal corridors for late successional plant species, since long corridors made of unsuitable habitat are of limited value for such plants (Wehling & Diekmann 2009).

The openness of the landscape is expected to favor anemochoric species, dispersing from the matrix and forest edges (Herlin & Fry 2000). However, the regional arboreal flora is predominantly zoochoric (Silva & Soares-Silva 2000), and thus, higher richness and abundance of zoochoric species indicate frequent visitation of the hedgerows by seed-dispersing fauna (Fritz & Merriam 1994; Herlin & Fry 2000). Moreover, the abundance of fruit resources, as well as the supply of shelter for animals, highlights the importance of hedgerows for increasing habitat diversity in agricultural landscapes (Harvey 2000).

Among the hedgerow structural variables (age, width, length, and origin), only width was correlated with plant abundance. Wider hedgerows were expected to have more animal-dispersed and late successional species (Herlin & Fry 2000). However, some studies have shown species-specific distributions in corridors with different widths (Cervinka *et al.* 2013). Our results show that there were more pioneer and early successional species in narrow hedgerows, possibly due to lateral light penetration, and higher zoochoric abundance, reflecting an increase in some animal-dispersed pioneer trees, such as *Tabernaemontana catharinensis*. Nonetheless, colonization by pioneer species is an important mechanism creating microhabitats favorable to late species and attracting more seed dispersing animals (Wunderle 1997; Florentine & Westbrooke 2004). Boughey *et al.* (2011) found that some bat species use hedgerows as narrow as 2 m, reinforcing the value of linear structures in providing food resources and shelter for these mammals.

Contrary to our expectations, direct connections between hedgerows and forest fragments did not influence zoochoric species richness or abundance. However, none of the sampled hedgerows were connected to such fragments at both ends, indicating that they are not real corridors (Beier & Noss 1998). Therefore, the greater proportion of zoochoric species in hedgerows is probably associated with dispersal by matrix-dwelling birds and bats (Toniato & Oliveira-Filho 2004).

In contrast, connected hedgerows had a greater richness of non-zoochoric species. Even though only 37% of species recorded in the hedgerows had anemo- or autochoric dispersal, our results suggest that connections with forest structure provide proximity with forest edges, which usually contain a greater abundance of wind-dispersed plants (Herlin & Fry 2000). In addition to connectedness, the landscape structures analyzed in this study (landscape diversity and proximity index) did not appear to influence woody species richness and abundance in hedgerows. There are two possible explanations for this finding. First, while landscape metrics have been used extensively to predict features of fragmented landscapes (Hargis *et al.* 1998), there are several important processes at a local scale that affect the structure and diversity of vegetation. As discussed above, the edge-like environment of hedgerows can strongly limit the number of species able to establish within them and is thus a proximate cause for the disconnection between hedgerow diversity and surrounding landscape structure.

Second, there are some elements of agricultural landscapes, like isolated trees, small tree clumps, and other hedgerows, which cannot be captured in maps based on mid-resolution satellite imagery (Turner *et al.* 2003), but can still be an important source of seeds for some species, notably pioneer trees. These structures can also provide forage and protection for animals crossing the matrix (Guevara *et al.* 1992), which probably spread seeds, and thus, homogenize plant assemblages from hedgerows and similar environments.

Hedgerows are home for mostly pioneer, animal-dispersed trees, and shrubs. This suggests that hedgerows

support a high level of activity of fruit-eating fauna, and thus, hedgerows are important structures for biodiversity conservation in rural landscapes. However, the limited presence of late successional species suggests that succession within hedgerows is arrested and that hedgerows are also of limited value as corridors or stepping stones for late succession plant species.

Acknowledgements

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