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Woody Species Regeneration in Atlantic Forest Restoration Sites Depends on Surrounding Landscape

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Abstract

Both passive and active restoration are limited by diaspore arrival from neighboring sources. Surrounding landscape is thus important for restoration success in fragmented landscapes, where reforestation, for long periods, may be limited to the planted species pool. We sampled woody species regeneration in 17 reforestation sites in Southern Brazil to investigate the effects of distance to seed sources and amount of remaining nearby Atlantic Forest habitat. The abundance and species richness of regenerating plants were explained by multiple regressions performed using plantation age and species richness, distance to the nearest patch, and surrounding habitat. Distance to the nearest forest remnant, through both the matrix in a straight line and riparian vegetation, was the best predictor of species richness and abundance of regenerating plants. Riparian corridors doubled the distance at which forest remnants influenced restoration sites. However, the area of forest remnants in the site neighborhood did not influence regeneration diversity, suggesting that the quality of both the seed source (including the status of seed dispersing fauna) and reforestation environment for the establishment of forest species should be investigated.

Key words: Forest Fragmentation, Seed Dispersal, Ecological Restoration, Secondary Succession.

Introduction

The Atlantic Forest has suffered extensive deforestation over the last five centuries due to agriculture, cattle raising, and urban growth. Today, in most regions the landscapes are fragmented, with forest cover limited to small patches and a huge amount of degraded area needing to be revegetated to comply with conservation goals and enhance landscape connectivity (Ribeiro *et al.* 2009).

The present landscape's spatial configuration may influence local ecological processes, mainly by decreasing biological flows such as seed dispersal (Hamilton 1999; Tabarelli *et al.* 1999; Tabarelli & Peres 2002). Thus, secondary succession, whether preceded by active restoration or not, may be delayed or even precluded if the local biota is constrained to a few already present or actively reintroduced species (Hobbs & Norton 1996; Holl *et al.* 2000). Active ecological restoration frequently relies on overcoming site limitations, such as an unfavorable microclimate and soil degradation, by means of planting or promoting the establishment of a limited pool of rustic species that is expected to change the site conditions (Parrotta *et al.* 1997; Sansevero *et al.* 2011).

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However, it is difficult, if not impossible, to manipulate a large set of species and functional groups to actively assemble a complex ecosystem without counting on spontaneous species arrival from neighboring sources (Parrotta *et al.* 1997). Although it is possible to introduce a relatively large number of species during the implementation of reforestation, many late species would not adapt to local abiotic conditions. Therefore, most unplanted species will depend on existing neighboring sources of propagules to reach restoration sites. Besides seed source distance, the size and quality of these sources can influence the arriving species richness as long as larger and better-conserved habitat tracts will hold more species (Fahrig 2003; Aparicio *et al.* 2008).

Differences in dispersal syndrome (White *et al.* 2004), seed mass (Laurance 1994; Moles & Westoby 2004), and microhabitat preferences (Holl 1999) among plants species can result in different abilities to cross the landscape and to arrive at successional sites. Most of the uncertainty regarding plant dispersal ability can be related to their dispersal agent's ability to cross the matrix among habitat patches, an issue that is of great interest to researchers (Taylor *et al.* 1993; Metzger & Décamps 1997; Wunderle Jr. 1997; Pivello *et al.* 2006). It is worth stating that both plants and their dispersal agents will show a great range in their dispersal abilities in fragmented landscapes (White *et al.* 2004). While wind-dispersed species benefit from a non-forest matrix, animal-dispersed species rely on the vagility of dispersing animal species. However, if there is a threshold in landscape fragmentation after which dispersal will fall to near zero (Metzger & Décamps 1997) regardless of species dispersal syndrome, knowing such a limit will be crucial for the planning, establishment, and management of restoration sites.

A few studies have been conducted relating fragmented landscapes and restoration sites, especially regarding passive succession in reforestation and the distance from seed sources. Some of these studies have shown that the recruitment of late-successional, forest specialist species is slower in isolated sites compared with sites adjacent to sources (Zanne & Chapman 2001; White *et al.* 2004). To mitigate the negative effects of distance from seed sources in fragmented landscapes, it is important to increase the connectivity of the matrix, and one of the best methods is to promote habitat restoration in some agricultural sites (García-Feced *et al.* 2011) and riparian lands (DeClerck *et al.* 2010). Furthermore, restoration sites and other early successional habitats represent a good opportunity to test hypotheses about biotic dispersal in fragmented landscapes, due to their simple structure and known history, unlike most forest remnants.

In this study, we investigate how and to what extent woody plant diversity in the understory of reforestation sites is related to the distance from seed sources and to the amount of neighboring Atlantic Forest habitat. We hypothesized that the abundance and richness of late successional, forest dependent species and animal-dispersed species will be low at further isolated sites.

Methods

Study sites

To analyze the influence of nearby landscape structures on native plant species regeneration, 17 reforestation sites of similar ages (75 to 101 months) at different distances from Atlantic Forest remnants were studied. The forest cover in a 1000-m radius from each site ranged from 2.3 to 35.3 ha (see Table 1 in the supplementary material**). Study sites were

Table 1. Results of multiple regression analysis for non-planted, native woody species diversity in restoration sites (N=17) in northern Paraná state, Brazil. A – total abundance, S – total species richness, A_L – abundance of late successional species, S_L – richness of late successional species, A_A – abundance of animal-dispersed species, S_A – richness of animal-dispersed species, D – distance to nearest forest remnant, D_V – distance to nearest forest remnant through riparian vegetation, Y – plantation age, P – planted species richness, V_{500} – surrounding forest area in 500 m radius, V_{1000} – surrounding forest area in 1000 m radius and A_{NF} – abundance of non-forest species. *Best models. Best independent variable: significance in simple linear regression with highest r^2.

Dependent Variable	Model	r^2	r^2 adjusted	*model p*	*best independent variable*	*beta*	*p*
A	$D\ Y\ P\ V_{500}\ A_{NF}$	0.495	0.265	0.13	-	-	-
	$D\ Y\ P\ V_{1000}\ A_{NF}$	0.642	0.454	0.03	D	–0.75	0.01
	$D_V\ Y\ P\ V_{500}\ A_{NF}$	0.586	0.398	0.05	D_V	–0.58	0.03
	$D_V\ Y\ P\ V_{1000}\ A_{NF}$*	0.731	0.609	0.006	D_V	–0.84	0.001
S	$D\ Y\ P\ V_{500}\ A_{NF}$	0.555	0.353	0.07	D	–0.57	0.04
	$D\ Y\ P\ V_{1000}\ A_{NF}$	0.632	0.465	0.03	D	–0.75	0.01
	$D_V\ Y\ P\ V_{500}\ A_{NF}$	0.627	0.457	0.03	D_V	–0.64	0.01
	$D_V\ Y\ P\ V_{1000}\ A_{NF}$*	0.705	0.571	0.01	D_V	–0.80	0.002
A_L	$D\ Y\ P\ V_{500}\ A_{NF}$	0.488	0.256	0.14	-	-	-
	$D\ Y\ P\ V_{1000}\ A_{NF}$	0.602	0.421	0.04	D	–0.74	0.01
	$D_V\ Y\ P\ V_{500}\ A_{NF}$	0.569	0.374	0.06	D_V	–0.57	0.03
	$D_V\ Y\ P\ V_{1000}\ A_{NF}$*	0.694	0.554	0.01	D_V	–0.81	0.002
S_L	$D\ Y\ P\ V_{500}\ A_{NF}$	0.489	0.258	0.14	-	-	-
	$D\ Y\ P\ V_{1000}\ A_{NF}$*	0.503	0.277	0.12	D	–0.68	0.03
	$D_V\ Y\ P\ V_{500}\ A_{NF}$	0.486	0.252	0.14	-	-	-
	$D_V\ Y\ P\ V_{1000}\ A_{NF}$	0.489	0.256	0.14	D_V	–0.64	0.04
A_A	$D\ Y\ P\ V_{500}\ A_{NF}$	0.494	0.263	0.13	-	-	-
	$D\ Y\ P\ V_{1000}\ A_{NF}$	0.578	0.387	0.05	D	–0.64	0.03
	$D_V\ Y\ P\ V_{500}\ A_{NF}$	0.551	0.347	0.07	-	-	-
	$D_V\ Y\ P\ V_{1000}\ A_{NF}$*	0.646	0.485	0.02	D_V	–0.70	0.01
S_A	$D\ Y\ P\ V_{500}\ A_{NF}$	0.596	0.412	0.04	D	–0.61	0.02
	$D\ Y\ P\ V_{1000}\ A_{NF}$	0.652	0.494	0.02	D	–0.76	0.008
	$D_V\ Y\ P\ V_{500}\ A_{NF}$	0.639	0.476	0.02	D_V	–0.64	0.01
	$D_V\ Y\ P\ V_{1000}\ A_{NF}$*	0.690	0.550	0.01	D_V	–0.77	0.004

**see supplementary material available at abeco.org.br.

located in the margins of the Capivara Reservoir (north of Parana state, Brazil; between 22° 45' 22" S, 51° 98' 38" W and 23° 06' 16" S, 50° 51' 27" W). The original vegetation cover was a seasonal form of the Atlantic Forest, which presently covers less than 2% of the region. The forest remnants are late successional and suffered limited timber extraction in the early 1980s, ranging from 4 to 180 ha in size.

The climate is classified as Köeppen's Cfa humid subtropical, with hot, humid summers. Frosts are infrequent, and rain is concentrated in the summer months (December-January), with no definite dry season. The average temperature in the warmest month (January) is approximately 23.8 °C and that in the coldest month (July) is 16.8 °C. Precipitation averages 201.4 mm in January (summer) and 56.5 mm in July (winter). The soil at all sites is a highly fertile eutrophic red latosol, originated from basaltic rock and used in soybean and maize rotation until the reforestation activities began. All the reforestation sites are also surrounded by maize and soybean plantations.

All reforestation sites were on strips of land between 334 m (maximum reservoir water level) and 338 m above sea level, by means of planting native, pioneer, and early secondary species, with 2 × 3 m spacing between seedlings. The planted species richness varied between 25 and 50 species. Weed control was done by mechanical and manual mowing until the end of the 2nd year after planting. During weed control, all regenerating individuals (native and non-native woody species) were also removed.

Data collection

In each site, ten 10- × 10-m plots were established along reforestation strips, with a minimum of a 20 m distance between them (see supplementary material). In each plot, all woody plants with a height equal or greater than 0.10 m were identified and counted. The regenerating plant species were also classified as early or late successional species (see supplementary material), by dispersal syndrome (self-, wind- or animal-dispersed), as native or exotic, and as forest or non-forest species. Regenerating individuals from exotic species, reforestation-planted species, and non-forest species were excluded from analysis because the arrival of the diaspores of these species does not depend on the remnant forest-originated seed rain. Abundance (A) and richness (S) were analyzed separately, and both were determined for three groups: (1) native species (A/S), (2) late successional species (A_L/S_L), and (3) animal-dispersed species (A_A/S_A).

To measure the amount of surrounding habitat and distance to the nearest forest remnant, a thematic map based on LANDSAT 7 imagery was generated (scene 222/76 from September 2003). Forest habitat area was measured in 500- and 1000-m radius neighborhoods for each reforestation site (V_{500} and V_{1000}, respectively). The distance to the nearest forest remnant of at least 4 ha was measured from the plots to the remnants, both directly in a straight line (D) and through a reforestation strip, thereby minimizing travel in the matrix (D_V) (see supplementary material). We also used the abundance of non-forest species (A_{NF}) to track possible differences in the negative effects of these species on native woody species among sites. The effects of both planted species richness (P) and stand age (Y) were also investigated.

Data analysis

All dependent variables were log-transformed for analysis. Multiple linear regressions were used to find better predictors for the abundance and richness of unplanted woody species native to Atlantic Forest. The model was deemed significant when $p \leq 0.05$. To identify the best model, the higher adjusted r^2 value was used.

Results

From the plots, 13,766 plants taller than 0.10 m distributed among 31 families and 80 species were sampled, mostly of native (84.6%), animal-dispersed (56.4%), and early successional species (78.2%). With the elimination of all planted, exotic, and non-forest species, only 1029 plants remained, distributed into 14 families and 20 species, mostly of animal-dispersed (90%) and late successional species (70%) (see the supplementary material for species list).

The multiple regression analysis identified some models that explained a significant portion of the variability in the diversity of woody plants in the studied sites. However, most of the variables included in the models were not significant alone, and no significant model accounted for late successional species (Table 1).

Both D and D_V were significant in models explaining abundance (A, A_L, and A_A) and species richness variables (S and S_A) (Table 1). An increase in distance reduced both the abundance (Figure 1) and species richness (Figure 2) of regenerating plants; at distances of approximately 4000 m (through matrix) or 8000 m (through riparian corridors), the number of non-planted regenerating plants tended toward zero.

Neither measure of neighborhood forest habitat (V_{500} or V_{1000}) served as a predictor of species richness in simple regressions (which are shown in supplementary material), but V_{1000} was significant in one of the models (Table 1).

Discussion

Given their restricted ranges of values, the abundance of non-forest species, stand age, and richness of planted species did not significantly influence woody species richness and abundance, and thus, can be considered to be controlled in this study.

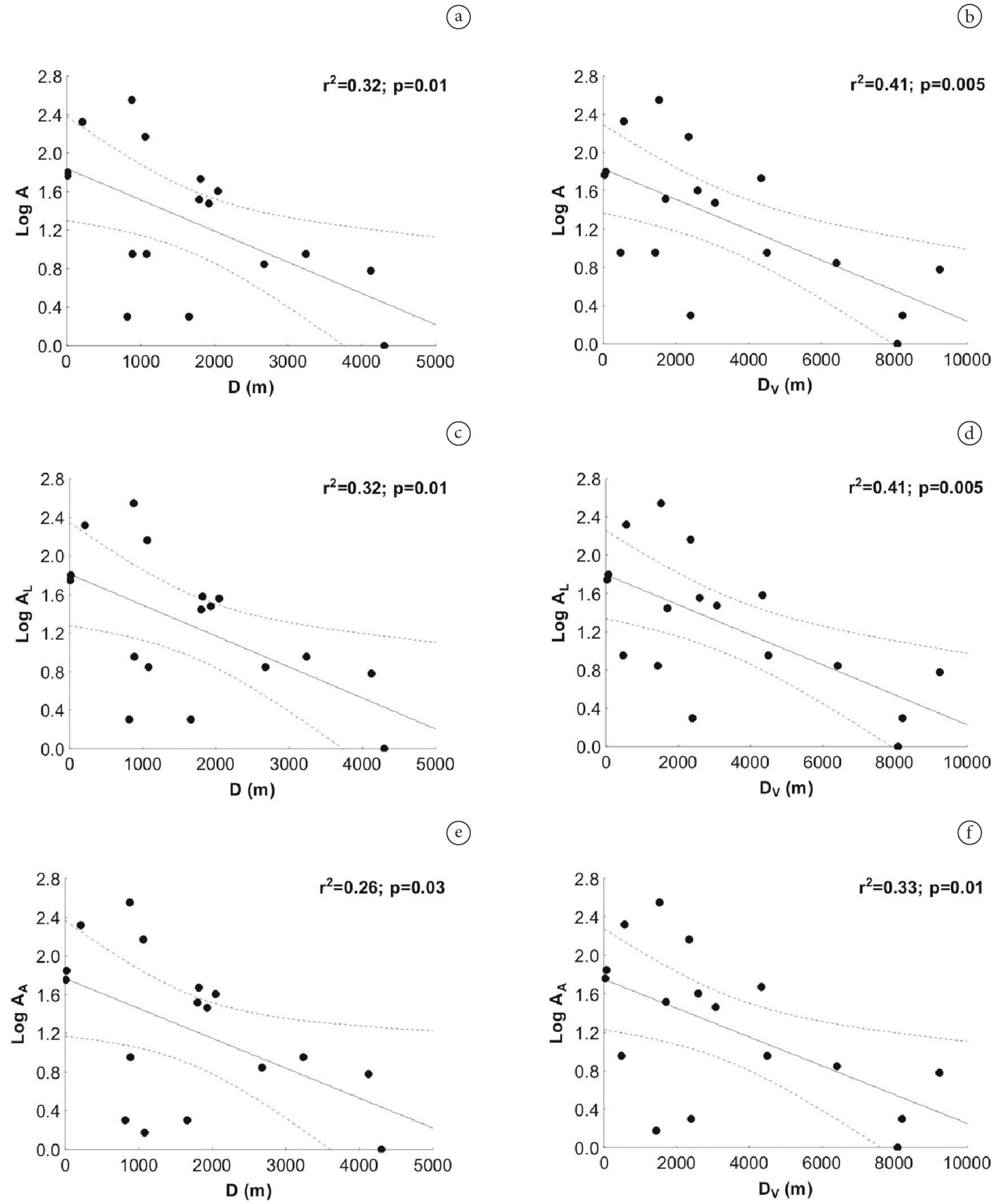

Figure 1. Relationship between distance to nearest forest fragment and abundance of woody, non-planted, native to Atlantic Forest species in restoration sites in the Capivara Reservoir, northern Parana state, Brazil. The three right plots show the relationship between the distance to the nearest forest fragment (in a straight line) (D) and abundance of all species (a), abundance of late successional species (c), abundance of animal-dispersed species (e). The three left plots show the relationship between distance to nearest forest fragment through riparian vegetation (D_V) and abundance of all species (b), abundance of late successional species (d), abundance of animal-dispersed species (f).

The landscape surrounding restoration sites proved to be important in both woody species richness and abundance, and thus it matters for the continuity of ecological succession at these sites (Wunderle Jr. 1997; Holl 1999; Holl *et al.* 2000). Both abundance and species richness were influenced by the distance to seed sources. Further, minimizing travel through the matrix by using riparian vegetation (our D_V measure) more than doubled the distance at which the forest fragments exerted their influence, particularly, for animal-dispersed and late successional species (up to 8000 m), suggesting a "corridor effect" that can increase connectivity in the fragmented landscape. Although this riparian vegetation is mostly comprised of early reforestation and spontaneous successional stands, forest animals can

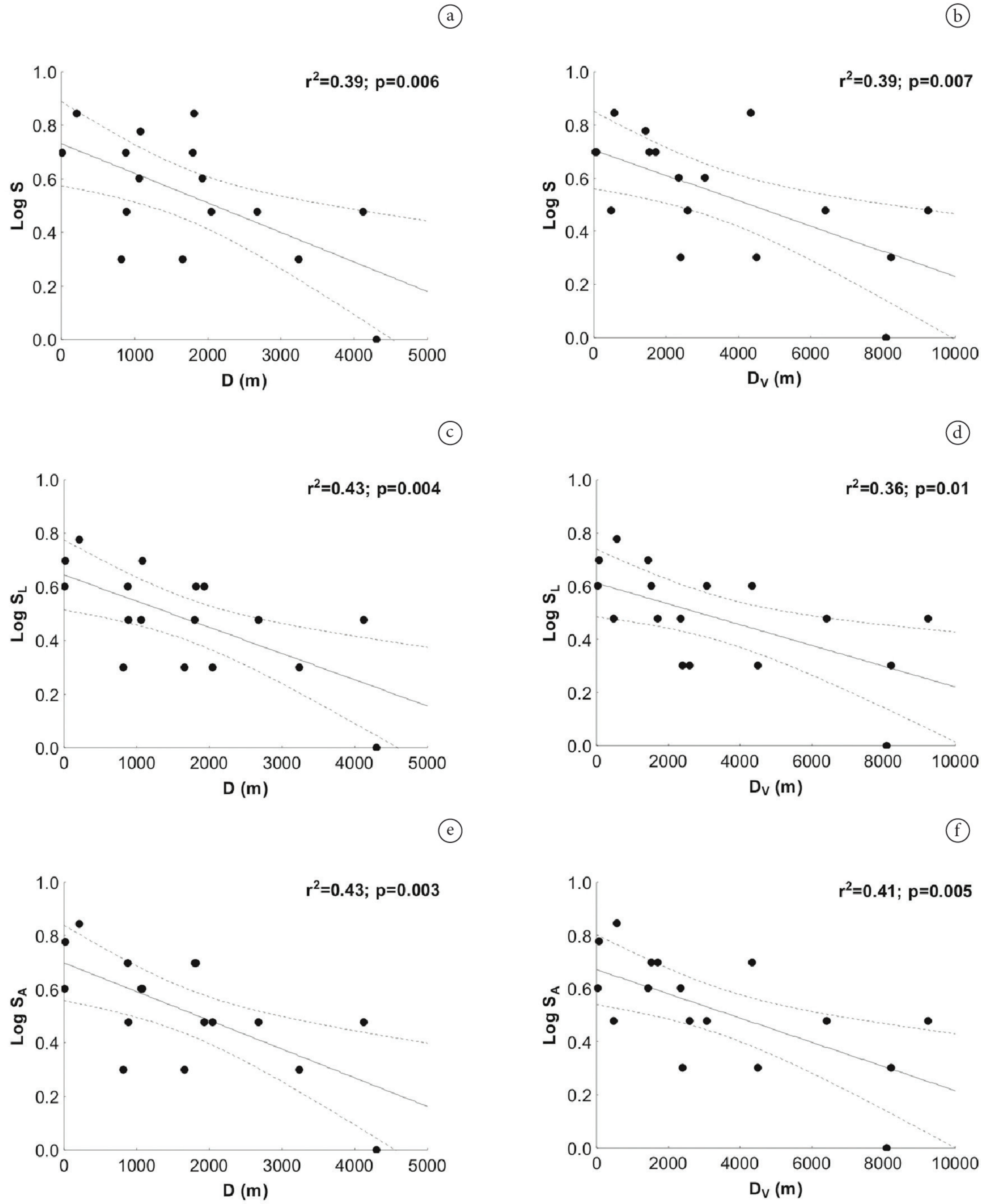

Figure 2. Relationship between distance to nearest forest fragment and species richness of woody, non-planted, native to Atlantic Forest species in restoration sites in the Capivara Reservoir, northern Parana state, Brazil. The three right plots show the relationship between the distance to the nearest forest fragment (in a straight line) (D) and total of species richness (a), richness of late successional species (c), richness of animal-dispersed species (e). The three left plots show the relationship between distance to nearest forest fragment through riparian vegetation (D_V) and total of species richness (b), richness of late successional species (d), richness of animal-dispersed species (f).

use it to avoid inhospitable matrices (Rosenberg *et al.* 1997; Wunderle Jr. 1997; Beier & Noss 1998). However, some generalist species may cross limited distances in the matrix (Bierregaard & Stouffer 1997) and, accordingly, our models suggests that limited seed dispersal may occur for up to 4000 m in a straight line from the seed source when associated with a larger area of surrounding forests.

One important issue regarding matrix resistance to animal movement is the existence of small-scale structures, such as isolated and grouped trees and small patches of vegetation, which can serve as "stepping stones" (Metzger 2000). Our measures of distance to the nearest forest fragment through the matrix do not take into account these structures, generally invisible in mid-resolution satellite imagery.

It is known that the distance from the seed source can be one of the major limiting factors for regeneration in degraded sites (Lamb *et al*. 1997; Parrotta *et al*. 1997; Wunderle Jr. 1997; Holl 1999; Holl *et al*. 2000; White *et al*. 2004). However, while the distance from the nearest seed source appears to be important for mass seed dispersal, i.e., strongly influencing woody species abundance, forest cover in the immediate vicinity of the restoration sites should be more important in determining species richness. Given that the seeds of a plant species can cross a certain distance threshold, irrespective of whether it is dispersed by animals or wind, it is legitimate to consider that lower distances to cross will imply a higher rate of successful dispersal (White *et al*. 2004). On the other hand, a greater area of surrounding habitat can mean that more species will survive in the remnant habitat (Tabarelli *et al*. 1999; Fahrig 2003), and thus more species that are able to disperse through the matrix will succeed in arriving at restoration sites (Parrotta *et al*. 1997). Our data, however, do not support these suggestions, since surrounding habitat area alone did not explain the abundance and species richness in the reforestation sites. We can speculate that this finding can be related to a limitation of the seed sources itself (poor habitat quality and/or dispersing fauna depletion) or a limitation of the physical environment in the restoration sites (mainly soil and air humidity affecting forest species' ability to establish).

Conclusion

Closer seed sources promote the arrival of more seeds, and dispersal distances through riparian vegetation strips can be twice those observed in matrix straight-line distances. Thus, restoration planning must take into account the presence of structures such as early successional stands, tiny riparian vegetation remnants, and existing reforestation sites that can serve as corridors.

Against our expectations, a larger area of remnant habitat in the neighborhood does not necessarily means more species are able to disperse to the restoration sites, which points to possible limitations of the potential of forest fragments as seed sources and also to the conditions for establishment in restoration sites. These limitations can be tested through assessments of seed dispersing fauna in the remnants and through seed and seedling transplant experiments; however, sampling the same restoration sites later (*e.g.*, 20 years after planting) will also shed light on the question.

Nonetheless, it is clear that Atlantic Forest remnants of any size and conservation status are crucial for continued succession in restoration sites (and for the ecosystem services expected from them) in the present highly-fragmented landscapes, highlighting the importance of conservation and management of such remnants, even in private lands.

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