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Matrix habitat and species richness in tropical forest remnants

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Abstract

The abilities of species to use the matrix of modified habitats surrounding forest fragments may affect their vulnerability in fragmented landscapes. We used long-term (up to 19-year) studies of four animal groups in central Amazonia to test whether species' abundances in the matrix were correlated with their relative extinction proneness in forest fragments. The four groups, birds, frogs, small mammals, and ants, had varying overall responses to fragmentation: species richness of small mammals and frogs increased after fragment isolation, whereas that of birds and ants decreased. For all four groups, a high proportion of nominally primary-forest species were detected in matrix habitats, with 8–25% of species in each group found exclusively in the matrix. The three vertebrate groups (birds, small mammals, frogs) exhibited positive and significant correlations between matrix abundance and vulnerability to fragmentation, suggesting that species that avoid the matrix tend to decline or disappear in fragments, while those that tolerate or exploit the matrix often remain stable or increase. These results highlight the importance of the matrix in the dynamics and composition of vertebrate communities in tropical forest remnants, and have important implications for the management of fragmented landscapes. © 1999 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Deforestation has led to striking fragmentation of natural landscapes throughout the world (Whitmore, 1997; INPE, 1998). Fragmented landscapes are composed of a patchwork of habitats of differing quality for fauna. With the exception of islands in hydroelectric reservoirs, human-fragmented landscapes maintain some degree of terrestrial connectivity via the matrix of modified habitats surrounding fragments. It has become increasingly apparent that understanding how species are affected by fragmentation requires information on their responses to all components of the landscape, i.e.

forest patches, remaining continuous forest, and the intervening matrix (Harris, 1984; Laurance, 1990, 1991, 1994; Malcolm, 1991; Fahrig and Merriam, 1994; Aberg et al. 1995; Lidicker, 1995; Flather and Sauer, 1996; Tocher et al., 1997).

The matrix is likely to be important in the evolution of fragment dynamics for several reasons. First, the matrix will often act as a selective filter (not an absolute barrier) for the movements of species across the landscape. The type of vegetation in the matrix will determine the pore size of the filter for movements of individuals. Tall second-growth forest, for example, would be analogous to a filter with large pores allowing more faunal movement because of its structural similarity to primary forest, while a pasture would have small pores that impede much movement (Malcolm, 1991). If this filter analogy is correct, one would expect a gradual increase in species richness, at least of those associated with primary habitat, from fine-pored (i.e. pasture) to larger-pored (i.e. second-growth) habitats. Forest species would be expected to vary in their pore-size requirements, with species that tolerate smaller pores being better able to persist in forest remnants (Laurance, 1990, 1991, 1994).

Second, the matrix may exert a strong influence on within-remnant community dynamics (Janzen, 1986;

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Laurance, 1990; Malcolm, 1991). For example, species associated with the matrix may invade forest remnants, altering the species composition of some taxonomic groups (Hutchings, 1991; Laurance, 1994; Brown and Hutchings, 1997; Tocher et al., 1997). Finally, different matrix types may influence fragment edge effects. Edge-related gradients in physical and biotic variables are likely to be less pronounced when the matrix is structurally similar to the original habitat, and this may reduce the ecological impacts of edge effects (Laurance and Yensen, 1991; Mesquita et al., 1999).

To investigate the importance of the matrix habitat in explaining species richness in forest fragments, we use results from long-term surveys of four taxonomically diverse groups (ants, small mammals, frogs, and birds) from the Biological Dynamics of Forest Fragments Project (BDFFP) in central Amazonia. To our knowledge, this is the first test of matrix effects using such a large and taxonomically diverse assemblage of species.

2. Methods

2.1. BDFFP history and study sites

The BDFFP, located 70 km north of Manaus, Brazil (Fig. 1), was initiated in 1979. A large area north of

Manaus was designated for development in the 1970s as part of a program to establish cattle ranches in the region as an economically viable solution for human settlement. With government incentives, large (5000–10,000 ha) ranches were carved out of primary rainforest (Lovejoy et al., 1986; Bierregaard et al., 1992). With cooperation from the ranchers, BDFFP researchers were able to design a large-scale experiment consisting of patches of forest of different sizes (1, 10 and 100 ha) that could be surveyed both before and after isolation from the surrounding forest (Lovejoy et al., 1986).

The project area comprises over 3000 ha of forest in designated study sites (reserves) spread over a 40 km-wide area (Fig. 1). Rainforest in the area is lowland (50–100 m elevation) *terra firma* forest (not subject to periodic flooding) with a canopy height of 30–37 m and very high tree diversity (Rankin-de-Merona et al., 1992). Palms dominate the understory (Scariot, 1996). The region's topography consists of rolling hills and numerous plateaus dissected by many streams and gullies.

2.2. The matrix habitat

The cattle ranches were created in the early 1980s by clearing and often burning the forest (Fearnside et al.,
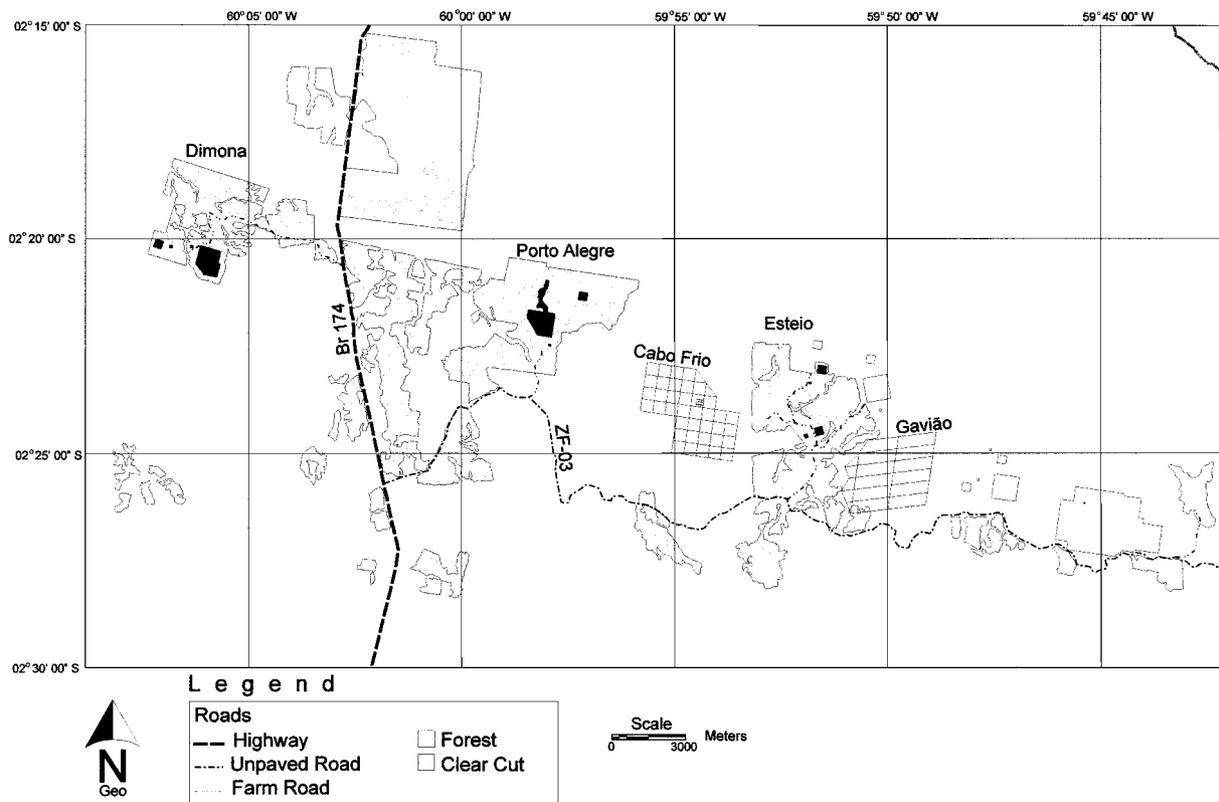

Fig. 1. Experimental landscape of the Biological Dynamics of Forest Fragments Project in the central Amazon of Brazil. Black areas are isolated forest patches, stippled areas are deforested land and white areas are primary forest.

1993). Most pastures were maintained for 5–10 years then, due to declining pasture productivity and a cessation of government incentives, were slowly abandoned. Regrowth forests quickly became established on many abandoned pastures. The regeneration pathways are fairly complex, but two trajectories are dominant: in areas where the forest was cut but not burned, regrowth is dominated by taller *Cecropia* spp., while in areas that were intensively used as pasture and subsequently abandoned, shrubby *Vismia* spp. dominate (Williamson et al., 1998). Although regrowth in some areas has reached 15–20 m in height, 100 m-wide bands of pasture or very low (< 2 m-tall) regrowth have been maintained around all experimental fragments to ensure some level of isolation.

2.3. Species abundance data

2.3.1. Small mammals

Abundance estimates for 15 species of small mammals were obtained from > 54,000 trap-nights of live-trapping effort (October 1987–March 1989) in fragmented, continuous, and matrix habitats (Malcolm, 1991). The sampling design involved trapping a series of 1-ha grids [each containing 12 terrestrial and 12 arboreal trap-stations, with one Tomahawk (14×14×40 cm) and one Sherman trap (8×8×23 cm) per station]. Each grid was trapped for eight consecutive nights on three different occasions. There was a total of 16 grids in four 10-ha fragments, four grids in four 1-ha fragments, 16 grids in continuous forest, and 11 grids in young (< 5 year-old) regrowth forest in the nearby matrix. Abundance estimates for 1- and 10-ha remnants were pooled to calculate an overall mean for the fragments, while the continuous forest and matrix abundance values were the overall means for those habitats.

2.3.2. Birds

Abundance estimates were available for 122 species of understory birds in fragmented and continuous forest (Bierregaard and Lovejoy, 1989; Stouffer and Bierregaard, 1995; Bierregaard and Stouffer, 1997). Lines of 8 mist-nets (2×12 m) were used for 1-ha remnants while lines of 16 nets were used for 10-ha fragments and continuous forest. Each line was netted for 1 day (0600–1400 h) at least 20 times over a period of 5 years. To determine abundances of birds in matrix habitats, three sites in each of the two major types of second-growth forest were sampled. At each site, 30 mist-nets were strung along previously cut trails. Nets were opened (0600–14-00 h) for two consecutive days. Each site was sampled six times at approximately monthly intervals from March to October 1993 (Borges, 1995). Abundance data for fragments, continuous forest, and the matrix (number of captures per 1000 net-hours) were the overall means for each habitat.

2.3.3. Ants

Abundance estimates for 127 terrestrial ant species were obtained from litter samples in fragments (3 of 1 ha, 3 of 10 ha, 2 of 100 ha), continuous forest (2 sites), pasture (1 site), *Vismia*-dominated regrowth (1 site), and *Cecropia*- dominated regrowth (1 site). Thirty-six 0.5 m² leaf litter samples were collected from each habitat. Ants were sorted from each sample and identified to species or morphospecies. The abundance of each species was defined as its frequency (percentage of samples present out of 36) in each habitat (Vasconcelos, in press; Vasconcelos et al., in press).

2.3.4. Frogs

Abundance estimates were obtained for 62 frog species in forest fragments and the matrix (Tocher, 1996) and continuous forest (Zimmerman, 1991). In each habitat, surveys of frog calls were conducted on pre-cut trails (cf. Zimmerman, 1994). Abundance estimates were obtained by dividing the total number of calls per species per trail by the product of the trail length (in km) and the number of times a trail was surveyed. A total of nine fragments (two of 100 ha, three of 10 ha, and four of 1 ha), eight regrowth sites, and four continuous forest areas were sampled.

2.4. Vulnerability index

For each species, an index reflecting its relative response to forest fragmentation was generated. This index was defined as the ratio of its overall abundance in fragments divided by its overall abundance in continuous forest. These ratios were then arbitrarily ranked on a five-point scale: 1 = 0–0.5; 2 = 0.51–0.9; 3 = 0.91–1.1; 4 = 1.11–1.5; 5 = > 1.51. Thus, species with low rankings were most vulnerable to fragmentation, and vice-versa. For each taxonomic group, Spearman rank correlations were used to test for associations between the vulnerability index of each species and its rank abundance in matrix habitats. Species that were captured too infrequently to allow confidence in the vulnerability ranking were eliminated from this analysis.

3. Results

On average, the four taxonomic groups responded quite differently to fragmentation (Table 1). As expected, species richness of birds and ants declined in forest fragments, but richness of small mammals and frogs actually increased. Birds and ants lost a large number of the original species complement in continuous forest, whereas few if any species were lost among small mammals and frogs. Some frog and small mammal species were mainly associated with matrix habitats and occasionally invaded fragments, contributing to the

Table 1
Ecological responses of different faunal groups to forest fragmentation in the central Amazon

Taxonomic group	Before and after species richness[a]	Loss of original species complement[b]	Invasion of matrix-associated species[c]
Birds	Decrease	High	No
Frogs	Increase	No	Medium
Small mammals	Increase	No	Medium
Ants	Decrease	High	No

[a] This index compares, for the same sized fragment the number of species for each group that were present before isolation to the number present after isolation.

[b] This index describes the proportion of species present before fragment isolation that disappeared after isolation.

[c] This index compares the proportion of the post-isolation community in fragments that is composed of predominantly matrix-associated species.

general increase in species richness in these two groups (Table 1).

A large proportion (40–80%) of nominally primary-forest species in all four groups were detected in pasture and/or regrowth forest (Fig. 2). In some cases, such as for certain frogs, primary-forest species are now breeding in the matrix (Tocher et al., 1997; Tocher, 1998). From 8 to 25% of the total species complement of each group was exclusively associated with the matrix (Fig. 3).

Correlations between matrix abundance and species vulnerability to fragmentation were positive and significant for all three vertebrate groups (frogs: $r_s = 0.753$, $n = 31$, $P < 0.0001$; birds: $r_s = 0.814$, $n = 115$, $P < 0.00001$; mammals: $r_s = 0.512$, $n = 15$, $P = 0.05$), but not for ants ($r_s = 0.121$, $n = 24$, $P = 0.57$; Fig. 4). Thus, vertebrates that use or exploit the matrix tend to increase or remain stable in fragments, whereas those that avoid the matrix often decline or disappear. Birds exhibited the strongest matrix-vulnerability correlation, followed by frogs and small mammals. Ants exhibited a fundamentally different pattern; many species that persisted in fragments were rare or absent from the matrix.

4. Discussion

Our results suggest that the matrix of modified habitats surrounding fragments is likely to have pervasive effects on vertebrate communities in forest fragments. First, many new species not originally present in continuous forest have "invaded" our experimental landscape and are now commonly encountered in the matrix, a situation also observed in other tropical areas (Janzen, 1986; Lawton et al., 1998; Moutinho, 1998; Vasconcelos and Cherrett, 1998). These species probably originated from the disturbed habitats along the highway leading from the major city of Manaus to our experimental area. In many cases, especially for frogs, these new arrivals are also invading forest fragments (Tocher et al., 1997; Tocher, 1998).

Second, and more surprisingly, a substantial number of nominally primary-forest species are capable of using matrix habitats, at least when large forest tracts which provide potential sources of immigrants are nearby, as is the case in our study area (see Malcolm, 1991; Tocher, 1998). For many forest species, however, primary forest is clearly of critical importance for long-
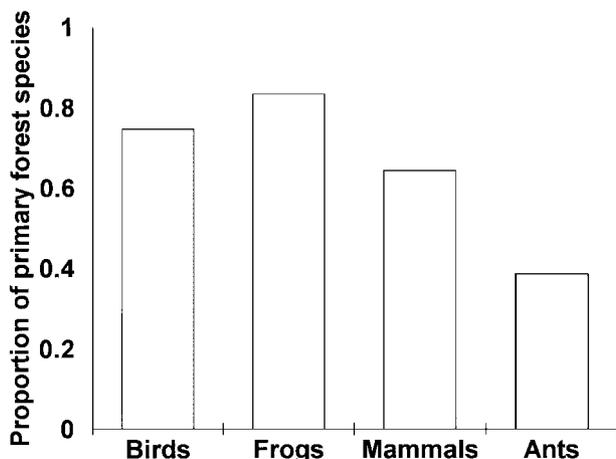

Fig. 2. Proportions of nominally primary-forest species that have been encountered in matrix habitats in central Amazonia.
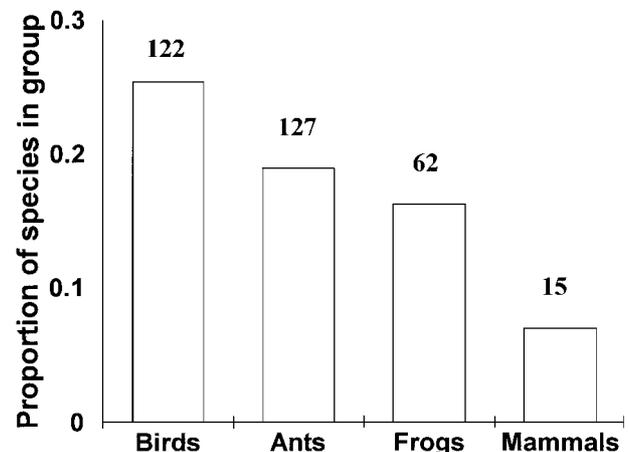

Fig. 3. Proportions of all species in each taxonomic group found exclusively in matrix habitats. Numbers above each bar represent the total number of species of encountered in the entire landscape.
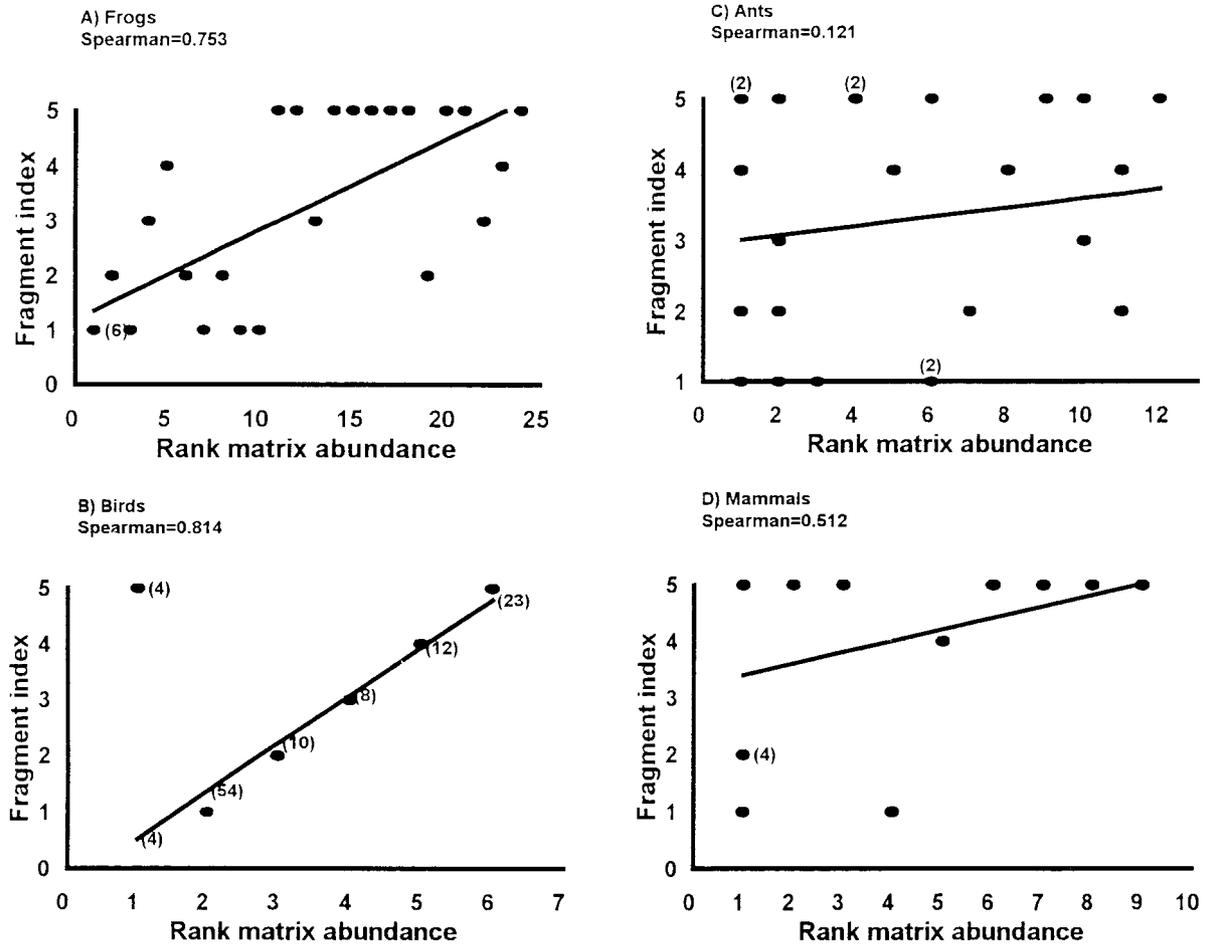
Fig. 4. Relationships between rank matrix abundance and the rank vulnerability of Amazonian species to forest fragmentation, for four different faunal groups. Fitted regression lines are for illustrative purposes only.

term survival, either because these species avoid modified habitats altogether or because these habitats are clearly suboptimal habitat (Borges, 1995; Tocher, 1998).

Matrix habitats vary considerably in their capacity to support forest species, and this is largely determined by the history and intensity of land use (Lawton et al., 1998), with more-disturbed sites generally having lower species richness (Tocher, 1998; Vasconcelos et al., in press). Forest frogs, for example, are most diverse in *Cecropia*-dominated regrowth which regenerates in areas not subjected to burning, and least diverse in cattle pastures (Tocher, 1998). Nevertheless, a high proportion of frogs in matrix habitats are associated with primary forest (Zimmerman and Bierregaard, 1986); in cattle pastures, for example, over 65% of the frogs are classified as primary-forest species (Tocher, 1998) whereas about 85% of forest species can be found in matrix habitants of all types including pastures and regrowth forest (Fig. 2).

These results demonstrate that the matrix acts as a selective filter and that some primary-forest species can use matrix habitats for movement and/or reproduction, a result that accords well with the findings of Laurance

(1991) for Australian tropical rainforest mammals. Faunal use of the matrix may help explain the highly varied responses of many species to fragmentation (Laurance, 1990, 1991; Malcolm, 1997; Tocher et al., 1997; Table 1). These responses can be predicted from a matrix-tolerance model (Laurance, 1991; Malcolm, 1991) in which the vulnerability of species in fragments is assumed to be directly related to their ability to use modified habitats: those that tolerate heavily degraded habitats (i.e. those most structurally dissimilar from the original forest) are predicted to be least vulnerable, and vice-versa.

The most plausible explanation for the matrix-vulnerability relationship is that populations of matrix-tolerating species in fragments are bolstered by the genetic and demographic contributions of immigrants (Brown and Kodric-Brown, 1977), originating either from other forest areas or the matrix itself. If such species disappear from fragments they are also more likely to be re-established by colonists. Finally, matrix-tolerant species may also be relatively tolerant of edge effects in fragments. For example, Malcolm (1991) found that small mammal communities in the matrix were more similar

to those in small, strongly edge-affected fragments (Malcolm, 1994; Laurance et al., 1998) than large ones. He reasoned that this pattern arose because mammals that used regrowth were also tolerant of edge conditions in fragments.

We are uncertain as to why leaf-litter ants failed to exhibit a significant matrix-vulnerability relationship, and this raises the possibility that there could potentially be a dichotomy in the way that terrestrial vertebrates and invertebrates respond to fragmented landscapes, or at least that similar processes are operating but at very different spatial scales. Other workers have found only weak correlations between vertebrate and invertebrate species richness across gradients of habitat disturbance (Lawton et al., 1998), hinting that such a dichotomy is possible. Clearly, further studies of matrix-vulnerability relationships comparing a range of animal taxa are needed.

This study represents the first taxonomically diverse demonstration of the importance of the matrix habitat on fragment dynamics (Fahrig and Merriam, 1994; Aberg et al., 1995; Flather and Sauer, 1996) and suggests a more important role for the surrounding landscape than has generally been suggested (Wahlberg et al., 1996; but see Laurance, 1991). The matrix-tolerance model has enormous conservation value because, in most tropical regions, extensive modified habitats exist that can be studied to predict species' vulnerabilities over much larger regions. An even more powerful tool would be to find an ecological correlate of matrix abundance to serve as a proxy variable, although attempts to identify such traits have so far met with little success (Laurance, 1991; Leach and Givnish, 1996). Regardless, these results highlight the importance of the matrix in remnant dynamics, and suggest the need for a whole-landscape approach to the conservation of fragmented populations.

Acknowledgements

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