ORIGINAL ARTICLE

The matrix effect: how agricultural matrices shape forest fragment structure and amphibian composition

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ABSTRACT

Aim Habitat loss and fragmentation are considered the main drivers of species population declines and extinctions in the world. The large-scale replacement of natural habitats with human-modified habitats, such as the replacement of forests with agricultural and livestock farming areas, creates a scenario where natural habitat patches are immersed in an inhospitable land use matrix. We sought to evaluate how forest fragments (FFs) are influenced by the different surrounding landscape components, where we assessed how agricultural matrices that differ in structure and seasonality affect the structure of FFs and their amphibian assemblages.

Location Atlantic Forest, Brazil.

Methods Using diverse methods including satellite imagery, historical land use and field data, we evaluated the effects of representative agricultural matrices on the structure of FFs and their amphibian composition, species richness and abundance.

Results Our results suggest that the structure of FFs and amphibian composition, species richness and individual abundance are intimately linked to the type of matrix and its proportion around FFs. The nature of the matrix is more likely to affect species richness, individual abundance and composition of amphibian assemblages than FF size, reducing the species-area relationship in FFs. There is strong support for the hypothesis that certain agricultural matrices facilitate FF exposure to the elements and a decrease in forest integrity within the fragment, which is reflected in a loss of strict forest inhabitants. Those matrices that allow for a greater exposure of FFs also appear to favour their occupation by habitat generalists.

Main conclusions Surrounding matrices affect the structure and dynamics of forest remnants and should therefore be considered in management plans of severely fragmented landscapes. The influence of the land matrix should be urgently assessed, as it has effects on species occurrences and distribution. This is especially relevant considering the increasing deforestation rates in biodiversity hotspots world-wide.

Keywords
amphibians, Atlantic Forest, conservation planning, edge effect, fragmentation, habitat quality, island biogeography theory, land use, landscape ecology, species turnover

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INTRODUCTION

The conversion and fragmentation of natural forests is a major threat to biodiversity globally (Lindenmayer & Franklin, 2002). In particular, forest fragmentation has been identified as one of the ubiquitous outcomes of anthropogenic land use dynamics (Tabarelli & Gascon, 2005). Among vertebrates, the greatest threat is habitat loss due to expanding agriculture, logging and modifications to freshwater systems (Baillie et al., 2010). In order to understand the

dynamics of forest fragments (FFs) in modified terrestrial landscapes, the theory of island biogeography (MacArthur & Wilson, 1967) has been used as a conceptual framework (Laurance, 2008). However, as this theory was originally intended to study islands, its suitability for FFs has been questioned (Laurance, 2008; Mendenhall *et al.*, 2014a). The main objection in the use of island biogeography is related with permeability and size of the matrix where the fragments are embedded. Furthermore, the framework provided by countryside biogeography shows that biodiversity distribution in fragmented landscapes is intrinsically linked to agricultural crops and not just FFs (Mendenhall *et al.*, 2014a,b). The landscape configuration plays an important role for species conservation considering the interactions between landscape elements (Villard & Metzger, 2014); where the proportion and placement of forest patches within the matrix can provide increased connectivity between FFs (Fahrig, 2013).

The biodiversity of FFs is strongly related to fragment size, shape and the distribution of fragments within any given landscape (Ranta *et al.*, 1998). These structural features have a direct effect on the quality of the FF (Rolstad, 1991; Forman & Moore, 1992; Murcia, 1995), where they interact to change the internal physiognomy of the FF and the ecotone of the transition between forest and the surrounding matrix, a phenomenon known as edge effect (Murcia, 1995). In FFs, the edge effect can cause both biotic and abiotic changes impacting the entire biota within (Saunders *et al.*, 1991; Forman & Moore, 1992; Stevens & Husband, 1998; Oliveira *et al.*, 2004). The edge effect has been identified as being globally responsible for changes within forests up to an average of 1 km (Haddad *et al.*, 2015). Edge effects and the magnitude of their impact are influenced by the relationship between area and perimeter, where very small fragments end up being completely impacted (Noss, 1983; Haddad *et al.*, 2015). The intensity of the edge effect tends to be less severe where the matrix and original habitat are structurally similar (Laurance & Yensen, 1991; Gascon *et al.*, 1999; Mesquita *et al.*, 1999). Studies have shown that matrices can be used as a connective medium between FFs by many species (Franklin & Lindenmayer, 2009), having a bearing on conservation of metapopulations and species facing a higher extinction risk (Laurance, 1991; Sisk *et al.*, 1997; Lindenmayer & Franklin, 2002).

Amphibians are considered to be the most threatened vertebrates in the world (IUCN, 2016). The structure of amphibian assemblages in agricultural landscapes is linked to the land use and natural forest gradients (Faruk *et al.*, 2013; Mendenhall *et al.*, 2014b). In this scenario, amphibian composition, richness and abundance is highly correlated with the environmental structure of FFs (Wanger *et al.*, 2010; Balaji *et al.*, 2014). Strict forest specialists, for instance, are often considered to be highly phylopatric and to have low vagility within their natural habitat, which makes them more vulnerable to isolation and susceptible to population declines and disconnect from appropriate reproductive habitat due to fragmentation (Becker *et al.*, 2007, 2009). Thus, populations in isolated forest patches can experience strong genetic erosion and inbreeding (Dixo *et al.*, 2009).

The Atlantic Forest has over 7.7% of all described amphibian species, where many are endemics (Haddad *et al.*, 2013) and some of these species have experienced population declines (Heyer *et al.*, 1988; Weygoldt, 1989; Eterovick *et al.*, 2005). While habitat loss and fragmentation represent the greatest issue to globally threatened amphibians in the Neotropics, affecting 90% of threatened amphibian species (Bolaños *et al.*, 2008), their mechanisms remain relatively understudied. Approximately 96% of Neotropical amphibians responded to edge effects in fragmented landscapes, and small FFs are inhospitable to forest-dependent species (Schneider-Maunoury *et al.*, 2016). Thus, understanding the effects of different land use matrices on FFs is an important priority given both growing land use change and amphibian declines.

The Atlantic rain forest is considered to be a global biodiversity hotspot, with high levels of species richness and endemism (Myers *et al.*, 2000). However, this biome is suffering from severe loss and fragmentation: there is only 7–8% left of its original distribution, although this proportion increases to 11.4–16% if secondary forests and small FFs are also considered. In addition, over 80% of FFs are smaller than 50 ha (Ribeiro *et al.*, 2009). These fragments are immersed within some sort of land use matrix, highlighting the need to understand the dynamics of these fragments with the matrices surrounding them. Our aim was to better understand how matrices that differ in structure and seasonality affect the structure of FFs and, consequently, their amphibian assemblages.

MATERIALS AND METHODS

Study site

We conducted this study in southern Minas Gerais state (21°25′38.42″ S; 45°56′53.21″ W, Fig. 1a), the Brazilian state with the highest index of deforestation in the Atlantic Forest. FFs in this area are composed of seasonal Semi-deciduous Atlantic Rainforest (SOS Mata Atlântica & INPE, 2014). The annual mean rainfall for the region is 1554 mm (Roldão *et al.*, 2012). The remaining fragments in the region are maintained primarily to ensure the persistence of headwater and water bodies used in agriculture, livestock farming and human consumption. These water sources are also used by several amphibian species for reproduction. Within this area, a total of sixteen FFs were used to survey amphibian assemblages. Fragments ranged in elevation from 786–885 m a.s.l. and from 5 to 226 ha over a total sampled area of 1472 km^2 (see Table 1 in Supporting Information Appendix S1 for further details). All observations were conducted between December 2011 and January–March 2012, which coincide with the rainy season in the region (Roldão *et al.*, 2012) and more generally with the amphibian breeding season in the Atlantic forest (Haddad *et al.*, 2013).
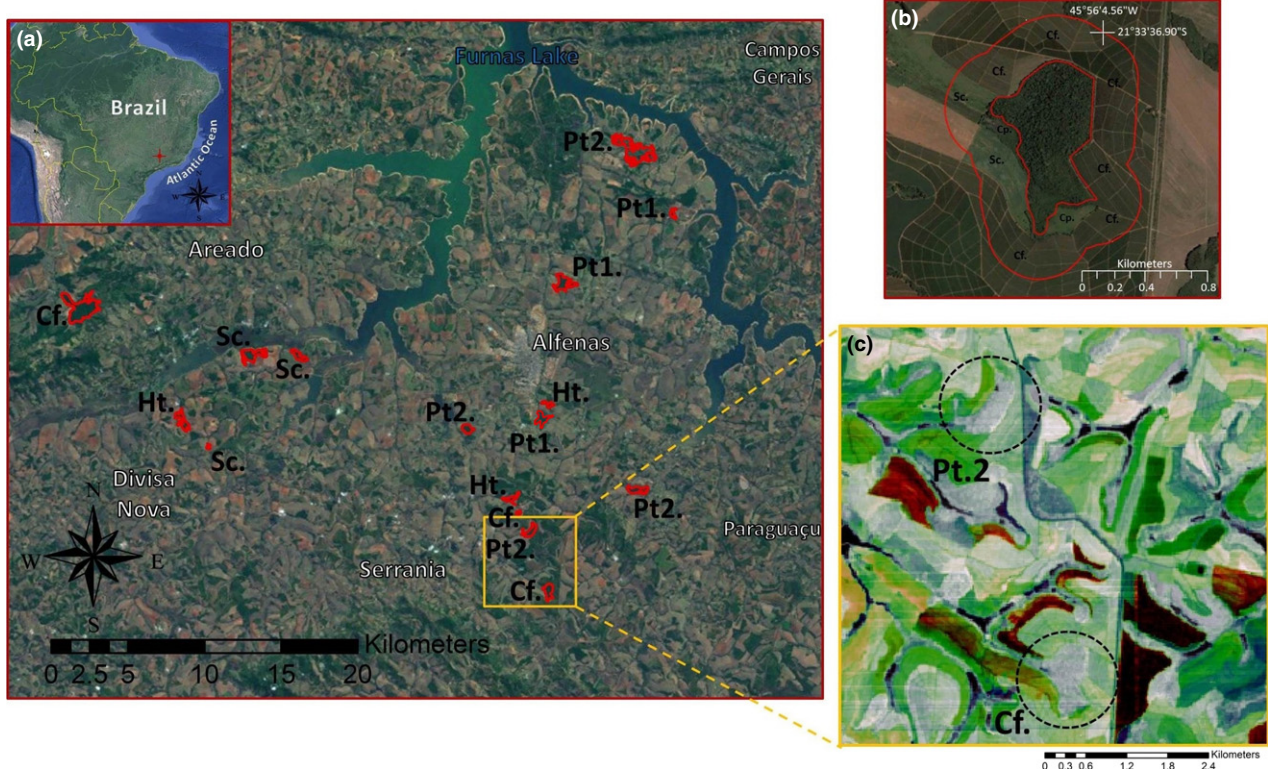
Figure 1 (a) Distribution of forest fragments within the landscape of south-eastern Brazil (21°25′38.42″ S; 45°56′53.21″ W). Fragment type: Cf. = Coffee; Sc. = Sugar cane; Pt1. = Fenced Pasture; Pt.2 = Presence of cattle within fragment; Ht. = Heterogeneous Landscape. (b) Quantification of buffer of a fragment's surrounding matrix (Cf. = Coffee: 77.76%; Sc. = Sugar cane: 13.25%; Cp. = 'Capoeira': 8%). (c) Mixture model of three pure components: vegetation (green), soil (red) and shade (blue); the black circles indicate the fragments in the landscape.

Sampling design

We selected 16 FFs according to the type of predominant agricultural matrices. These matrices have been classified as (1) coffee, (2) sugar cane, (3) pastures, (4) heterogeneous landscape without a dominant crop (< 50% crop dominance), and (5) fragments with livestock presence, where cattle have access to the fragment for water, shelter and food. All coffee plantations in this landscape are sun coffee crops. We selected three fragments embedded in each of these five predominant matrix types, with the exception of fragments with livestock, which had four fragments (Supporting Information S1, Table 1). To identify and define the fragments to be studied, we manually classified satellite imagery {Esri, Digital Globe [i-cubed 15 m eSAT to scale (1:6000)]}, employing a V-LATE 2.0 beta extension of Esri's spatial software ArcGIS for Desktop 10. We defined fragments including all of the vegetation types that were not broken by a physical barrier which could potentially impact movement patterns of habitat specialists, such as roads, highways, open areas or other human-induced barriers. This allowed for the selection of fragment groups with similar sizes (analysis of variance, ANOVA; $P = 0.760$), shapes (ANOVA; $P = 0.813$), degree of isolation (ANOVA; $P = 0.957$), and elevation (ANOVA; $P = 0.251$); all fragment parameters are detailed in

Appendix S1, Table 1. We determined the matrix type through Esri Digital Globe satellite imagery and visually confirmed with field inspections, taking into account all matrix types and the matrix's history, which was investigated with interviews with landowners. In order to determine the main surrounding matrix type we used a 300 m buffer from the FF's edge, and quantified the percentage of each type of matrix in direct contact with the fragment (Fig. 1b). We then calculated the proportion of each matrix type within the buffer with the same spatial software. We determined the predominant matrix type as being > 50% of the buffer area. The fragments classified as heterogeneous landscapes comprise three fragments surrounded by five or more matrix types and with < 50% crop dominance. We used a Shannon–Wiener diversity index based on the proportions of each matrix type to assess landscape heterogeneity in the buffer area of each fragment.

We used visual encounter surveys (Crump & Scott, 1994) and playbacks of previously recorded advertisement calls of local species to survey adult and juvenile anurans. Three people surveyed 300 m transects running parallel to a fragment's water body during each survey session. Surveys were carried out at night and each fragment was surveyed three times resulting in fifteen survey hours per fragment. In total each person surveyed 240 h, and the total survey time of all FFs

Table 1 Classification of anuran species by ecological guilds (forest specialists and generalists).

Scientific name	Species Guild/ Umbrella Group
Adenomera thomei (Almeida & Angulo 2006)	Generalist
Aplastodiscus leucopygius (Cruz & Peixoto, 1985 '1984')	Forest
Bokermannohyla luctuosa (Pombal & Haddad, 1993)	Forest
Dendropsophus minutus (Peters, 1872)	Generalist
Elachistocleis cesarii (Miranda-Ribeiro, 1920)	Generalist
Haddadus binotatus (Spix, 1824)	Forest
Hylodes aff.*sazimai* Haddad & Pombal 1995	Forest
Hypsiboas albopunctatus (Spix, 1824)	Generalist
Hypsiboas aff. *beckeri* (Caramaschi & Cruz, 2004)	Generalist
Hypsiboas faber (Wied-Neuwied, 1821)	Generalist
Hypsiboas aff. *latistriatus* (Caramaschi & Cruz, 2004)	Forest
Hypsiboas lundii (Burmeister, 1856)	Forest
Leptodactylus fuscus (Schneider, 1799)	Generalist
Leptodactylus latrans (Steffen, 1815)	Generalist
Lithobates catesbeianus (Shaw, 1802)	Generalist
Phyllomedusa burmeisteri (Boulenger, 1882)	Generalist
Proceratophrys boiei (Wied-Neuwied, 1825)	Forest
Rhinella ornata (Spix, 1824)	Forest
Rhinella schneideri (Werner, 1894)	Generalist
Scinax fuscovarius (A. Lutz, 1925)	Generalist
Scinax longilineus (B. Lutz, 1968)	Forest

comprised 720 h. Water bodies originated within each FF, with water flowing towards the FF's edge. Thus, the patches are not being affected by habitat disconnect with the aquatic environment, an important consideration in terms of the life cycle of amphibians (Becker *et al.*, 2007, 2009). Sampling sufficiency was assessed with species accumulation curves (Supporting Information Appendix S3).

We also measured intrinsic structural variables of FFs. Vegetation, canopy and leaf litter density data were collected for each transect. Leaf litter thickness and canopy cover were measured for 10 sampling points every 30 m for each 300 m transect (Supporting Material Appendix S2). We analysed degradation of vegetation considering all fragments in one mixture model generated with the software SPRING 5.2 (Câmara *et al.*, 1996), using three pure components for mixture model (vegetation, soil and shade) (Fig. 1c) based on Shimabukuro & Smith (1991). We used a mixture model for the patch structure analysis, where the average number of pixels represents the density of vegetation inside the FF, and pixel variation represents the presence of clearings within the FFs. Satellite imagery RESOURCESAT-1 via the sensor LISS-III (Linear Imaging Self-Scanner), spatial resolution 23.5 m, was acquired by the National Institute for Space Research (INPE 2014) and we used it to assess the structure of FFs for the mixture model. Chronologically, the imagery corresponds with the end of the field season. We took measurements for every fragment with the software ArcGIS for Desktop 10

using the zonal statistics spatial analyst tool in the internal polygon area, avoiding the edge so as not to include pixels from the matrix.

Study species

We conducted an *a priori* ecological classification of species based on information from Haddad *et al.* (2013), Ferrante *et al.* (2014), The IUCN Red List of Threatened Species (2016) and field observations. The classification of species groups (Table 1) was based on the ecological guilds of forest dependence (strict forest inhabitants or with forest-based reproduction) and generalist habits (species with functional connectivity in all components of the landscape: forests, forest edges, degraded and open areas).

Statistical analyses

To test the similarity of FF structure surrounded by each type of matrix we used a Shapiro–Wilk normality test, followed by a Bartlett test for homogeneity of variances and a comparison of similarity between the fragment groups using an ANOVA. All tests were set to 5% significance level. We used a principal components analysis (PCA) to assess the relationship of agricultural crops (coffee, sugar cane, pasture, cattle access to the fragment and landscape heterogeneity) with the fragments' intrinsic structural variables (integrity of vegetation structure, presence of clearings in the FFs, canopy cover and depth of leaf litter). We used non-metric multidimensional scaling (NMDS) to evaluate the relationship between intrinsic FF structural variables, matrix characteristics and the overall anuran assemblage composition. We performed the NMDS analysis with frequency standardizations per FF and the Bray–Curtis index as distance measurement. We then fitted the environmental variables to the NMDS ordination using the envfit-function of R package vegan (Oksanen *et al.*, 2016). The correlation of point projections (anuran species composition in each FF) with the predictor vectors (FF intrinsic structural variables and matrix characteristics surrounding each FF) was estimated with 999 permutations. We used pie charts to represent the number of forest specialist and generalist species sampled in each FF.

Habitat fragmentation is a random process (Lindenmayer & Franklin, 2002), making it difficult to investigate its effects in natural landscapes with an efficient sampling design. Testing a sample (n) with multiple regressions, as suggested by Burnham & Anderson (2002), in order to achieve adequate replicates would be impossible, given the unique combination of characteristics of each fragment in the landscape. Thus, we used hierarchical partitioning (Mac Nally, 2000) to reduce collinearity and select the most relevant environmental variables for each model. The hierarchical partitioning method determines the independent contribution of each environmental variable to the response variable and separates it from the joint contribution, resulting from correlation with other variables (Mac Nally, 2000). The dependent

variables used in the models were anuran species richness and abundance for each guild (habitat specialists and generalists). Specialist and generalist anuran species richness and abundance were based on bootstrap procedure to estimate standard errors (Magurran, 2004). The predictor environmental variables used in hierarchical partitioning were: FF area, isolation of the fragment in the landscape, proportion of forests surrounding FF, integrity of vegetation, presence of clearings in the FFs, canopy cover, leaf litter depth, cattle access within the fragment and the percentage of the predominant matrix type within the landscape: coffee, sugar cane and pasture. To avoid possible bias in the nominal ranking of importance of the explanatory variables in models with more than nine explanatory variables (Walsh & Mac Nally, 2013), we ran different hierarchical partitioning models, changing the entering order of the variables but keeping nine explanatory variables in the models. We then selected the four most relevant explanatory variables from the hierarchical partitioning analysis and fitted them using a generalized linear model with Gaussian residual distribution for species richness and Poisson residual distribution for species abundance. The probabilities of species abundance models were estimated by computing the analysis of deviance table for the full model and the null model (only the intercept). McFadden's R^2 (McFadden, 1974) was used as a measure of model fit for the species abundance models. Partial regression plots were used to graphically show the influence of each variable in the model; partial regression plots show the expected effect of a variable when the other variables in the

model are held statistically constant (Velleman & Welsch, 1981). These plots are easier to interpret than three-dimensional graphics, in which the interpretation depends on the angle at which the graph is projected. All 16 surveyed fragments were used, so that even small proportions of each matrix type were considered, allowing for proportional representation of each matrix in a 300 m radius around the FF from the fragment's edge.

RESULTS

Relationships between land use and structure of forest fragments

Two general groups emerged from the PCA, depicting the relationships between the proportion of each matrix type around the FF and the structural variables of FFs (Fig. 2a). Based only on PC1, one group comprised leaf litter depth, canopy cover, integrity of vegetation with a greater proportion of more perennial matrix (coffee), landscape heterogeneity (Shannon Index) and the sugar cane matrix, and the second group was formed by pasture matrix, cattle presence within the fragment and presence of clearings within the FFs. However, the sugar cane matrix has a more intermediate pattern between the groups. The direction of each matrix axis represented in the PCA analysis shows the differences between the three matrix types (pasture, sugar cane and coffee). These results suggest an inverse relationship between leaf litter depth and the proportion of pasture or presence of
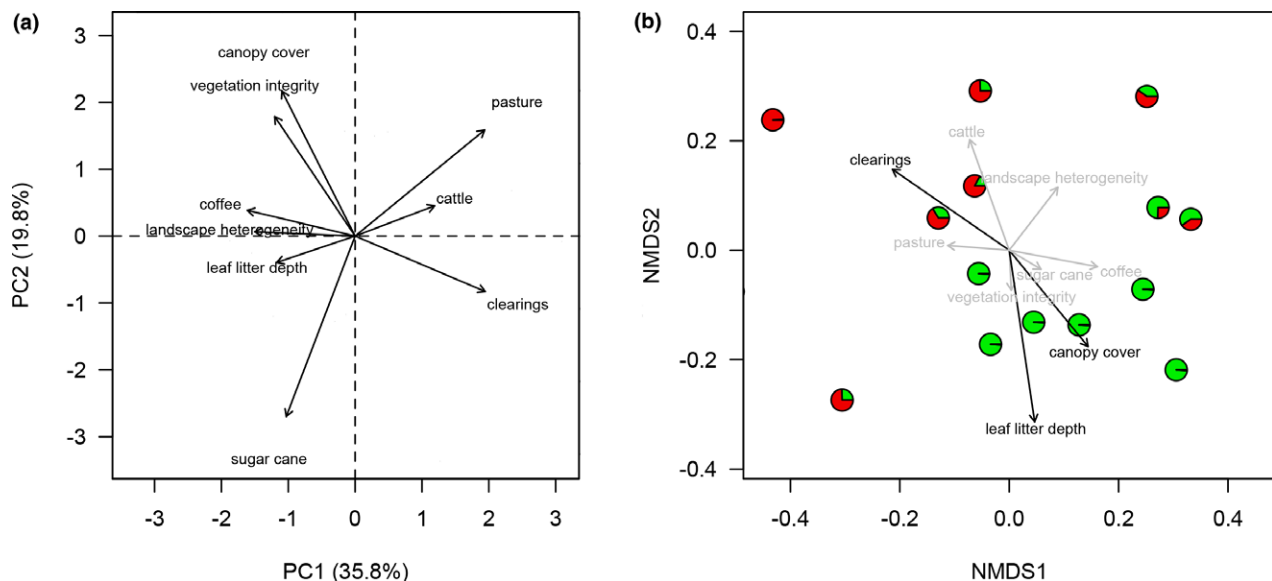

Figure 2 (a) Principal Components Analysis involving agricultural crops and activities (coffee, sugar cane, pasture, cattle access within the fragment and landscape heterogeneity) on the fragments' structural variables (canopy cover; depth of leaf litter; vegetation integrity and presence of clearings) in south-eastern Brazil. (b) The Non-metric Multidimensional Scaling analysis representing the relationship between the assemblage structure with the environmental variables: agricultural matrix (coffee, sugar cane, pasture, cattle access within the fragment and landscape heterogeneity) and a forest fragment's structural variables (canopy cover; depth of leaf litter; vegetation integrity and presence of clearings). The circles represent the forest fragments and the proportion of green and red colours represents the percentage of forest and generalist species in each assemblage, respectively.

cattle within a FF. The highest level of vegetation integrity (highest pixel average of the mixture model) and the highest average of leaf litter depth show greatest similarity with the coffee matrix. There is a negative relationship between pixel variation in the mixture model and coffee, indicating limited variation in vegetation and lack of open areas in fragments surrounded primarily by coffee. Forest fragments whose surrounding landscape had a higher diversity (Shannon) index grouped with coffee matrix, greater leaf litter depth, higher average of vegetation integrity and canopy cover, while its inverse relationship with pixel variation in the mixture model (soil, shadow and vegetation) suggests these fragments had less vegetation loss and forest clearings.

Response of amphibian assemblages to land use

We found 21 frog species belonging to eight families within FFs: Bufonidae, Craugastoridae, Hylidae, Hylodidae, Leptodactylidae, Microhylidae, Odontophrynidae and Ranidae. The structure of amphibian assemblages in relation to the environmental variables of each fragment and the landscape around them is represented by the NMDS analysis depicted in Fig. 2b (stress = 0.106). Two FFs were removed from the NMDS analysis because no anuran individuals were detected. Three variables of fragment structure (canopy cover, leaf litter depth and presence of clearings) were associated with amphibian assemblage structure. However, the two-dimensional NMDS results suggest two general groups of variables structuring the amphibian assemblage: the highest

proportion of generalist species in the assemblage is associated with more clearings, cattle access to FF and the pasture matrix, and the highest proportion of forest-associated species is associated with increased canopy cover and leaf litter depth, better vegetation integrity, coffee and sugar cane. The heterogeneity of the landscape surrounding FFs was found to have an intermediate pattern in relation to both forest-associated and generalist guilds.

Based on the hierarchical partitioning analysis, the forest-associated species richness was more highly associated with coffee, sugar cane, pasture and the FF area (Table 2). The overall model explained 49% of the forest-associated species richness ($P = 0.018$, Table 3), but only the proportion of coffee in the matrix was relevant ($P = 0.011$, Fig. 3a). These results suggest that, for every 10% increase of coffee area in the FF surroundings, an increase of almost one (0.92) forest-associated species would be expected. Although the FF area is among the most important variables analysed, there is no trend (see Table 3 and Fig. 3b), suggesting that the surrounding matrix is more important than area of FFs for forest-associated species richness in FFs. According to the model for forest-associated species richness (Table 3), each matrix type has a different correlation strength on species richness (Fig. 3a,c,d).

The hierarchical partitioning analysis suggests that the presence of cattle in the fragment, proportion of sugar cane, pasture and coffee in the surrounding area of the fragment were the most relevant predictors for the abundance of forest-associated species (Table 2). There was also a negative

Table 2 Percentage-distribution of independent effects calculated from hierarchical partitioning for forest-specialist and generalist guilds of amphibians for species richness and individual abundance.

FOREST GUILD		GENERALIST GUILD	
FOREST SPECIES RICHNESS		**GENERALIST SPECIES RICHNESS**	
Predictor variables	Independent contribution (%)	Predictor variables	Independent contribution (%)
Coffee	32.55	Leaf Litter Depth	48.64
Forest Fragment Area	14.09	Forest Fragment Area	9.50
Pasture	13.57	Landscape Heterogeneity	9.03
Sugar cane	11.04	Canopy Cover	7.86
Integrity of Vegetation	8.39	Fragment Isolation	6.73
Fragment Isolation	6.25	Presence of clearings	5.21
Canopy Cover	6.14	Pasture	5.01
% of Forests Surrounding FF	4.42	Coffee	4.67
Leaf Litter Depth	3.55	% of Forests Surrounding FF	3.34
FOREST SPECIES ABUNDANCE		**GENERALIST SPECIES ABUNDANCE**	
Cattle presence in the FF	23.65	Canopy Cover	17.90
Coffee	17.36	Leaf Litter Depth	16.27
Pasture	15.18	Cattle presence in the FF	15.18
Sugar cane	10.61	Fragment Isolation	12.47
Forest Fragment Area	9.13	Sugar cane	10.82
Landscape Heterogeneity	7.49	% of Forests Surrounding FF	7.76
% of Forests Surrounding FF	6.80	Pasture	6.81
Canopy Cover	5.82	Forest Fragment Area	6.70
Fragment Isolation	3.97	Coffee	6.10

Table 3 Results of multiple regression models for the effects of the four most relevant predictor variables based on hierarchical partitioning analysis.

VARIABLES	b	P	VARIABLES	b	P
FOREST SPECIES RICHNESS	$r^2 = 0.49$	$P = 0.018$	**GENERALIST SPECIES RICHNESS**	$r^2 = 0.86$	$P < 0.001$
Coffee	0.092	0.011	Leaf Litter Depth	−1.360	0.001
Forest Fragment Area	0.007	0.193	Landscape heterogeneity	−2.133	0.005
Pasture	0.051	0.111	Canopy cover	−0.061	0.025
Sugar cane	0.065	0.058	Forest Fragment Area	−0.005	0.322
FOREST SPECIES ABUNDANCE (glm quasipoisson)	pseudo-$r^2 = 0.49$	$P < 0.001$	**GENERALIST SPECIES ABUNDANCE** (glm quasipoisson)	pseudo-$r^2 = 0.81$	$P < 0.001$
Cattle presence in the FF	−1.593	0.137	Canopy cover	−0.054	0.006
Sugar cane	0.070	0.051	Leaf Litter Depth	−1.185	0.002
Pasture	0.079	0.019	Cattle presence in the FF	1.607	0.002
Coffee	0.083	0.02	Fragment Isolation	0.003	0.034

trend between presence of cattle within a FF and abundance of forest-associated individuals (Table 3, Fig. 3e). The multiple regression analyses with these four variables indicate that the abundance of forest-associated individuals was affected by the proportion of coffee, pasture and sugar cane matrices (pseudo-$R^2 = 0.49$, $P < 0.001$, Table 3). The number of individuals was higher in FFs surrounded by more perennial matrices, such as pastures ($P = 0.01$, Fig. 3g) and coffee ($P = 0.02$, Fig. 3h), while there was only a marginal effect ($P = 0.051$) between the sugar cane matrix and forest-associated individual abundance (Fig. 3f). Given its seasonal nature, the sugar cane matrix was likely not as conducive to high numbers of forest-associated individuals as its more perennial counterparts (coffee and pastures).

For generalist species richness, the four most relevant predictor variables were leaf litter depth, landscape heterogeneity, canopy cover and FF area (Table 2). Generalist species richness was negatively associated with leaf litter depth ($P = 0.001$, Fig. 3i), landscape heterogeneity ($P = 0.005$, Fig. 3j) and canopy cover ($P = 0.025$, Fig. 3k). The overall model explained 86% of the variance of generalist species richness ($P < 0.001$). For every 1 cm increase in leaf litter there was a loss of 1.36 generalist species, and for every 10% increase of canopy cover there was a decrease of 0.25 generalist species.

Canopy cover, leaf litter depth, presence of cattle in the fragment and fragment isolation were the most relevant predictor variables for generalist species abundance (Table 2). The abundance of generalist species within FFs was negative in relation to canopy cover (Fig. 3m, $P = 0.006$) and leaf litter depth (Fig. 3n, $P = 0.002$), and positive in relation to presence of cattle in the forest interior (Fig. 3o, $P = 0.002$) and the FF's isolation (Fig. 3p, $P = 0.034$). The overall model explained 81% of the variance of generalist species individual abundance, $P < 0.001$ (Table 3).

DISCUSSION

The role of the surrounding matrix and the forest patch quality are already identified as key knowledge gaps in fragmentation studies (Ibáñez et al., 2014). Our study demonstrates the importance and relationship of both to conservation of FFs. Each land use matrix type has a different effect on the internal structure of FFs, which in turn impacts anuran species composition, richness and abundance. Furthermore, edge effects may vary as a result of the proportions of the surrounding matrix's structure and seasonality. Edge effects have been recognized to cause changes in the structure, composition, dynamics and microclimate of a FF (Harper et al., 2005), all of which can influence amphibians and other taxonomic groups (Gascon et al., 1999; Urbina-Cardona et al., 2006; Cubides & Urbina-Cardona, 2011). However, limited attention has been given to the contribution of different surrounding matrices on edge effects. Our results support the notion that island biogeography theory is not an adequate model for managing a fragmented landscape, as previously pointed out (Laurance, 2008; Mendenhall et al., 2014b). Given the terrestrial connectivity on land, the biogeography theory does not account for edge and matrix effects. In addition, different types of matrices surrounding the FFs and the structure of FFs are more likely to affect forest-associated species richness and abundance than FF area. In contrast, countryside biogeography includes in its scope both human-modified landscapes and the biodiversity associated to these systems, making it possible to understand biodiversity patterns and collapses in agricultural landscapes (Mendenhall et al., 2014a,b).

It has been suggested that the proportion of forests surrounding FFs influences the patch isolation (Fahrig, 2013). Our study has not found evidence of positive effect of proportion of forest surrounding FFs on the species richness and number of individuals of both forest specialist and generalist guilds. This also suggests that strict forest specialists have their populations restricted to the patch, with perhaps weak metapopulation structures for this guild (although this would need to be assessed genetically). While other taxonomic groups such as birds and mammals can disperse over the landscape much more easily using intervening forest patches in the landscape as stepping stones (Uezo et al.,
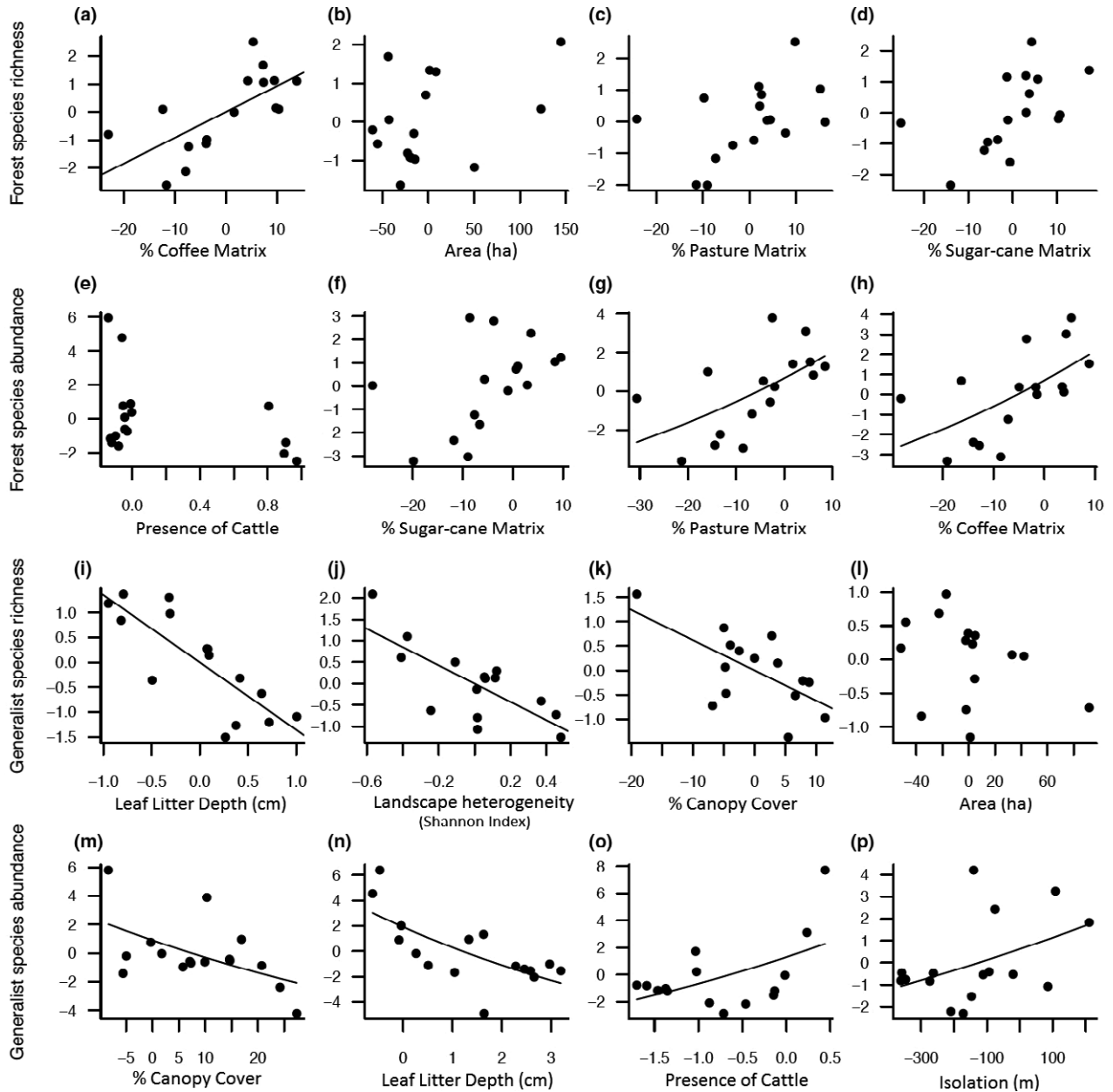
Partial regression plots

Figure 3 Partial regression plots for the four most relevant predictor variables based on hierarchical partitioning analysis.

2005), forest-associated amphibians have low functional connectivity between forest patches (Dixo *et al.*, 2009), and generalist amphibians have high tolerance to matrix variability, not being substantially affected by fragmentation (Dixo & Metzger, 2010). Generalist species are also favoured by the isolation of FFs in the landscape (see Table 2 and Fig. 3p), demonstrating their high tolerance to matrix variability. However, it is worth mentioning that the proportion of forests surrounding forest patches was very small, which could

have been insufficient to influence the connectivity in this particular landscape.

Agricultural matrices such as sun coffee and pasture can host different amphibian species, with a community structure that differs between these matrices and FFs, where some species may occur in a variety of habitats, whereas others (those only in FFs) are strict forest dwellers (Mendenhall *et al.*, 2014b). Agricultural matrices usually do not host species with very specific habitat requirements; those species tend to

be dependent on FFs that are in direct contact with an agricultural matrix. Our results suggest that different types of matrices, their structure and proportions have a bearing on the structure of FFs, and consequently on amphibian species richness and composition. Thus, the composition of the amphibian assemblages and species richness and abundance are intimately linked to fragment structure, leaf litter depth, canopy cover and presence of clearings, where surrounding matrices play a critical role in the maintenance of FF dynamics. The composition of amphibian assemblages mediated by environmental variables such as presence of clearings, canopy cover and leaf litter depth indicates a variation of vegetation gradients between different FFs in the landscape, which are shaped by the history of each individual FF. Thus, the fragment's vegetation structure has acted as an environmental filter, shaping the fragment's amphibian assemblage. This is because vegetation density is closely linked to the availability of reproductive sites, shelters and temperature and humidity variation of soil and water within FFs.

Given that generalist and forest specialist species respond differently to intrinsic variables of FF structure and the matrix, special attention should be given to the species' ecological needs, and processes such as colonization, competition and ecological succession to truly understand anuran biodiversity distribution in a fragmented landscape. The differences observed between the three matrix types (pasture, sugar cane and coffee) support the hypothesis that matrices with different structure and seasonality have different effects on FFs, with taller and more perennial matrices acting as protective barriers around FFs. More exposed landscapes offer less resistance to winds (Laurance & Curran, 2008), leading to an increase in wind speed in open areas (Savill, 1983), which in turn affects the microclimate and tree survival on a FF's edge (Laurance et al., 2002; Laurance, 2008). This would also appear to be the case for pastures and sugar cane (post-harvest).

The loss of plant matter in the FFs due to greater exposure of the FF at the canopy or leaf litter level may favour the increase of generalist species (Sartorius et al., 1999; Urbina-Cardona et al., 2006), which in turn tends to increase predation and competition within the FF (Urbina-Cardona et al., 2006). Species richness and abundance of individuals in the generalist and forest-associated guilds were inversely proportional (Fig. 2b), suggesting a succession process where generalist species out-compete strict specialists in FFs. In addition, the absence of strict specialists is influenced by less perennial matrices and/or cattle presence. These results support our study's working hypothesis, where a more perennial and complex surrounding matrix favours those environmental variables that increase forest–associated species richness within a FF.

The sugar cane matrix presents an interesting pattern. This matrix cannot block external effects like the coffee matrix does because it exposes the FFs in post-harvest periods. However, FFs surrounded by this matrix had many forest-specialist species when compared to completely exposed

landscapes, such as landscapes surrounded by pastures. Landscape heterogeneity and the coffee matrix grouped with leaf litter depth, canopy cover and the higher level of vegetation integrity, and were opposite to the presence of clearings, cattle within the FFs and the pasture matrix (Fig. 2a). This suggests that both a homogeneous matrix with more perennial arboreal structure and a diverse landscape with varied proportions of matrices may protect forest structure. The most heterogeneous landscapes in this study are composed mostly of tall vegetation structure [coffee, sugar cane, 'capoeira' (uncultivated grasses and shrubs, see Scheibler & Christoff, 2007), eucalyptus and forests close to FFs, see Supporting Material], which show greater similarity with forest structure than other matrices, giving FFs a degree of protection to external pressures. The environmental heterogeneity favours a higher amphibian species richness, but it does not identify the needs for species or guild management or conservation plans (Silva et al., 2011). Our study indicates that FFs surrounded by heterogeneous landscapes have a diverse assemblage of species, with both strict forest specialists and habitat generalists (see Fig. 2b). However, generalist species richness is negative relative to diverse landscapes. Generalist species are opportunistic and explore different kinds of habitats, so it may be possible that some species could avoid competition with specialists within FFs.

The presence of cattle within FFs favours generalist species richness and abundance both directly and indirectly. Cattle act as ecosystem engineers, removing and degrading the leaf litter that acts as shelter and breeding sites for terrestrial and direct developing forest-associated anurans. Cattle also trample and compact the soil on the margins of water bodies, thus destroying suitable habitat for forest-associated anuran tadpoles. The constant presence of cattle within a FF may reduce plant recruitment due to trampling, and affect availability of calling and breeding sites of forest-associated treefrogs. Cattle can also generate temporary puddles and pools through trampling, which can in turn be used by generalist species such as *Dendropsophus minutus*, *Hypsiboas albopunctatus*, *Hypsiboas* aff. *beckeri* and *Hypsiboas faber* for reproductive purposes. This would explain the large number of individuals of these species observed in FFs with cattle presence. Population declines and eventually local extirpations are to be expected for those forest-associated species that are more sensitive to the internal disturbance of FFs. This will, in turn, also affect amphibian species composition within fragments, as generalist species will tend to further colonize the FF. The processes above would therefore result in biodiversity and ecosystem service losses at the landscape level and within the Atlantic Forest biome. This outcome is of particular concern considering the high number of endemic species occurring in FFs embedded in agricultural areas.

CONCLUSIONS

Our study demonstrates that conservation of FF structure is directly dependent on the surrounding matrix. Unsuitable

matrices impact not only fragment edges but also their inner structure, and in this process habitat specialists can potentially experience population declines and local extinction, while the amphibian assemblage may change as a result of colonization by generalist species. This has major implications not only for conservation planning for the establishment of future reserves, but also for existing reserves and management of severely fragmented landscapes, as their vegetation integrity and community structure may already be influenced by surrounding agricultural matrices. Our study suggests a potential alternative in the form of matrix management for maintenance of remaining fragments and associated faunal communities in the Atlantic rain forest. Given the number of crops that are currently cultivated globally, it would be important to support and stimulate similarly focused research on other crops and in other regions of the world where forest fragmentation is a pervasive issue.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Key landscape parameters.
Appendix S2 Forest fragment structural variables.
Appendix S3 Species sampling.

BIOSKETCH

Lucas Ferrante's main research interests are animal behaviour, biogeography, diversity, evolution, landscape ecology, natural history and conservation.

Author contributions: L.F. designed the research; L.F., M.F.O.S., T.S. conducted fieldwork and examined material; L.F. and R.C.J. conducted GIS analyses; L.F., E.B.F. and F.B.B. conducted statistical analyses; L.F., A.A., E.B.F., F.B.B. wrote the manuscript; L.F., A.A., E.B.F., F.B.B., M.F.O.S., T.S. and R.C.J. revised the manuscript.

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