RICARDO RIBEIRO DE CASTRO SOLAR

PARTIÇÃO DA DIVERSIDADE DE FORMIGAS EM UMA PAISAGEM FRAGMENTADA

Dissertação apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Entomologia, para obtenção do título de *Magister Scientiae*.

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APROVADA: 26 de julho de 2010.

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Dedico este trabalho inteiramente à minha mãe, que sempre me foi exemplo de luta e dedicação.

> "Prefiro tentar subir para a ponta dos finos pêlos do coelho;
> assim posso olhar bem dentro dos olhos do mágico do universo;
> [...] e não me habituar completamente com tudo."
> *Jostein Gaarder*

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Resumo

SOLAR, Ricardo Ribeiro de Castro, M. Sc., Universidade Federal de Viçosa, julho de 2010. **Partição da diversidade de formigas em uma paisagem fragmentada.** Orientador: José Henrique Schoereder. Co-orientadores: Og Francisco Fonseca de Souza e Carlos Ernesto Gonçalves Reynoud Schaefer.

Eventos de fragmentação florestal são caracterizados como uma das maiores ameaças à biodiversidade e são a causa primária de perda de espécies nas florestas tropicais. Formigas são organismos que apresentam diversas características favoráveis ao seu uso em trabalhos ecológicos, o que as torna frequentes em estudos sobre fragmentação. Portanto, o objetivo deste estudo é responder a seguinte pergunta: Por que há mais espécies de formigas nos fragmentos florestais em relação ao entorno? Para responder a essa questão, hipóteses explicativas foram lançadas, baseadas em recursos e condições. Além disso, diferenças nas respostas em diferentes microhabitats foram analisadas. A amostragem foi realizada em quatro fragmentos florestais e quatro entornos adjacentes na cidade de Viçosa, Minas Gerais, Brasil. As formigas foram amostradas nos microhabitats epi- e hipogéicos, com armadilhas *pitfall* sem iscas. Foram coletadas amostras de solo para obter variv́eis explicativas. A diversidade de formigas foi particionada seguindo a equação $\gamma = \alpha + \beta$. O pressuposto, de que o fragmento é mais diverso que o entorno foi testado através de ANOVA. As variáveis explicativas foram testadas através de partição hierárquica, para detectar as variáveis mais importantes na explicação da diversidade e estas variáveis foram testadas através de *glm* para demonstrar a relação e a tendência. Estimativas de riqueza de espécies foram realizadas para se estimar o efeito na escala de paisagem. A composição de espécies foi testada através de NMDS, e a significância acessada através de ANOSIM. Nosso pressuposto se confirmou apenas a nas escalas de diversidade β e γ e para o hábitat epigéico. Além disso, as variávies mais importantes para explicação foram %areia (-); CTC (+); concentração de ferro (-) e matéria orgânica do solo (unimodal). Além disso, estas variávies apresentam o mesmo padrão de variação que o pressuposto, sendo fortes candidatas a fatores causais. A composição de espécies variou, sendo distinta quando comparamos fragmento *vs.* entorno e quando comparamos entre microhábitats epi- e hipogéicos. No último, observamos resposta apenas para o ambiente florestal. A confirmação do nosso pressuposto, bem como a explicação provida pelas variáveis ambientais suportam o fato de que alterações causadas na qualidade do ambiente pela fragmentação são responsáveis pela perda de espécies observada. Ainda, a composição de espécies revelou que existem subconjuntos de espécies específicos de cada local, matrizes e florestas. Ainda, a ausência de diferença na composição de espécies entre os microhabitats na matriz revela uma acentuada perda de algumas espécies que existiam no ambiente florestal, mas que não mais estão presentes.

Abstract

SOLAR, Ricardo Ribeiro de Castro, M. Sc., Universidade Federal de Viçosa, July, 2010. **Ant diversity partitioning in a fragmented landscape.** Advisor: José Henrique Schoereder. Co-advisors: Og Francisco Fonseca de Souza and Carlos Ernesto Gonçalves Reynoud Schaefer.

Forest fragmentation events have been characterized as one of the main threats to biodiversity in modern times, and are the primary cause of species loss in tropical forests. Ants are organisms that present many suitable traits to be used in ecological studies, therefore they are frequently used in fragmentation surveys. However only epigaeic microhabitat have been considered in these studies, neglecting other important microhabitats. Hence, with this study we aimed to answer the following question: Why are there more ant species in forest remnants compared to matrices? We made explanatory hypotheses, in which environmental variables were taken as surrogates of resources and conditions. The study was carried out in four forest remnants and four surrounding matrices in Viçosa municipality, Minas Gerais state, Brazil. Ants were sampled with pitfall traps in two microhabitats, epigaeic and hypogaeic, with unbaited pitfall traps. The diversity was partitioned, following the equation $\gamma = \alpha + \beta$. An ANOVA was made at each scale to test the assumption that fragment harbour more species than matrices. Explanatory variables were analysed through hierarchical partitioning to find out which variables are more important in explaining species richness and using GLM to depict the relationships among variables. Estimators of species richness were employed to asses the effect of fragmentation in the landscape. Species composition was tested through NMDS and significance values were obtained by ANOSIM. We confirmed our assumption only for β and γ diversity. The most important variables to explain diversity were %Sand (-), CEC (+), iron concentration (-) and soil organic matter (unimodal). Variation among environmental parameters in relation to fragmentation explained the variations in species richness. We found differences in species composition, with forest habitats being distinct from matrices at both epi- and hypogaeic microhabitats. A distinction between epigaeic/hypogaeic communities was found only in forest environments. We confirmed our assumption and confirmed that some variables are important for explaining species loss caused by fragmentation. It give support to the fact that alterations caused on environmental quality are important and must be considered. Moreover, species composition revealed that there are specific subsets in each local, matrices and forests. Still, the lack of difference in species composition between microhabitats in matrices reveals the strong effect of fragmentation on some hypogaeic species, that should depend on litter, that is not available after vegetation clearance.

1 Introduction

The human population is growing fast, which exerts a lot of pressure on tropical forests with consequent destruction of these forests (Gascon *et al.*, 1999; Debinski & Holt, 2000). One of the major consequences of deforestation is the subdivision of pristine forests into large numbers of forest fragments (Sobrinho *et al.*, 2003). This subdivision is also called forest fragmentation and it has many causes, such as agriculture, livestock and urbanization processes (Schoereder *et al.*, 2004; Sobrinho & Schoereder, 2007). Populations of organisms that live in pristine forest are now being divided, changing their ecological dynamics (Vasconcelos *et al.*, 2006), including dispersion rates, invasions by exotic species and modification of extinction rates (Carvalho & Vasconcelos, 1999; Soares *et al.*, 2001; Schoereder *et al.*, 2004; Bruna *et al.*, 2005). Given all these negative effects, forest fragmentation is currently one of the main threats to biodiversity (Debinski & Holt, 2000; Ribas *et al.*, 2005; Vasconcelos *et al.*, 2006; Sobrinho & Schoereder, 2007), being the process itself a primary cause of species loss.

A landscape of forest patches is composed of a mosaic of environments, with different degrees of degradation, isolation, sizes and shapes (Sobrinho & Schoereder, 2007). Commonly, these patches maintain some connection to each other via matrix, which is the usual term to refer to areas among remnants (Gascon *et al.*, 1999). The role played by the matrix goes far beyond being simply a barrier to species dispersion among forest patches (Gascon *et al.*, 1999; Laurance *et al.*, 2002; Schoereder *et al.*, 2004; Ribas *et al.*, 2005). Gascon *et al.* (1999) proposed to see the matrix not as a barrier, but rather as a filter, which constrains an individual movement in the environment. Matrix physical characteristics (i.e. vegetation, humidity, *etc.*) will determine the pore size of that filter and species characteristics will determine their capacity to cross these pores and the adversities of the environment (Carvalho & Vasconcelos, 1999; Gascon *et al.*, 1999). Therefore, to understand the mechanisms by which fragmentation changes biological communities, it is necessary to consider the entire landscape, including the matrix as a crucial and active actor (Carvalho & Vasconcelos, 1999; Gascon *et al.*, 1999; Debinski & Holt, 2000; Vasconcelos *et al.*, 2006).

Given the great diversity of landscapes formed after fragmentation, biological communities are suffering from different levels of impact on ecological processes. These processes can act on different taxa and along different spatial scales (Ribas *et al.*, 2003). On the local scale, interactions among individuals over ecological time are more important in determining ecological dynamics. On the other hand, at the regional level processes of colonization/extinction play a more important role over ecological and evolutionary time (Srivastava, 1999).

Classically in ecology, local processes are reported to have greater influence on community dynamics (Soares *et al.*, 2001), mainly due to the patchy distribution of some species (Ribas & Schoereder, 2002, 2004), although regional processes can play an important role on community regulation (Salomon *et al.*, 2010). Therefore, biodiversity must be analysed on other scales, like regional scale (γ diversity) and between-locality diversity (βdiversity) (Loreau, 2000; Veech *et al.*, 2002).

In a recent review, Veech *et al.* (2002) suggest to use the additive partitioning of diversity to deal with these different spatial scales, as it is an operationally better method and gives more accurate information about diversity partitioning. Additive partitioning means that $\gamma = \alpha + \beta$, in which α is the local richness, γ is the regional richness and β is the among-locals diversity (or the differentiation measurement) (Loreau, 2000; Veech *et al.*, 2002). Through this approach, all scales have the same unit of measurement (species) and the diversity can be partitioned on multiple levels. γ diversity in given level is equal to α diversity in the immediate higher level (Veech *et al.*, 2002).

Ants have been extensively used in surveys dealing with forest fragmentation effects (Ribas & Schoereder, 2002; Brühl *et al.*, 2003; Sobrinho *et al.*, 2003; Schoereder *et al.*, 2004; Bruna *et al.*, 2005; Ribas *et al.*, 2005; Vasconcelos *et al.*, 2006; Sobrinho & Schoereder, 2007). Ants comprise a vast group of insects, dominant in tropical forests with a crucial ecological role for ecosystem functioning (Wilson, 2008; Underwood & Fisher, 2006). Moreover, ants are easily sampled and identified, being a suitable model for ecological surveys (Folgarait, 1998; Schmidt & Solar, 2010). Several studies have demonstrated the negative effect of forest fragmentation on tropical forests ant communities (Carvalho & Vasconcelos, 1999; Vasconcelos *et al.*, 2006; Sobrinho & Schoereder, 2007). Moreover, continuous forests harbour more species than fragments and matrices are expected to have less species than forest fragments. Nevertheless, some causes of this species loss are still unknown. New studies are recommended to clarify the effects and recovery of forest fragmentation process (Gascon *et al.*, 1999; Debinski & Holt, 2000; Vasconcelos *et al.*, 2006) as well as assess these effects in seldom surveyed microhabitats, such as the hypogaeic.

Often, only epigaeic and arboreal habitats are considered when dealing with the effects of forest fragmentation on ant communities (but see Underwood & Fisher, 2006; Schmidt & Diehl, 2008; Schmidt & Solar, 2010) . Nonetheless, in the last few years, myrmecologists have begun to consider the vertical stratification of ant communities (Wilkie *et al.*, 2007; Brandão *et al.*, 2008; Schmidt, 2008; Schmidt & Solar, 2010) and much attention has been devoted to hypogaeic and canopy ants, which have different species composition with peculiar ecological and evolutionary stories (Rabeling *et al.*, 2008; Schmidt & Solar, 2010).

With this survey, we aimed to answer the following question: Why are there more species inside the forest fragments compared to the matrices? To answer that, the following hypotheses (not self-exclusive) were tested:

- Ant species alpha diversity is higher inside fragments than in the matrices because food resources are more abundant and conditions are more suitable inside the forest.

- β diversity is higher inside the fragments than in matrices due to matrix simplification (lower heterogeneity, measured by coefficient of variation) due to agriculture and livestock activities.

- Regional species richness (γ) is higher inside fragments than in the matrices because average resources are more abundant and average conditions are more suitable inside the forest.

Moreover, we also used the data to infer for the following statements:

- Species composition differ with different types of matrices and matrices will differ from forest fragments. Moreover, microhabitats present specific subsets of species.
- The above relationships are more evident in epigaeic than in hypogaeic microhabitats, as subsoil is more buffered, presenting a delayed response.

2 Material and Methods

2.1 Location of study

This study was carried out in Viçosa municipality, Minas Gerais state, Brazil (23k x 720570 / y 7703630). The dominant forest type in this region is the semidecidous seasonal rainforest, which belongs to the Atlantic Rain Forest biome (Veloso *et al.*, 1991). The previous pristine forest suffered from heavy fragmentation in the past (i.e. 30's and 40's), being replaced by crops, pastures, livestock (Sobrinho & Schoereder, 2007; Pinto *et al.*, 2008) and in the last few years, silviculture has become a more common activity (Schmidt, 2008). Nowadays, the scenario is composed of a plethora of forest fragments (mainly secondary) with different shapes, sizes and matrices, forming an excellent model system to survey forest fragmentation and land-use effects.

2.2 Sampling procedure

In order to encompass the economic activities that are prone to causing fragmentation in the Viçosa region, four forest fragments were arbitrarily chosen along with four adjacent matrices (Table 1). To avoid interdependence among samplings, areas were chosen at least two kilometres from each other, as can be seen in the map (Figure 1).

Table 1: Table with sampled areas separated by vegetation type (more representative and sampled) and UTM coordinate (Zone 23). Due to the continuity of pastures, their area cannot be calculated.

Vegetation type	Area (ha)	Coordinates (UTM x/y)
Forest Fragment	92	722271.34 / 7703135.86
Pasture	n.a.	723098.36 / 7703758.28
Forest Fragment	9.30	722739.33 / 7707141.48
Coffee Crop	18	722696.70 / 7707061.42
Forest Fragment	55.49	721562.28 / 7701452.78
Eucalyptus Crop	5	721840.47 / 7701364.28
Forest Fragment	34.27	724147.87 / 7698976.39
Pasture	n.a.	724433.60 / 7699081.77

Figure 1: Map with the sampled fragments and adjacent matrices. Source: GoogleEarth

Sampling was carried out during the rainy season (March-May 2009) and all samples were made at least 50 meters from the edge aiming to diminish edge effects on the forest (Sobrinho & Schoereder, 2007) and a possible forest effects on the matrix. Samples were made with a pair of grids (Figure 2) in each group "fragment + adjacent matrix". Each grid was composed of nine sampling points, which consist of a pair of pitfall traps, one epigaeic and one hypogaeic (Schmidt & Solar, 2010), both unbaited and half-filled with a solution composed by ethanol (70%) and glycerine in a proportion of 9:1 (Figure 3). We opted to use unbaited pitfalls because our hypotheses are dealing with resources controlling local richness, hence the use of baits is prone to artificially increase local resource availability.

Pitfalls remained in the field for 96 hours. Collected ants were immediately transferred to an ethanol solution at 80% where they were kept until identification. Specimens were identified to genus (Bolton, 1994; Fernández, 2003) and then morphospeciated (Oliver & Beattie, 1996). Voucher specimens are deposited in the reference collection of Community Ecology Laboratory, Federal University of Viçosa.

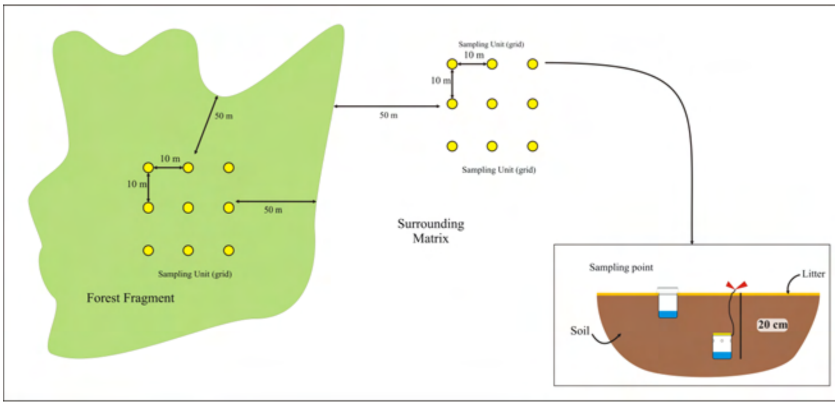

Figure 2: Scheme of the sampling design. Each grid was composed of nine pairs of epigaeic/hypogaeic pitfall traps (sampling point). Each sampling point was located 10 meters apart the others.

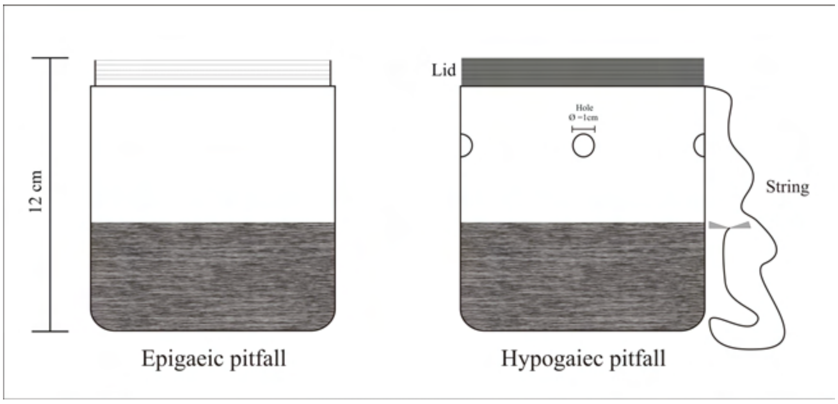

Figure 3: Pitfall trap design. On the left, the epigaeic pitfall trap, buried level with soil surface . On the right, the hypogaeic pitfall trap, which is buried 20cm below soil surface. The epigaeic pitfall trap is covered with a roof-like piece to avoid flooding. The hypogaeic pitfall trap has four radial holes, where ants can gain access to the trap, as it must be buried with the lid.

2.3 Sampling of environmental variables

At each sampling point, some soil variables were taken in order to clarify the processes operating on the found pattern. These variables were divided into surrogates of conditions and surrogates of resources. Soil granulometry was taken as a surrogate of conditions, as it may affect nest construction. Cation Exchange Capacity (CEC), Iron (Fe), Phosphorous (P), Potassium (K) and Soil Organic Matter (SOM) were taken as surrogates of resources, given that all of these variables may be direct or indirect resources to most ant species. Specific methods to obtain each measurement are described below.

Soil was sampled at two different depths, 0-5cm representing epigaeic microhabitat and 15-30 cm representing hypogaeic microhabitat. Soil samples were taken inside the hole made to install the trap, being careful to avoid mixture of soil layers during the burying process. In the laboratory, samples were air dried for three days (72 hours) and then sifted in a sieve with a mesh of 2mm. The resultant soil was sent to soil analyses in the Soil Department, Federal University of Viçosa.

2.4 Statistical Analyses

2.4.1 Additive partitioning of diversity

To analyse the response of ant communities to fragmentation in different spatial scales, we opted to use the additive partitioning of biological diversity (Veech *et al.*, 2002). In this model, biological diversity is seen as a sum of three components:

- Alpha (α) diversity - Also called Local diversity, is the diversity measured in a scale which species can interact with each other (Srivastava, 1999).
- Gamma (γ) diversity - Also called regional diversity, is the diversity measured in a scale which historical factors are more important (dispersion ability, evolutionary effects, *etc.*).
- Beta (β) diversity - Also called differentiation diversity, or among-locals diversity, is the difference between α and γ, and should represent heterogeneity and turnover.

In our study, at least two scales are possible to be identified; the fragment and the landscape scales. In fragment scale, α_{frag} means the species richness in each sampling point inside each fragment/matrix (i.e. each pitfall); γ_{frag} is the accumulated species richness in each sampled fragment/matrix and β_{frag} is the difference between γ_{frag} minus α_{frag}, following equation 1

$$\beta_{frag} = \gamma_{frag} - \alpha_{frag} \tag{1}$$

At the scale above (landscape scale) we can take each fragment/matrix on the local scales. Hence, at this level, $\alpha_{land} = \gamma_{frag}$. Total species richness of fragments/matrices are now taken as γ_{land}, which consists of all species that occur in fragments/matrices. On the landscape scale, β_{land} can be considered as the difference between γ_{land} minus α_{land}, following equation 2

$$\beta_{land} = \gamma_{land} - \alpha_{land} \tag{2}$$

One of the greatest advantages of this method is that the total species richness of the survey (in this case, of the landscape scale) can easily be expressed as expressed in equation 3, for all fragments/matrices:

$$\gamma_{land} = \alpha_{frag} + \beta_{frag} + \beta_{land} \tag{3}$$

2.4.2 Test of the assumption

At fragment scale (α_{frag}, γ_{frag} and β_{frag}), we tested the assumption that matrices harbour fewer species than fragments. We made an ANOVA testing the influence of landscape compartment (Forest, pasture, coffee and *Eucalyptus*) on ant species richness in each microhabitat. Species diversity was always the response variable and habitat type the explanatory variable. As often as possible, we lumped levels in order to simplify the model. Moreover, we tested for the effect of area on species richness, by testing species diversity as the response variable and area as the explanatory variable. All models followed Poisson distribution, corrected for under- or over-dispersion when needed (Logan, 2010). At the α_{frag} scale, we used generalized linear mixed models in order to avoid pseudo-replication. Models and distribution of errors were checked via residual analyses in all cases (Crawley, 2007). Tests were performed on the software R (R Development Core Team, 2009) using GLM and with the package *lmer* to fit mixed models under the Poisson assumption.

On the landscape scale (γ_{land} and β_{land}), as we do not have enough repetitions to apply a statistical test, we used a 1^{st} order Jackknife estimator of species richness, which is based on presence/absence data and is very precise among non-parametric estimators (Chiarucci *et al.*, 2003). Differences between forest fragments and matrices were inferred from the confidence intervals. We also inferred differences based on the slope of species accumulation curves. Calculations of estimators and species accumulation curves were performed on the software R (R Development Core Team, 2009) with the package *vegan*.

2.4.3 Explanatory variable analyses - Hierarchical Partitioning

In this study, many environmental parameters were sampled as explanatory variables (X) of species diversity (Y). However, in most cases these variables are not necessarily uncorrelated and multicollinearity is the main problem when analysing these kind of data. Hence, to gauge the independent effect (I) of each explanatory variable upon species diversity in each scale, we opted to use hierarchical partitioning (Chevan & Sutherland, 1991).

Hierarchical partitioning (HP) is a statistical protocol in which all practicable models in a multiple regression are considered in an attempt to identify the most [supposedly] causal factors (Mac Nally, 2000). H.P. is also able to recognize that goodness-of-fitness measures - such as log likelihood [1] - are not unconditional indicators of model suitability, but measure suitability compared to other models. In that way, HP is very suitable in identifying the polarity and relative magnitudes of the effects (importance) of predictor variables (Logan, 2010).

We used HP to depict the independent effect of eight environmental variables (SOM, K, P, Fe, CEC, %Sand, %Clay and %Silt) upon species richness.

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[1] but note that other g.o.f. measures are available

The latter was measured in three different scales: α_{frag} (each sampling unit), γ_{frag} (each fragment/matrix) and β_{frag}. Furthermore, Coefficient of Variation (CV) of each explanatory variable was calculated as a proxy of habitat heterogeneity and its influence upon β_{frag} diversity.

Despite HP can give us a very good idea of the independent effects of variables, it does not give any significance value to be compared. Hence, how can the results of HP be trustworthy and usable? A randomization routine is the best available method to solve this query (Mac Nally, 2002). By randomizing data several times (1000 is recommended) and comparing the random I_{random} with the observed I_{obs} it is possible to decide which variables to retain and which variables to dismiss. The randomized outcomes can be used to calculate Z-score [2], and the critical values for $p < 0.05$ and $p < 0.01$ are $Z \geqslant 1.65$ and $Z \geqslant 2.33$ respectively.

We adopted Poisson distribution of errors, which is recommended to deal with count data. As HP did not allow us to correct the dispersion parameter, we transformed data of β_{frag} diversity by applying square root transformations. When following Poisson errors, the goodness of fit measurement used was $log - likelyhood$ and when under Gaussian assumption, we used R^2 as the goodness of fit measurement (Crawley, 2007).

Hierarchical Partitioning and randomization tests were applied using the software R (R Development Core Team, 2009) with the package *hier.part*.

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[2] $[I_{obs} - \overline{I}_{rand}]/sd\{I_{rand}\}$

2.4.4 Explanatory variable analyses - Generalized Linear Models

After assessing the independent effects of variables with HP, we ran generalized linear models to test the effects of each variable on species richness at each level (α, γ and β diversity). We choose to test the variables with significant independent effects on species richness and variables with independent effects higher than 11%, since we observed that it is possible to find significant effects only above this value.

Complete models were simplified until only significant effects remained. The final model was tested against a null model to ensure of its explanatory power. When multicollinearity effects were perceived, we checked the Akaike Information Criteria (AIC) of both models, and we kept the models with smaller AIC value. If models did not differ in AIC value or this values were not available, we opted to keep the variables with higher independent effect in HP.

All models followed Poisson errors, corrected for under- or over-dispersion when needed (Logan, 2010). At the α_{frag} scale, we used generalized linear mixed models in order to avoid pseudo-replication. Models and distribution of errors were checked via analysis of residuals in all cases (Crawley, 2007). Tests were performed with the software R (R Development Core Team, 2009) with *glm* models and with the package *lmer* to fit mixed models under the Poisson assumption.

We also tested the response of environmental variables to habitat type. We tested only the response of variables that presented significant effect on ant diversity. We made an ANOVA for each variable using Gaussian errors.

All models were checked by residual analysis and data were log transformed when needed.

2.4.5 Composition analyses

Composition was tested by Non-metric Multidimensional Scaling (NMDS). This technique differs in many aspects from usual ordination methods. First, at NMDS, a small number of axes are explicitly chosen prior to the analysis and the data are fitted to those dimensions; there are no hidden axes of variation. Second, most other ordination methods are analytical and therefore result in a single unique solution to a set of data. In contrast, NMDS is a numerical technique that iteratively seeks a solution and stops computation when an acceptable solution has been found, or it stops after some pre-specified number of attempts. As a result, an NMDS ordination is not a unique solution and a subsequent NMDS analysis on the same set of data and following the same methodology will likely result in a somewhat different ordination (Kindt & Coe, 2005).

The major drawbacks of NMDS when compared to other ordination techniques were related to computational limitations. However, many of this problems have been already solved, making NMDS the most powerful multivariate analysis for ecological data (Kindt & Coe, 2005).In this study, we opted to use Raup-Crick dissimilarity index, once it seems to be more suitable to presence-absence data (Hammer *et al.*, 2001).

To run NMDS, we pre-established four different divisions, as follows:

1. Forest *vs.* Matrices (separated by type);

2. Forest *vs.* Matrices (all matrices together);
3. Forest *vs.* Matrices (at each microhabitat);
4. Epigaeic *vs.* Hypogaeic (at each landscape compartment).

Following NMDS, we used analysis of similarity (ANOSIM) to test for the significance between multivariate groups formed. Similarity percentage (SIMPER) was made to access the individual contribution of each species toward distinguishing differences community structure among groups (Clarke, 1999). Analyses were performed with the free software PAST (Hammer *et al.*, 2001).

3 Results

We collected 69 ant species, from 31 genera and eight subfamilies (Table 3). A total of 27 species occurred only in forest and 19 species occurred only in matrix. We highlight the sampling of *Acantostichus laticornis* Forel, 1908 and *Carebara* sp.a, that was exclusively sampled at hypogaeic forest environments; and *Leptogenys* sp.a, which occurred at only one sampling point.

3.1 Assumption

Epigaeic β_{frag} and γ_{frag} diversities presented significant relationships to habitat type. In both cases, we statistically lumped Forest + Coffee and *Eucalyptus* + Pasture. Both β_{frag} ($F_{1,6} = 14.04$; p=0.009; Figure 4a) and γ_{frag} ($F_{1,6} = 12.47$; p=0.012; Figure 4b) diversities were higher in forests and coffee crops than in *Eucalyptus* and pastures.

We did not find significant relationships between α_{frag} diversity and habitat in either epigaeic microhabitats ($\chi^2 \backsimeq 7$; df=4; p=0.16) or in hypogaeic microhabitats ($\chi^2 < 4$; df=4; p=0.82). We found no significant relationship for hypogaeic β_{frag} ($F_{3,4} = 0.47$; p=0.71) and hypogaeic γ_{frag} ($F_{3,4}$=0.4115; p=0.76) diversities.

On the landscape scale, we inferred that γ_{land} diversity is higher in forest than in matrix for both epigaeic ($Jack1_{for} = 72.31 \pm 6.85$

and $Jack1_{mat} = 53.56 \pm 4.88$; Figure 5a) and hypogaeic microhabitats ($Jack1_{for} = 34.61 \pm 4.37$ and $Jack1_{mat} = 20.83 \pm 2.76$; Figure 5b). When we joined microhabitats, we also found that forest harbour more species than matrix ($Jack1_{for} = 69.76 \pm 4.74$ and $Jack1_{mat} = 55.79 \pm 4.19$; Figure 5c). We confirmed this trend by comparing species accumulation curves for epigaeic (Figure 5d), hypogaeic (Figure 5e) and joint (Figure 5f) microhabitats.

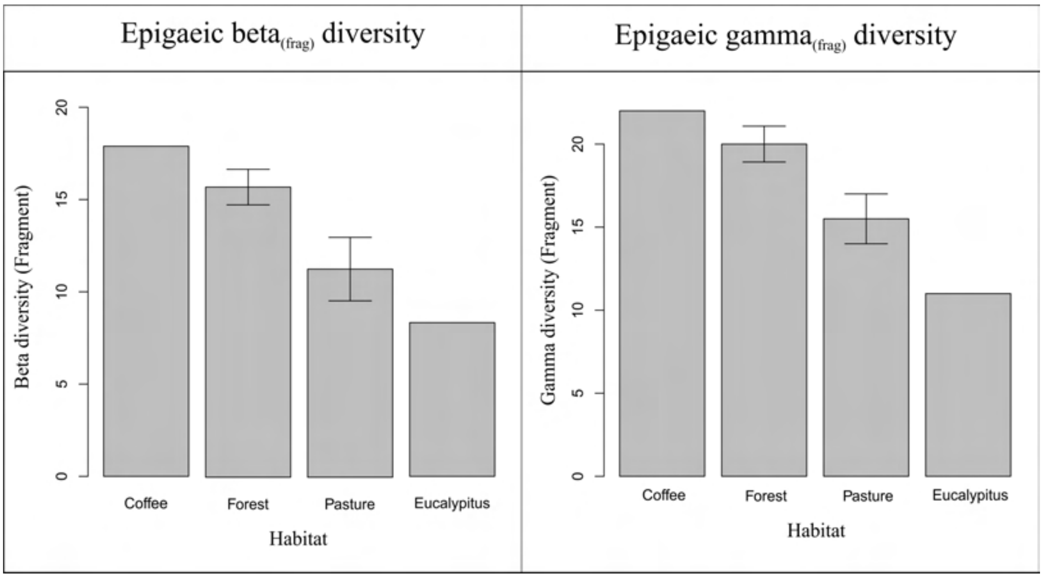


Figure 4: Tests of assumption results. At (a) β_{frag} diversity is shown to be higher in forests and coffee habitats when compared to pastures and *Eucalyptus* habitats (p=0.009). The same result is shown in (b) for γ_{frag} diversity (p=0.012). Error bars are standard errors.

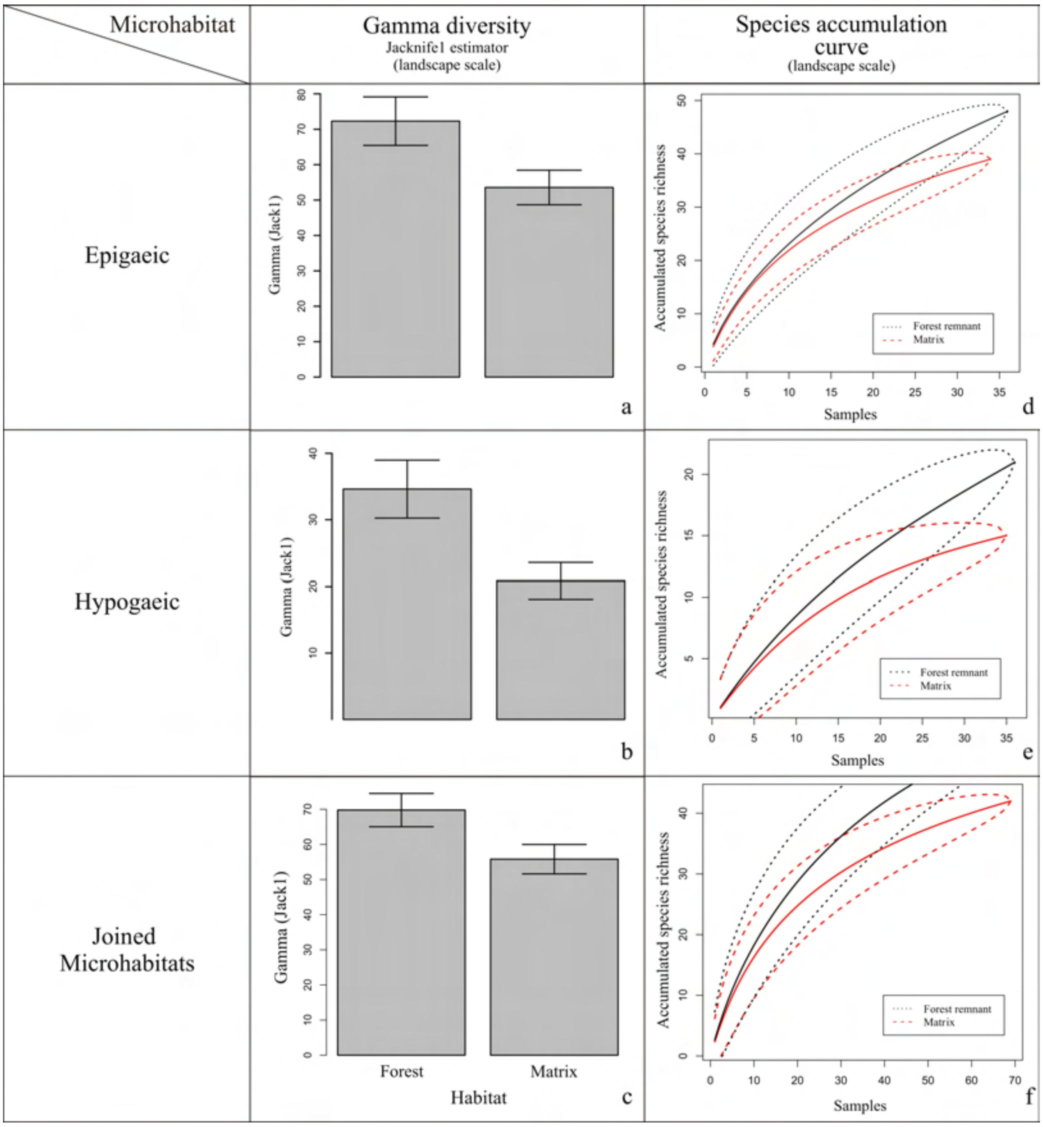


Figure 5: Tests of assumption results. 1^{st} order Jackknife yielded the same results for both forests and matrices, as well as for joined microhabitats. Epigaeic (a), hypogaeic (b) and joined (c) microhabitats have more species in forests when compared to matrices. Error bars are standard errors. Species accumulation curves confirm these results by checking the slope and confidence interval of each curve. Black curves are forest habitats and red curves are matrix habitats.

3.2 Environmental variables effects on ant diversity

3.2.1 Hierarchical partitioning

Hierarchical partitioning (Figure 6) revealed a positive independent effect of SOM on hypogaeic α_{frag} diversity (46.08%; Z-score=3.71; $p < 0.01$; Figure 6b) also, it revealed a positive independent effect of K on hypogaeic β_{frag} (28.25%; Z-score=2.01; $p < 0.05$; Figure 6f) and hypogaeic γ_{frag} (26.45%; Z-score=1.80; $p < 0.05$; Figure 6h). A negative independent effect of sand percentage was detected on epigaeic γ_{frag} diversity (30.09%; Z-score=2.29; $p < 0.05$; Figure 6g).

3.2.2 Generalized linear models

We found that hypogaeic α_{frag} diversity has a significant unimodal relationship with SOM ($\chi^2_{2,5}$=13.54; p=0.001; Figure 7a). β_{frag} diversity presented a significant negative relationship with both Fe ($F_{1,6}$=11.73; p=0.018) and %Sand ($F_{2,5}$=9.52; p=0.027), represented by Figure 7b. Still, γ_{frag} has a significant positive relationship with CEC ($F_{1,6}$=25.95; p=0.003) and a significant negative relationship with %Sand ($F_{2,5}$=19.59; p=0.006), represented by Figure 7c.

3.3 Habitat effect on environmental variables

Since we lumped forest + coffee together, as well as *Eucalyptus* + pasture in the test of assumption, we kept the same simplification here, as we aim to check for the same variation in environmental variables. We found no significant relationship for epigaeic SOM ($F_{1,6}$=1.31; p=0.28, Figure 8a) and

%Sand ($F_{1,6}$=3.83; p=0.09; Figure 8d). Conversely, we found a significant relationship for CEC ($F_{1,6}$=10.44; p=0.017; Figure 8b) Fe ($F_{1,6}$=8.19; p=0.03; Figure 8c). CEC is higher in forests and coffee crops and Fe concentration is higher in *Eucalyptus* and pastures. In spite of some non-significant results, all observed trends were in accordance with explanations to ant diversity results with relation to fragmentation.

The other variables did not have relationship with fragmentation. Even using forests *vs.* matrices (without simplification), any significant result was found (minimum p-value=0.35).

3.4 Species composition changes

NMDS analysis revealed differences in species composition between forest/matrix as well as between epigaeic/hypogaeic communities. The former presented differences in both microhabitats (Stress_{epig}=0.31 and Stress_{hypo}=0.29; Figure 9a;b) and the latter presented differences only in forest fragments (Stress_{for}=0.32; Figure 9c). Matrices did not differ in species composition between microhabitats (Stress_{matr}=0.40; Figure 9d).

ANOSIM confirmed results yielded from NMDS, that forest/matrix separation is significant for both epigaeic ($p<0.001$) and hypogaeic (p=0.031). Epigaeic/hypogaeic difference was confirmed only for forest habitats ($p<0.001$), but it was not significant for matrix habitats (p=0.10).

Results of SIMPER revealed the ant species that contributed with groups separation are presented in the Table 2. We listed species that accumulated contribution sums 50% to sites dissimilarity.

Table 2: SIMPER results with species that contributed to group formations. Results are presented for separation between forest *vs.* matrices groups in each microhabitat and separation between epigaeic *vs.* hypogaeic groups in forest habitats. Species are listed until they reach a contribution of 50%. Symbols are indicating the habitat where each species was most frequent.

Forest* *vs.* Matrix§		Epigaeic† *vs.* Hypogaeic‡
Epigaeic	Hypogaeic	Forest
Camponotus rufipes *	*Rogeria* sp.a §	*Pachycondyla striata* †
Pachycondyla striata *	*Pheidole* sp.j §	*Camponotus rufipes* †
Pheidole sp.c §	*Labidus* sp.a §	*Gnamptogenys* sp.a †
Gnamptogenys sp.a *	*Labidus* sp.b *	*Camponotus* sp.a †
Pheidole sp.b §	*Solenopsis* sp.b §	*Labidus* sp.b ‡
Camponotus sp.a *	*Solenopsis* sp.c §	*Solenopsis* sp.a ‡
Ectatomma sp.a *	*Nomamyrmex* sp.a *	*Ectatomma* sp.a †
Atta cf. laevigata §	-	*Nomamyrmex* sp.a ‡
Labidus sp.a §	-	*Pheidole* sp.c †

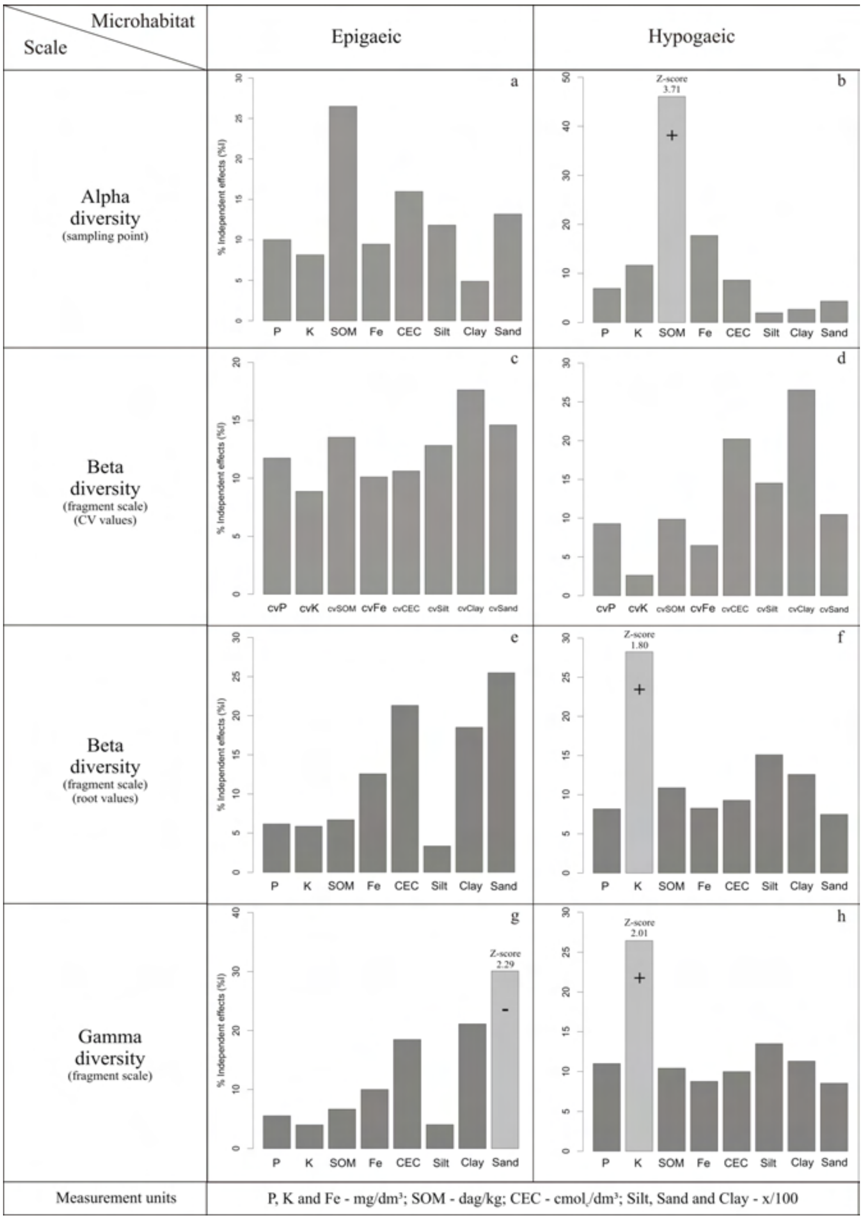


Figure 6: Distribution of the independent effects of each environmental variable (%) on ant species diversity as determined by hierarchical partitioning. Diversity was measured at three scales (α_{frag}, β_{frag} and γ_{frag}) and in two microhabitats (epigaeic and hypogaeic). Lines represent ecological scales and columns represent microhabitats. Lighter coloured bars are significant effects ($p<0.05$) and + or − symbols represent the trend. Phosphorous (P), Potassium (K), Soil Organic Matter (SOM), Iron (Fe) and Cation Exchange Capacity (CEC).

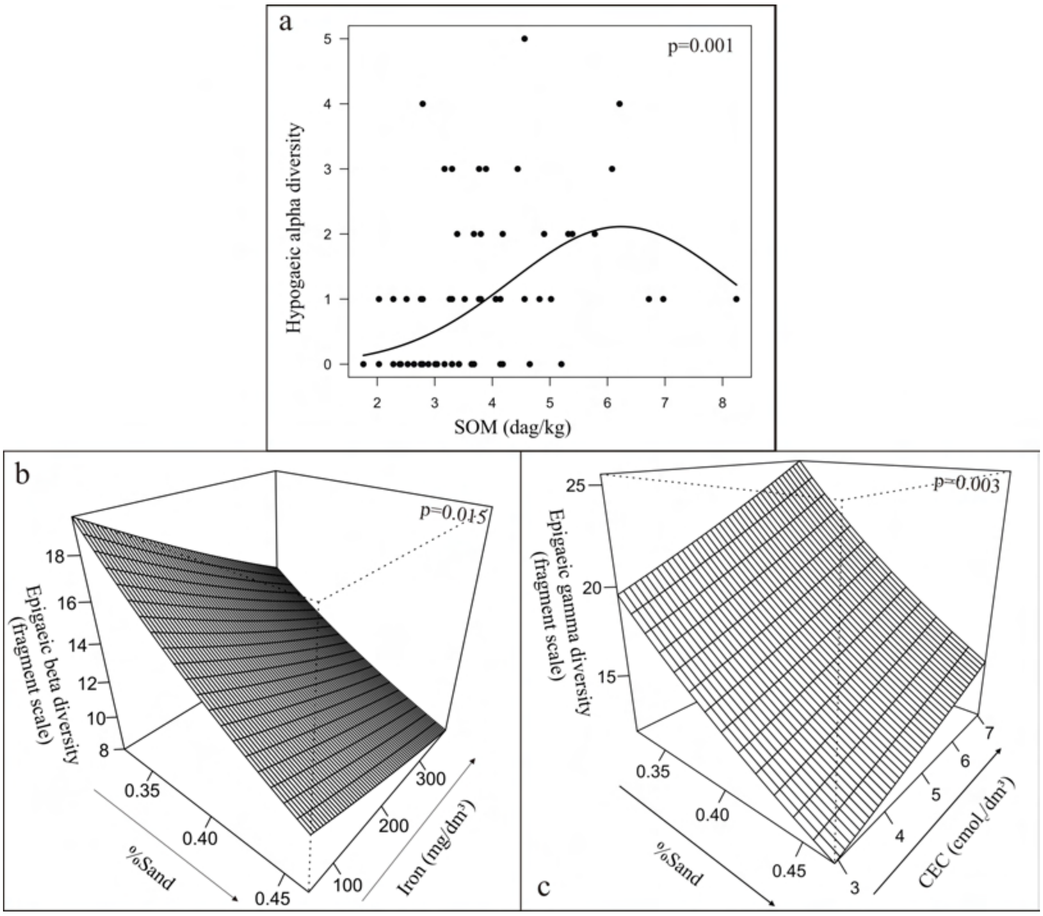


Figure 7: Results for regression analyses with environmental variables extracted from HP. (a) represents the quadratic significant influence of soil organic matter (SOM) on hypogaeic α_{frag} diversity (p=0.001), where is possible to see that hypogaeic α_{frag} diversity increases until it reaches an upper limit when it begins to decrease. (b) shows the negative influence of both %Sand and Iron (Fe) on epigaeic β_{frag} diversity (p=0.015). Finally, (c) represents a positive influence of cation exchange capacity (CEC) and a negative influence of %Sand on epigaeic γ_{frag} diversity (p=0.003).

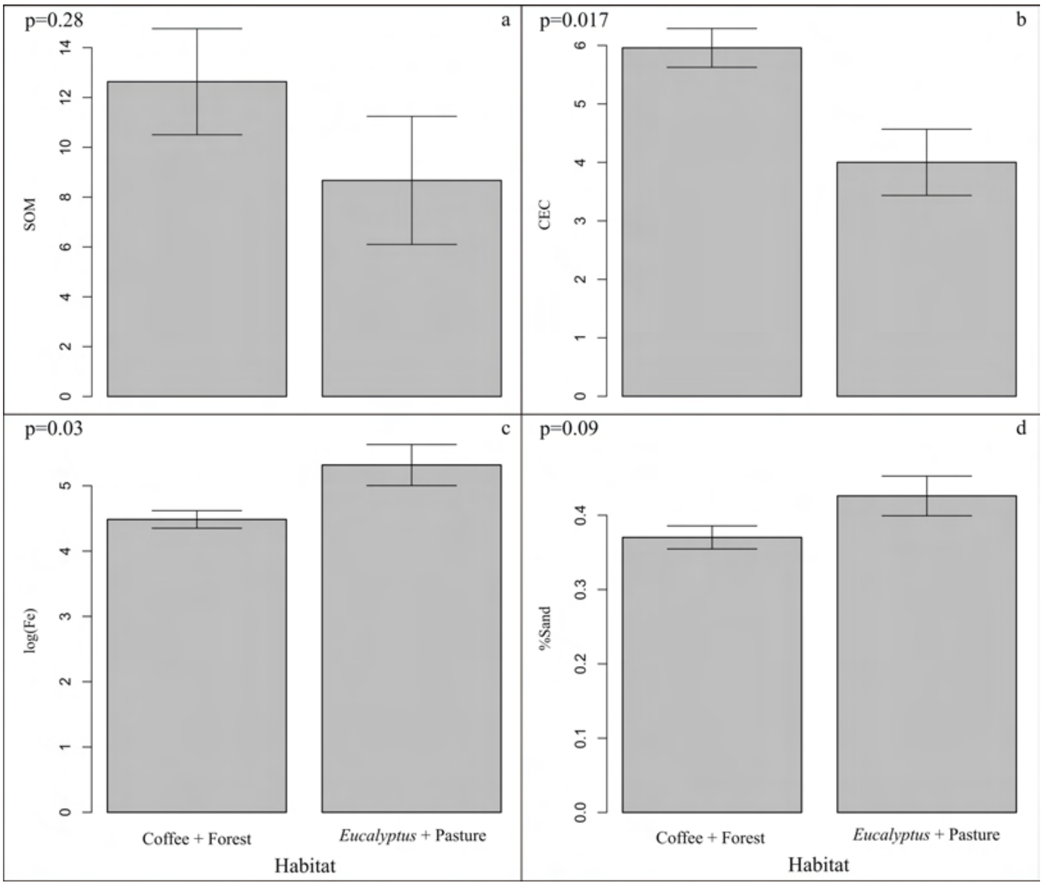
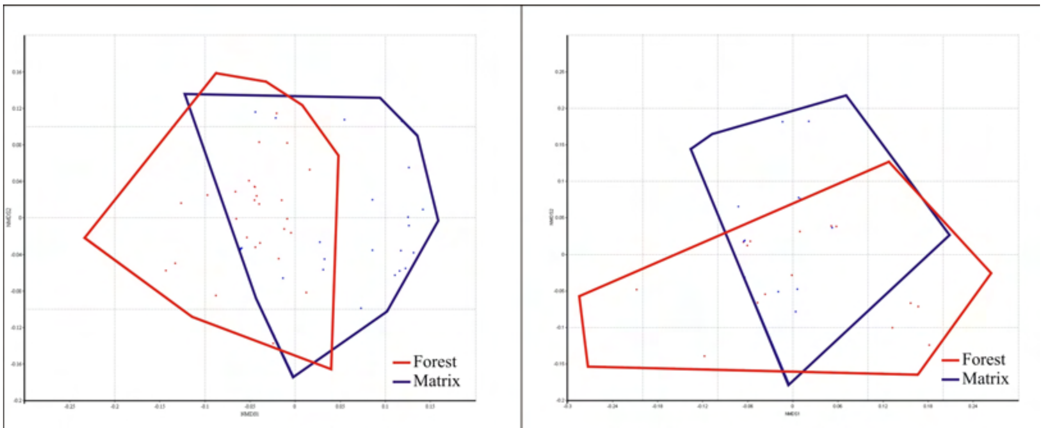
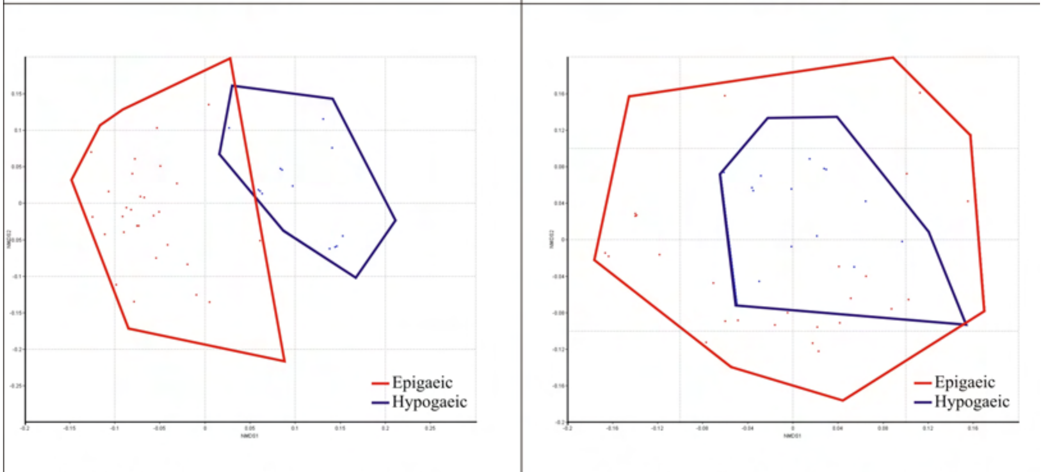


Figure 8: Relationship between environmental variables and habitat type. Significant results were found at (b) CEC *vs.* habitat and (c) Fe *vs.* habitat. Despite non-significant results, it is possible to notice that the trend in all cases corroborate the ant diversity results found.



Composition of epigaeic ants between landscape compartments

Composition of hypogaeic ants between landscape compartments



Composition of forest ants between microhabitats

Composition of matrix ants between microhabitats

Figure 9: NMDS results. Groups were formed using the Raup-Crick index. (a) is the difference between forest and matrix for epigaeic ants ($p<0.001$); (b) is the difference between forest and matrix for hypogaeic ants ($p=0.03$); (c) is the difference between epi- and hypogaeic ants in forest habitats ($p<0.001$) and (d) shows a lack of difference between epi- and hypogaeic ants in matrix habitats ($p=0.10$).

Table 3: Table of ant species recorded at this survey. Bold names are subfamilies. Numbers are frequencies in each area (based on presence/absence in traps.

	Epigaeic					Hypogaeic			
Species	Forest	Coffee	Pasture	*Eucalyptus*		Forest	Coffee	Pasture	*Eucalyptus*
Cerapachinae									
Achanthostichus laticornis Forel, 1908					2				
Dolichoderinae									
Linepithema sp.A	1	2	1						
Linepithema sp.B		1							
Tapinoma sp.A	3								
Tapinoma sp.B	1								
Ecitoninae									
Labidus sp.A	1		8		3	1	1	1	
Labidus sp.B	1		1		5			1	
Neivamyrmex sp.A						1			
Nomamyrmex sp.A	1				4				
Ectatomminae									
Ectatomma sp.A	7	1	4						
Ectatomma sp.B	3								
Gnamptogenys sp.A	12		2	3	3				
Gnamptogenys sp.B	5								
Gnamptogenys sp.C					1				

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Table 3: Continuation of Table 3

	Epigaeic					Hypogaeic			
Species	Forest	Coffee	Pasture	*Eucalyptus*		Forest	Coffee	Pasture	*Eucalyptus*
Formicinae									
Brachymyrmex sp.A			1						
Brachymyrmex sp.B		1							
Camponotus crassus Mayr, 1862	2			3					
Camponotus rufipes (Mayr,1775)	2	4							
Camponotus sp.A	1	5				1			
Camponotus sp.B	3	1		3					
Camponotus sp.C	6			2					
Camponotus sp.D	2								
Camponotus sp.E	1								
Camponotus sp.F	1		1						
Myrmicinae									
Apterostigma sp.A	1								
Atta cf. *laevigata* (Smith), 1858	2		9				2		
Carebara sp.A					3				
Crematogaster sp.A			4	1					
Crematogaster sp.B		1	1						
Cyphomyrmex sp.A	1				1				
Cyphomyrmex sp.B	2		1		1				
Cyphomyrmex sp.C			1						
Hylomyrma sp.A	1				1				

Continues at next page

Table 3: Continuation of Table 3

	Epigaeic					Hypogaeic			
Species	Forest	Coffee	Pasture	*Eucalyptus*		Forest	Coffee	Pasture	*Eucalyptus*
Megalomyrmex sp.A	1				1				
Monomorium sp.1						1			
Mycocepurus sp.A			1						
Mycocepurus sp.B			2						
Pheidole sp.A	1	1	3		1	1			
Pheidole sp.B	4	3	7	1		1	2		
Pheidole sp.C	7	4	9	1	1	1	1		
Pheidole sp.D	1	1	1						
Pheidole sp.E	4								
Pheidole sp.F	1	1	2		1				
Pheidole sp.G	2								
Pheidole sp.H		1							
Pheidole sp.I	1	1							
Pheidole sp.J	1	2				3	2		
Pheidole sp.K	1								
Pheidole sp.L		1			1			1	
Pheidole sp.M		1	1						
Rogeria sp.A					1				
Sericomyrmex sp.A	1								
Sericomyrmex sp.B	1								
Solenopsis sp.A	3	2	2	1	3	1	1	1	

Continues at next page

Table 3: Continuation of Table 3

	Epigaeic					Hypogaeic			
Species	Forest	Coffee	Pasture	*Eucalyptus*		Forest	Coffee	Pasture	*Eucalyptus*
Solenopsis sp.B	1	1			1	1	1	1	
Solenopsis sp.C	1					1	1	1	
Solenopsis sp.D		1	1				3		
Strumigenys sp.A				1					
Trachymyrmex sp.A	2				1				
Trachymyrmex sp.B			1						
Wasmannia sp.a	4								
Ponerinae									
Hypoponera sp.A	1				1				
Hypoponera sp.B	2								
Leptogenys sp.A	1								
Odontomachus chelifer (Latreille),1802	2								
Odontomachus sp.B	1								
Pachycondyla striata Smith, 1858	22		3	7					
Pachycondyla sp.B	1	1		1	1				
Pseudomyrmecinae									
Pseudomyrmex sp.A			1						

4 Discussion

4.1 Ant fauna

The number of species sampled in this study (69) is slightly smaller than previous studies at the same region (Sobrinho *et al.*, 2003; Ribas *et al.*, 2005; Sobrinho & Schoereder, 2007), that sampled from 100 to 119 ant species, as they employed a greater sampling effort. Our sampling is congruent with the recent findings of Schmidt (2008), that sampled 77 ant species in eight areas, with equivalent sampling effort, though his survey also sampled the arboreal microhabitat. Hence, we have no reason to believe that there are any sampling artefact in our survey. Moreover, we expanded our sampling to include the still neglected hypogaeic microhabitats, which have been poorly documented in fragmentation and ant ecology surveys (Brandão *et al.*, 2008; Rabeling *et al.*, 2008). The sampling of this stratum revealed hidden results about fragmentation.

Since the development of the hypogaeic pitfall trap by Schmidt & Solar (2010), some subterranean ant species once considered to be rare have now been commonly sampled. This is the case of *A. laticornis*, which was thought to be a rare ant prior to the use of this trap, has now been sampled in all surveys, though with low abundance. It confirms the assertion of Brandão *et al.* (2008), who called attention to the use of inappropriate criteria to determine rarity in ant species. Interestingly, *A. laticornis* were sampled in Viçosa only in forest undergrounds, calling for a potential bioindicator property of this ant species. Some other traits of this species are also suitable for its using as a bioindicator, like conspicuous morphology to the naked eye, fidelity to forest habitats and easy sampling (since the development of the hypogaeic trap).

We also highlight the sampling of *Leptogenys* sp.a. Our register is the second time that this ant species is recorded in Viçosa region, the first being in Schmidt (2008). Moreover, it was sampled at the same remnant as ours. This remnant, is the oldest and supposedly has not been clear cut. This patch is prone to harbour some species that do not have elevated dispersion abilities through the matrix, and may be eliminated from other patches. Even with exhaustive sampling at Viçosa region, this ant genus was only recorded twice and in this remnant (Soares *et al.*, 2001; Sobrinho *et al.*, 2003; Schoereder *et al.*, 2004; Ribas *et al.*, 2005; Sobrinho & Schoereder, 2007; Schmidt, 2008; Paolucci *et al.*, 2010). Hence, *Leptogenys* sp.a can be a good bioindicator of conservation status of forest patches, indicating the healthiness of a given remnant and the success of forest recovery. Rare sampling and inconspicuous morphology to the naked eye remain as drawbacks to its use as a good bioindicator.

Despite fragmentation and other human-induced impacts can limit distribution of some species, others are favoured when matrices are formed (DeSouza *et al.*, 2001). Above, we discussed the case of some species negatively affected by forest fragmentation, but for the same region, Schoereder *et al.* (2003) described the occurrence of *Camponotus genatus* Santischi, 1922. This ant species was formerly recorded in Cerrado environments, but is now found in matrices and forest gaps in the Viçosa region, due to transformation of previous forest habitats into open fields. In our data, the higher abundance of *Atta laevigata* in matrices (mainly pastures) are in agreement with Laurance (2008), that reports a higher incidence of leaf-cutter ants in human modified lands.

4.2 Why do more ants prefer forest fragments?

We found that ant species diversity responded to forest fragmentation, but this response was only detectable at higher scales than local (α). At the fragment scale (i.e. α, β and γ diversity at the level of each fragment/matrix), pastures and *Eucalyptus* crops presented smaller β diversity and lower total species richness (γ_{frag}) than coffee crops and forest remnants. Additionally, the majority of responses related to species richness were found in epigaeic microhabitat, confirming our hypotheses that this stratum is more sensitive to habitat change. Environmental variables responded to fragmentation in epigaeics, but did not present variation below-ground. Therefore, undergrounds should be more buffered from above soil modifications, since soil acts as a stabilizer, retarding effects of changes (Rabeling *et al.*, 2008). Hence, we observe two apparently antagonistic situations, given the same environmental conditions and impacts. However, above- and below-ground communities are actually distinct in time, as below-ground communities have delayed response compared to above-ground. Given time is an important variable to responses in soil level (Bardgett *et al.*, 2005) and the buffering capacity of soils, a delay is expected in communities protected by low soil variation (Resende *et al.*, 2007; Rabeling *et al.*, 2008).

The coffee crop containing as much species diversity as forest patches seems to be an odd result, but it can be justified by the fact that explanatory variables show the same trends in both forest remnants and the coffee crop, demonstrating that the latter can be seen as a large-pored filter matrix (Gascon *et al.*, 1999). Moreover, this coffee crop is inserted between two well conserved fragments, possibly protecting this crop from matrix effects, enabling species to either cross or live within the matrix.

On the landscape scale (i.e. forest and matrix habitats summed), estimated species richness was higher in forest remnants than in matrices combined. This result confirms our assumption and, moreover confirms that despite heterogeneous matrices (coffee, pasture and *Eucalyptus*), forest remnants can harbour more ant species. It shows that it is not only simplification caused by fragmentation that is responsible for species loss (Sobrinho & Schoereder, 2007), but also the substitution of original conditions and original habitat is much more important for forest species, that cannot live in matrices. Still, despite serving as a filter rather than a barrier, matrix remains an unsuitable habitat, incapable of sustaining biodiversity in comparison to forest habitats. This result calls attention to the need to preserve and recover forest habitats and not only create corridors through matrix.

Results on both scales, fragment and landscape, indicate that β diversity plays an important role in the higher species richness in forest fragments. There is an evidence that microhabitat variation found in forest remnants is very important in maintaining ant species diversity (Tilman & Pacala, 1993). The same explanation may holds true for many other taxa depending on specific resources, which in turn vary throughout the habitat, allowing more species to co-exist in a given habitat due to preferences for specific condition or due competition avoidance (Ribas & Schoereder, 2002).

Regarding environmental variables, SOM presented a unimodal relationship with hypogaeic α_{frag} diversity. α_{frag} not responding to fragmentation is explained by the absence of variation in SOM among fragments and matrices. SOM can be used as direct food resource for detritivorous ants (Blüthgen & Feldhaar, 2010), as well as an indirect resource, since many ant preys (as termites) feed on SOM (Jouquet *et al.*, 2004). The majority of ant taxa sampled in forest undergrounds are predatory ants, being indirectly affected by prey availability. Nevertheless, why does ant species richness (α_{frag}) begin to decrease above certain level of SOM? It can be explained by the theory of heterogeneity *versus* productivity, as SOM can be a good proxy of primary productivity. Locals with low productivity ($\downarrow$ SOM) are similarly resource-poor as well as locals with high productivity ($\uparrow$ SOM) are similarly resource-rich and at both cases, we find homogeneous places. On the other hand, locals with intermediate productivity are composed of micro-patches with elevated productivity as well as micro-patches with debilitate productivity. Under this scenario, following Tilman's competition model, intermediate resource will be the place with higher species diversity, as they can maintain more species due to higherheterogeneity (Tilman & Pacala, 1993).

The positive relationship between CEC and epigaeic γ_{frag} diversity seems to explain the higher diversity found in forest remnants and coffee crops, since both habitats presented higher levels of CEC when compared to pastures and *Eucalyptus* crops. Higher CEC soils are able to grow and sustain more plant and microorganism diversity which are both direct or indirect resources and can represent conditions to ant species. For example, Ribas *et al.* (2003) found that tree species richness is positively correlated with ant species richness in Brazilian savannah. In coffee crops it is common to use soil correctors and agricultural inputs, which can improve CEC conditions, being indirectly responsible to increase of ant diversity in this habitat.

Surprisingly, β_{frag} diversity was negatively affected by Fe. However, similar results were found by Murphy *et al.* (2003) for aquatic plant species richness. Elevations in redox potential are prone to cause elevation in Fe^{+2} concentrations and, under this condition, Fe presents elevated toxicity. In terrestrial environments, high Fe concentrations are associated with micro-wetting locations, which can be caused by soil compression, impairing soil drainage. Elevated Fe concentrations are not normally found in well drained soils, being normally found in swamps. Moreover, Fe was higher in pastures and *Eucalyptus* and lower in forest and pastures, being a potential predictive variable for our assumption that matrices have fewer species than forests. To our knowledge and after an exhaustive research at the ISI Web of Knowledge, this is the first record of the effects of Fe in terrestrial ecosystems.

On the other hand, K presented significant positive influence on β_{frag} and γ_{frag} in HP. Despite K not varying with fragmentation, it is interesting to note that ants are responding to this nutrient. K is associated with osmotic regulation in insects (Klowden, 2007). Some insects are highly dependent on K to maintain very alkaline pH (up to 12) in mid- and hind-gut, as do termites (reviewed by Sarcinelli *et al.* 2009). In ants, this nutrient may be important in osmotic regulation as well as in synaptic and neuronal transmissions (Klowden, 2007). Also, this study presents the first record of effects of K in terrestrial ecosystems.

Granulometry of soil is a condition known to restrict species distributions. It is widely known for termites (Jouquet *et al.*, 2002, 2004; Abe *et al.*, 2009) that clay-rich soils favour the establishment of termite mounds. Conversely, it is known that some ant species such as *Mycetophylax simplex* Emery, 1888 and *Atta robusta* Borgmeier, 1939 are known to be endemic of *restinga* environments that are specially sandy (Teixeira *et al.*, 2004; Klingenberg & Brandão, 2009). Nevertheless, sandy soils are poorer in organic matter and, at the same time need to spend more of the same resources to stabilisation of nest walls. Accordingly to this assumption, we found that the soil sand percentage had negative effect on both β_{frag} and γ_{frag} diversities. We suggest that this higher sand percentage, associated with limited organic matter, is prone to imposing limitations on ant diversity. Interestingly, we found that %Sand is higher (despite not significantly) in the environments with lower species richness, which can reinforce the idea of a causal explanation. Exposed soils (i.e. without vegetation cover) are prone to clay loss, as rain water can hit with higher intensity the soil, washing clays and concentrating sand (Resende *et al.*, 2007). This is confirmed by the absence of this effect on undergrounds, that are protected by upper soil layers. Both pasture and *Eucalyptus* suffer from this effect. Pastures are obvious, since they are open fields, directly affected by rainfall. *Eucalyptus* crops are constantly cut and this area was pasture in the last few years. This characteristic is common among crops, since after being exhausted as pastures, farmers normally change the land use to resistant crops such as *Eucalyptus* and *Pinus*. The coffee crop sampled is located in between two forest fragments, which can protect the soil and avoid the damages caused by rain.

Similar results were found in a higher ecological scale, that we called the landscape scale, in which forest harbour more species than matrices. At this scale, we were not able to test for environmental explanatory variables, however, we think that the same group of resources and conditions are varying at this scale. These alterations caused by fragmentation on landscape structure and soil conditions are capable of limiting species distribution and establishment. Andersen (2008) had shown that the ability to establish in a new environment is a determinant of the species richness and composition of a given place.

When analysing species composition, all groups presented high stress values, which requires much care when looking for plots resulting from these analyses. Despite of it, we found many significant differences. We found that matrices keep a different sub-group of species, and that these species are not potential colonizers to the fragments. Most importantly, it indicates that ant species that come from fragments not usually establish at matrices, not being ready to re-establish populations in fragments where these species were lost. We also found that hypogaeic species suffered more in relation to species composition, since we found that hypogaeic ant species are just a subsample of epigaeic ants in matrices. On the other hand, in forest fragments, hypogaeic ants are composed of a very distinct group of ants. Still, the restricted occurrence of *A. laticornis* and *Carebara* sp.a in forest undergrounds (Schmidt, 2008; Schmidt & Solar, 2010) indicates that this ant genera became restricted after fragmentation. The extreme example is the ant *Leptogenys* sp.a, which is restricted to only one fragment (Schmidt, 2008). This absence of response in matrix habitats indicates that litter comprises an important stratum of habitat to hypogaeic ants. When it is either completely removed (e.g. pasture and coffee) or substituted for homogeneous litter (e.g. *Eucalyptus*), it directly affects the hypogaeic ant community, that is probably dependent on other micro-Arthropoda and nesting resources available only in the forest litter. Hence, fragmentation affects species composition in both habitats, and affects the distribution of ant diversity in the landscape. Another important assertion is that, in many matrices, the arboreal stratum is completely removed, and this ant group goes locally extinct immediately.

SIMPER results shown that relatively common ant species were responsible for group separation. *Camponotus rufipes* and *Pachycondyla striata* were the two species that had higher contribution to separate forest and matrix in analyses, when considering epigaeic microhabitat. These ant species are very common in all surveys in this region (Soares *et al.*, 2001; Sobrinho *et al.*, 2003; Schoereder *et al.*, 2004; Ribas *et al.*, 2005; Sobrinho & Schoereder, 2007; Schmidt, 2008; Paolucci *et al.*, 2010), however they varied in frequency, being much more common inside forest fragments, compared to matrices. Hence, despite both species occurring in fragments and matrices, it is important to consider the frequency in determining the effect. At the hypogaeic microhabitat, forest/matrix separation was more difficult to determine, as can be seen by the higher stress value. This difficulty was due mainly to the low number of species and low species frequency, both common of hypogaeic microhabitats. *Rogeria* sp.a was the species with the highest influence in group separation, followed by two other species that were more frequent in matrix, *Pheidole* sp.j and *Labidus* sp.a.

Differences between epi-/hypogaeic ants were analysed only in forest *via* SIMPER, since in matrix these groups did not differ. In this case, groups are much more separated and species that were responsible for this separation occurred preferentially in one microhabitat, either epi- or hypogaeic. *P. striata* and *C. rufipes* were the species with highest contributions and both species were sampled only in epigaeic traps. This result was expected, as they are large ants that nest on upper soil layers, normally having most of the nest emerging from soil. Moreover, these ants did not forage underneath soil, normally being found walking above soil.

5 Conclusions

Forest fragmentation and consequent human modified landscapes are affecting ecological communities in many ways. They affect species richness, as well as species composition, being factors capable of inducing and increasing disturbances in matrices and juxtaposed forest fragments (Laurance, 2008).

In this study, we demonstrated that forest fragmentation and habitat conversion is capable of inducing biodiversity loss, acting as either primary or secondary effect by presenting strong support to the fact that forest fragmentation is affecting soil, landscape, conditions and resources. These effects are playing a strong role in secondary effects of species loss (Sobrinho *et al.*, 2003). Vegetation clearance represents the main primary effect of forest fragmentation causing destruction of habitats and separation of previous joint communities. Secondary effects begins to play a role on species loss in fragmented landscapes ranging from genetic constraints to increased competition inside the fragments, that now are now unable to harbour as many species in comparison to previous conditions.

Moreover, we demonstrated the importance of considering the landscape of having many compartments (i.e. ecological scales). By demonstrating that different responses can arise from the different scales, we are able to discuss which factors are more important in determining species diversity. It is also important of considering explanatory hypotheses. This information enables to detect possible causes of the impact and provide information about why organisms are suffering from the impact.

We have shown the importance of analysing species composition based on species frequencies, as it gives information about common species that may be important to assess the healthiness of a given fragment. However, we cannot discount information regarding biology of specific groups, and some few species may indicate much about conservation status and history of land use.

Despite the great number of studies considering fragmentation, it is still unclear why it affects species richness. Studies now have to assess the direct causes of species loss, as well as clarify how this loss reflects on environment. Besides, it is urgent to understand how ecosystem services delivered by biodiversity are affected by human activities, as it can affect human beings. Studies considering the effect of forest fragmentation and consequent species loss over ecosystem function and services are then desired.

6 References

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