TATHIANA GUERRA SOBRINHO

RESPOSTAS DA COMUNIDADE DE FORMIGAS À FRAGMENTAÇÃO DE HABITATS

Tese apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Entomologia, para do título de "Doctor Scientiae".

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APROVADA: 03 de fevereiro de 2005

Prof. Júlio Neil Cassa Louzada	Prof. Frederico Santos Lopes
Prof. Og Francisco Fonseca de Souza (Co-orientador)	Prof. Carlos Frankl Sperber (Co-orientador)

Prof. José Henrique Schoereder
(Orientador)

Dedicatória

Dedico este trabalho à Fátima Guerra, minha mãe.

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RESUMO

SOBRINHO, Tathiana Guerra. D.Sc., Universidade Federal de Viçosa, fevereiro de 2005. **Respostas da comunidade de formigas à fragmentação de habitats.** Orientador: José Henrique Schoereder. Co-orientadores: Carlos Frankl Sperber e Og Francisco Fonseca de Souza.

A fragmentação de habitats tem sido apontada como uma das principais causas de alterações na riqueza, abundância e composição de espécies em ambientes tropicais. O objetivo da tese foi testar hipóteses relativas a alterações no número e composição de espécies de formigas devido a mecanismos biológicos gerados pela fragmentação florestal. Os principais testados foram: invasão por espécies da matriz, colonização e extinção, efeitos de borda e de forma. Os dados do primeiro e segundo artigo foram coletados, respectivamente em17 e 18 fragmentos na região de Viçosa com áreas variando de 3 a 300 ha e em dez pastagens ao redor destes. As coletas nos fragmentos foram realizadas durante três anos consecutivos, o que permitiu o estudo das taxas de extinção local e colonização, enquanto as coletas na matriz foram realizadas apenas em um dos três anos. Foram usadas armadilhas do tipo ‘pitfall’ com diferentes iscas e as coletas foram feitas com três diferentes níveis de amostragem de acordo com a área dos fragmentos. Para a realização do terceiro artigo foram feitas coletas em dez fragmentos com áreas variando entre 3 e 100 ha aproximadamente, nos quais foram feitas dez amostras de 1m^2 de serapilheira na borda e dez no centro. A serapilheira foi peneirada e colocada num extrator de Winkler para a extração das formigas. A área e o isolamento dos fragmentos foram determinados a partir de fotos aéreas. Quando foi usado esforço amostral proporcional observou-se aumento do número de espécies com aumento da área dos remanescentes. Além disso, fragmentos menores mostraram-se mais homogêneos em termos de composição de espécies do que os maiores e potencialmente mais sujeitos à invasão por espécies de matriz, uma vez que apresentaram, proporcionalmente, um maior número de espécies em comum com a matriz que os grandes. Embora o grau de isolamento não tenha influenciado na taxa de colonização, as taxas de extinção local foram maiores nos fragmentos menores, padrão que pode ser explicado pela menor densidade populacional apresentada pelas formigas nestes remanescentes. Ainda que as taxas de colonização não tenham variado, formigas generalistas colonizam mais freqüentemente os fragmentos pequenos, enquanto formigas especialistas de florestas colonizam mais os grandes. Também há diferenças em relação às taxas de extinção, sendo que formigas generalistas apresentam uma maior extinção dentro dos fragmentos que as especialistas, independentemente da área. Há mais espécies de formigas no centro do que na borda dos fragmentos e não se observou aumento do número de espécies à medida que se distancia da borda. Conclui-se, portanto, que a fragmentação causa alterações na composição de espécies de formigas e que estas alterações são mais pronunciadas em fragmentos pequenos, os quais sustentam populações menores e estão mais sujeitos à invasão e a efeitos de borda e de forma, uma vez que apresentam uma maior borda relativa.

ABSTRACT

SOBRINHO, Tathiana Guerra. D.Sc., Universidade Federal de Viçosa, February 2005. **Response of ant community to habitat fragmentation.** Adviser: José Henrique Schoereder. Co-advisers: Carlos Frankl Sperber and Og Francisco Fonseca de Souza.

Habitat fragmentation has been pointed as a main cause of changes of species richness, abundance and composition in tropical environments. This thesis aimed to test hypotheses relative to alterations of ant species richness and composition generated by forest fragmentation. The mechanisms tested were: invasion by matrix species, colonization and extinction, and edge and shape effects. Data from the first and second paper presented were collected in 17 ad 18 remnants, respectively, in the region of Viçosa, varying from 3 to 300 ha and in ten pastures around the remnants. Sampling have been carried out during three consecutive years, allowing the study of the local extinction and colonization rates, whereas sampling in the matrix occurred in only one of these three years. Baited pitfall traps were used and the number of samples in the remnants was proportional to their areas. Sampling of the third paper of this thesis were carried out in ten remnants with areas ranging from 3 to 100 ha, in which ten 1m^2 samples of litter were collected in the edge of the remnants, and other ten in the center of the remnants. Litter samples were sifted and put into a Winkler extractor, to remove the ants. Remnant areas and isolation were determined using aerial photographs. Proportional sampling showed an increase of species richness with increase of remnant area. Furthermore, smaller remnants were more homogeneous in species composition than larger remnants, and potentially more invasion-prone by matrix species, because they presented proportionally more species in common with the matrix than larger remnants. Even though the degree of isolation has not influenced the colonization rate, the local extinction rates were higher in the smaller remnants, pattern that may be explained by the smaller ant population density in these remnants. Although the colonization rates did not vary with remnant area, generalist ants colonized more frequently the smaller remnants, whereas specialist ants colonized more the larger remnants. There were also differences in relation to the extinction rates within remnants, and generalist ants presented higher extinction in the forests, independently of their areas. There were higher species richness in the center than remnants edge, and there were no relationship between species richness and the distance from the forest edge. Concluding, forest fragmentation caused alterations on ant species composition and these changes are more pronounced in smaller remnants, which sustain smaller populations and are more prone to invasion and to edge and shape effects, because they present a higher relative edge.

INTRODUÇÃO GERAL

A fragmentação de habitats consiste na destruição de áreas contínuas e não perturbadas, subdividindo-as em fragmentos isolados (Lovejoy *et al.* 1986, DeSouza *et al.* 2002, Schoereder *et al.* 2003), intercalados por áreas de matriz antrópica (pastagens, culturas agrícolas, entre outras) (Turner 1996, Didham 1997). Nas últimas décadas, a fragmentação tem sido apontada como uma das principais causas de perda de biodiversidade em ecossistemas tropicais (Bierregaard Jr. *et al.* 1992, Didham *et al.*1998, Majer *et al.* 1997, Vasconcelos & Delabie 2000) e por isso tem sido um assunto bastante estudado.

Freqüentemente, tem sido relatada uma diminuição do número de espécies de diversos *taxa* com a diminuição da área dos fragmentos (DeSouza & Brown 1994, Turner 1996, Vasconcelos 1999, Carvalho & Vasconcelos 1999). Esse padrão de diminuição do número de espécies é muitas vezes confundido com a relação espécie-área, que não considera os processos que ocorrem em uma paisagem fragmentada (Schoereder *et al.* 2003). Essa diminuição no número de espécies pode ser explicada por simples efeito de amostragem ou de perda de habitat (Preston 1962, DeSouza *et al.* 2002). Isso significa que a porção de área que foi isolada devido à fragmentação possui somente uma parcela do número total de espécies ou uma menor heterogeneidade de habitats em relação à área contínua original (Suarez *et al.* 1998).

Entretanto, outros mecanismos, gerados pela fragmentação, podem causar alterações na riqueza e composição de espécies, como por exemplo, diminuição no tamanho das populações, isolamento dos fragmentos, invasão de espécies dos novos ambientes criados (áreas de matriz), efeitos de borda e de forma (DeSouza *et al.* 2002). Estes mecanismos podem agir tanto em escala local, ocorrendo dentro dos remanescentes, quanto regional, alterando as dinâmicas de colonização e extinção de espécies nos fragmentos.

A matriz antrópica na qual os fragmentos se encontram pode exercer uma forte influência sobre as comunidades dos mesmos. Espécies da matriz atrópica tendem a ser mais generalistas e tolerantes a efeitos de borda, podendo invadir os fragmentos e contribuir para alterações na composição de espécies (Gascon *et al.* 1999). Entretanto, essa influência da matriz deve variar de acordo com algumas características dos remanescentes, como por exemplo, área e grau de isolamento. Quanto maior o grau de isolamento menor será o número de imigrantes vindos de outros fragmentos e, conseqüentemente, menor a recolonização por espécies extintas localmente ("efeito resgate") (DeSouza *et al.* 2002). Portanto, fragmentos mais isolados tendem a ser mais colonizados por espécies da matriz do que por espécies de outros fragmentos, o que pode levar a alterações na composição de espécies nos mesmos.

O efeito de borda é conseqüência da transformação de áreas anteriormente contínuas em borda e do aumento da proximidade do centro do fragmento até seu exterior (Murcia 1995, Zheng & Chen 2000, DeSouza *et al.* 2002), levando, conseqüentemente, a um aumento na proporção de borda exposta a outros habitats (Kapos *et al.*1997). A criação de borda acarreta mudanças microclimáticas na porção que vai da margem do fragmento até mais ou menos 100m em direção ao seu interior (Lovejoy *et al.* 1986, Laurance & Yensen 1991, Murcia 1995, Laurance 1997, Turton & Freiburger 1997), bem como altera a comunidade de plantas (Laurance & Yensen 1991, Kapos *et al.* 1993, Laurance *et al.* 1998). Essas mudanças no microclima e na vegetação na borda podem provocar importantes alterações nas comunidades de diversos taxa de animais, como pássaros, mamíferos e invertebrados em geral (Lovejoy *et al.* 1986, Fowler *et al.* 1993, Didham 1997, Brown & Hutchings 1997, Didham *et al.* 1998).

Além disso, características do fragmento como forma e isolamento devem ser consideradas, uma vez que as mesmas interagem de forma a determinar a intensidade dos efeitos de borda (Turton & Freiburger 1997). Quanto à forma, fragmentos estreitos tendem a ser mais afetados por efeito de borda do que aqueles que apresentam uma forma circular ou arredondada, pois apresentam uma maior borda relativa. A complexidade de forma dos fragmentos deve ser avaliada como um mecanismo potencialmente gerador de alterações nas comunidades residentes em habitats fragmentados.

Muitas vezes torna-se complicado isolar e testar os diversos mecanismos que atuam sobre as comunidades de áreas fragmentadas, já que estes estão interligados. Portanto, a falta de uma metodologia que consiga isolar os efeitos da fragmentação acaba confundindo e comprometendo os resultados dos trabalhos. Além disso, a grande maioria dos trabalhos investiga apenas se há alterações no número de espécies em decorrência da invasão, do isolamento, e dos efeitos de borda e de forma sem se preocupar em estudar alterações na composição de espécies, bem como a maneira como estes mecanismos biológicos causam essas alterações. Dessa forma, torna-se necessário um estudo mais detalhado de como as variáveis geradas pela fragmentação influenciam a riqueza e composição de espécies em fragmentos de diferentes áreas. Do ponto de vista prático, o conhecimento dos principais efeitos da fragmentação de habitats sobre as comunidades é importante para que soluções sejam apontadas e para que políticas de conservação e manejo sejam implantadas de forma correta.

Nesta tese procurou-se conhecer o efeito de alguns dos processos gerados pela fragmentação sobre as comunidades de formigas em um ambiente fragmentado. A escolha da comunidade de formigas para o desenvolvimento do trabalho é no mínimo coerente, uma vez que as mesmas são diversas, abundantes, facilmente coletáveis e de identificação relativamente fácil. Além disso, elas desempenham vários papéis ecológicos no ambiente (Wilson 2000) e algumas espécies afetam a composição e abundância de outros insetos e até mesmo de algumas plantas (Hölldobler & Wilson 1990).

Os objetivos desta tese foram: (i) testar o pressuposto de que a fragmentação de habitats altera a composição de espécies de formigas, verificando se a proporção de espécies em comum com a matriz aumenta com a diminuição da área dos fragmentos; (ii) testar as taxas de colonização e extinção local em relação à área dos fragmentos; (iii) testar a hipótese de que fragmentos menores são mais invadidos pelas espécies de matriz do que os grandes e que existe uma extinção maior de espécies generalistas em relação às especialistas de florestas no interior dos fragmentos; (iv) testar o pressuposto de que o número de espécies de formiga aumenta à medida que diminui a distância da borda dos fragmetos; (v) testar a hipótese que efeitos de borda e de forma alteram a riqueza e composição de espécies de formigas.

Esta tese foi dividida em três artigos científicos, escritos em inglês. O primeiro artigo foi publicado na revista *Sociobiology*, o segundo na revista *Austral Ecology* e o terceiro foi escrito nas normas da revista *Biodiversity and Conservation*, para a qual o mesmo foi submetido. Os dois primeiros artigos foram reproduzidos da forma original como se encontram nos respectivas revistas.

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PRIMEIRO ARTIGO

Does Fragmentation Alter Species Composition in Ant Communities (Hymenoptera: Formicidae)?

by

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ABSTRACT

We tested if fragmentation alters ant species (Hymenoptera: Formicidae) composition, through the similarity of species composition within the remnants with matrix habitat. We sampled 17 tropical forest remnants and adjoined grassland matrix. Species composition was altered by fragmentation, because although total species richness increased with remnant area, the proportion of generalist ant species (occurring both in the matrix and in the forest) decreased. Four mechanisms may explain the above patterns: (i) fragmentation changed conditions inside the remnants, favoring species formerly only present in forest gaps; (ii) isolation effects changed the pool of species able to colonize different remnants; (iii) fragmentation increased invasion by generalist species, through the increase in perimeter/area ratio and conditions more similar to matrix habitats; and (iv) area reduction is higher than perimeter reduction. Smaller remnants lose more species than larger ones and receive less species from the matrix than large remnants, which explains the patterns found.

Keywords: conservation, deforestation, Formicidae, invasion, landscape ecology, species composition.

INTRODUCTION

Habitat fragmentation results from the subdivision of continuous habitat into one or more isolated and smaller remnants (Lovejoy *et al.* 1986, Murcia 1995, Bender, Contreras & Fahrig 1998, DeSouza *et al.* 2001), surrounded by matrix (pastures, monocultures, etc.) of different habitat (Offerman *et al.* 1995, Turner 1996, Gascon & Lovejoy 1998). Fragmentation is considered a main process responsible for the loss of biodiversity in tropical ecosystems (Turner 1996, Turner & Corlett 1996, Didham *et al.* 1996, Majer, Delabie & McKenzie 1997, Didham *et*

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al. 1998a, Vasconcelos 1999, Vasconcelos & Delabie 2000). The positive relationship between remnant area and species richness has been frequently documented (Rosenzweig 1995, Grashof-Bokdam 1997, Carvalho & Vasconcelos 1999), and this relationship is considered one of the few "laws" in Ecology (Ricklefs & Lovette 1999).

Several studies have reported a decrease in species richness after fragmentation (DeSouza & Brown 1994, Vasconcelos 1999, Carvalho & Vasconcelos 1999, Wettstein & Schmid 1999). Such a decrease may be due to a sampling effect (Preston 1962) or to habitat loss (De Souza *et al.* 2001), i.e., the resulting remnant contains only a portion of the original species richness or a smaller structural heterogeneity in relation to the pristine habitat (Suarez, Bolger & Case 1998). These effects may be considered primary, because they occur soon after the fragmentation event. Nevertheless, several other mechanisms may lead to secondary local extinctions (Turner 1996, DeSouza *et al.* 2001), including demographic constraints (increase in endogamy, genetic drift, etc.) and environmental stochasticity (Davies & Margules 1998, Gascon & Lovejoy 1998, Suarez, Bolger & Case 1998, Ricklefs & Lovette 1999, DeSouza *et al.* 2001). Furthermore, population decrease may jeopardize positive interactions or the pressure of negative interactions (Davies & Margules 1998, DeSouza *et al.* 2001). Consequently, population loss and particularly the disappearing of key species may generate cascade effects, causing alterations in the dynamics of other populations, and further species loss in the community (Offerman *et al.* 1995, Fisher 1998, Suarez, Bolger & Case 1998, Fagan, Cantrel & Cosner 1999, Boswell, Britton & Franks 1998). Smaller remnants, hence, may have higher extinction rates, because they support small populations, which have already been observed in ant communities (Schoereder *et al.* unpublished data).

An important consequence of fragmentation is the shift of continuous habitat areas into edges, and subsequent decrease in the distance between remnant edge and center (DeSouza *et al.* 2001). Species richness may decrease along edges of forest remnants (Carvalho & Vasconcelos 1999), but for some species the edge may represent the favorable habitat, and edge creation may benefit these species (DeSouza *et al.* 2001). For example, some insects, such as ants, beetles and butterflies, are edge specialists (Majer, Delabie & McKenzie 1997, Brown & Hutchings 1997, Didham *et al.* 1998a, Shahabuddin & Terborgh 1999) and are positively affected by fragmentation. Other species avoid edges and, depending on remnant area and on the extension of edge effects, may become locally extinct (Didham *et al.* 1996, Didham *et al.* 1998a, Zheng & Chen 2000). In addition to causing changes in remnant species composition, edges can create a habitat that facilitates the entrance of invading species.

The matrix habitat the fragments are nested within may also exert a strong influence on the community dynamics in the habitat remnants. Specifically, species associated with the matrix may invade the fragments, altering their composition. Matrix species are usually more tolerant to remnant edges ('ecotones') than to interior habitats. Therefore, edge effects on these species are probably more significant in smaller remnants, because they have a higher perimeter/area ratio, or in remnants where the matrix vegetation is very dissimilar to the pristine community (Kapos *et al.* 1997, Gascon & Lovejoy 1998, Carvalho & Vasconcelos 1999, Gascon *et al.* 1999).

It is necessary to know not only the mechanisms generated by fragmentation that may lead to species richness loss, but also those altering species composition, such as those noticed by several authors (Didham 1997, Brown & Hutchings 1997, Davies & Margules 1998, Didham *et al.* 1998a, Didham *et al.* 1998b, Vasconcelos & Delabie 2000).

In this paper we tested the assumption that fragmentation alters ant species composition, increasing the proportion of matrix species in smaller remnants. We also put forward some hypotheses to explain the pattern and tested the hypothesis that such a change in species composition may result from the relationship between the remnant area and perimeter.

METHODS

Study area

The study was carried out in Viçosa, southeastern Brazil (20°45'S, 42°50'W). This region was covered by forests up to the last century, when an accelerated process of fragmentation has begun. The pristine forest was fragmented and intermingled with pastures and coffee plantations mainly in the 1930's and 1940's (Gomes 1975), and the remaining vegetation has been restricted to few islands, particularly in hilltops. From the 1960's onwards, the agriculture diminished in the region and several forest areas regenerated into secondary forests. Nowadays a mosaic of forest remnants forms the region with areas varying from three to 300 hectares, forming an ideal system to study the effects of fragmentation.

Sampling procedure

We chose 17 remnants, with areas ranging from ca. 3 ha to ca. 100 ha, to carry out the sampling procedure. We sampled the remnants during summer (February 1995), which is the rainy season in the region. We sampled the ants by pitfall traps, using human feces, carrion and decomposing fruit as baits. Pitfall traps consisted of plastic containers (diameter 19 cm, height 11 cm), with an inner recipient containing the bait, and were left in the field for 48 hours. Ants attracted by the bait fell into the pitfall, dying in a 5% detergent solution.

We set the pitfalls in groups of three, each one containing a bait type. We set the pitfalls within the groups two meters apart from each other, and the minimum distance among groups was 50 m, avoiding forest edges and gaps. We sampled the larger remnant (93 ha) using 24 pitfall groups, each of the four medium-sized remnants (30 ha, 39 ha, 46 ha and 61 ha) using 12 pitfall groups, and each of the 12 smaller remnants (ranging from 3.2 ha to 8.6 ha) using four pitfall groups. Sampling effort, therefore, was represented by three levels of sampling, depending on remnant area.

We also sampled ten locations in the pasture matrix surrounding the sampled remnants, using similar baited pitfall design. We set four groups of three pitfalls in each pasture.

We considered generalist ant species those found both in the pitfalls disposed in pasture and in the pitfalls disposed in the remnants. Although pasture species may occur only in matrix (matrix species) or also in the forest remnants, we considered only the latter as generalists because we are interested in the species that are effectively able to occur in the remnants. Forest species were those collected only in forest remnants.

We sorted, mounted and identified the ants to genera with the help of identification keys (Hölldobler & Wilson 1990, Bolton 1994). Whenever possible, we identified the ants to species level. When species identification was not possible, we sorted ants according to their external morphology. We deposited voucher specimens in the reference collection of the Community Ecology Lab of the Departamento de Biologia General of the Universidade Federal de Viçosa.

Statistical analyses

Several papers criticize the use of proportional sampling, i.e., a sampling design that uses sampling effort proportional to remnant area (Hill, Curran & Foody 1994), because it may introduce a sampling bias. Nevertheless, the effect of sampling effort may be removed using a model that includes such an effect (Schoereder *et al.* unpublished data). If, after the removal of sampling effect, a significant portion of deviance is still explained by remnant area, we accept the species-area relationship.

We started our analyses testing the species area relationship, using an analysis of covariance and ant species richness in each remnant as the response variable. The explanatory variables were the logarithm of remnant area, the three levels of sampling effort, and the interaction term. The complete model was fitted using Poisson errors (Crawley 2002) with significance being accessed by step-wise omission of nonsignificant terms, beginning from the maximal model, using the software R (Ihaka & Gentleman 1996). The complete model was submitted to residual analysis.

To test the assumption that fragmentation alters ant species composition, we used the proportion of generalist ant species in relation to the total ant species in each remnant as response variable. Because we do not know species composition of the pristine vegetation, we use remnant area as a surrogate of fragmentation effects. The explanatory variables were the logarithm of remnant area, the three levels of sampling effort, and the interaction term. We used an analysis of covariance, with binomial errors (Crawley 2002). We expected this proportion to decrease with area, showing that smaller remnants have species composition more similar to the matrix than larger ones.

If the above assumption was accepted, we tested the hypotheses causing species composition alteration, through analysis of covariance, using ant species richness as response variable. The explanatory variables were logarithm of remnant area, category of ants (generalist or forest species), and the interaction between these two variables. The complete model was fitted, using Poisson errors corrected for overdispersion (Crawley 2002), with significance being accessed by step-wise omission of nonsignificant terms, beginning from the maximal model. The complete model was submitted to residual analysis. We expected that the interaction term in the above model was significant, because each ant species category would increase differentially with remnant area. Therefore, forest and generalist ant species would respond differently to remnant area increase.

RESULTS

We collected 93 ant species in all remnants together and 49 ant species in the matrix, totaling 117 ant species distributed in seven subfamilies. From these species, we sampled 24 exclusively in the matrix, 68 only in the remnants and 25 were sampled in the two habitats (Table 1).

The total number of ant species increased with remnant area ($F_{1,15}$ = 408.30; $p<0.0001$; $r^2 = 0.97$; Fig. 1). Both sampling effort and the interaction between sampling effort and area were not significant.

The proportion of generalist species decreased with remnant area ($F_{1,15} = 19.41$; $p < 0.0001$; $r^2 = 0.70$; Fig. 2), according to our assumption.

Table 1. Species sampled in forest remnants and in matrix of grasslands in the region of Viçosa, MG, Brazil.

	Remnants	Matrix
Subfamily Cerapachyinae		
Sphinctomyrmex	X	
Subfamily Dolichoderinae		
Dolichoderus attelaboides	X	
Linepithema sp. 1	X	
Linepithema sp. 2	X	
Linepithema sp. 3	X	X
Linepithema sp. 4	X	
Linepithema sp. 5	X	
Subfamily Ecitoninae		
Labidus praedator	X	X
Nomamyrmex sp. 2	X	
Subfamily Formicinae		
Brachymyrmex sp. 1	X	
Brachymyrmex sp. 3	X	X
Brachymyrmex sp. 5	X	X
Brachymyrmex sp. 7	X	
Brachymyrmex sp. 8	X	
Brachymyrmex sp. 9	X	
Camponotus rufipes	X	X
Camponotus sp. 1	X	
Camponotus sp. 4	X	
Camponotus novogranadensis	X	X
Camponotus melanoticus	X	X
Camponotus sp. 8	X	
Camponotus sp. 9	X	
Camponotus sp. 10	X	
Camponotus sp. 11	X	
Camponotus sp. 13	X	
Camponotus sp. 14	X	
Camponotus sp. 16	X	
Camponotus sp. 19	X	
Camponotus sp. 21	X	
C. (Myrmobrachys) crassus		X
C. (Myrmaphaenus) sp.1		X
C. (Myrmaphaenus) sp.2		X
C. (Myrmaphaenus) sp.3		X
C. (Myrmaphaenus) leyoligi		X
Paratrechina sp.2		X
Mirmelachista	X	
Plagiolepis	X	

Table 1. (Cont.) Species sampled in forest remnants and in matrix of grasslands in the region of Viçosa, MG, Brazil.

	Remnants	Matrix
Subfamily Myrmicinae		
Acromyrmex niger	X	
Apterostigma jubatum	X	
Apterostigma sp.1		X
Atta sexdens rubropilosa	X	X
Cyphomyrmex transversus	X	X
Cyphomyrmex sp. 2	X	
Cyphomyrmex sp. 3	X	
Cyphomyrmex sp. 4	X	
Mycetarotes sp.2		X
Mycocepurus smith		X
Mycocepurus goeldi		X
Myrmicocrypta	X	
Trachymyrmex sp. 1	X	
Trachymyrmex sp. 2	X	
Trachymyrmex sp. 4		X
Wasmannia auropunctata	X	X
Wasmannia sp. 2	X	
Cephalotes atratus	X	
Cephalotes minutus		X
Procryptocerus marginatus	X	
Crematogaster sp. 2	X	X
Crematogaster sp. 5		X
Crematogaster sp. 6		X
Glamyromyrmex	X	
Gymnomyrmex	X	
Neostruma	X	
Strumigenys sp. 1	X	
Strumigenys sp. 2	X	
Cardiocondyla minutior		X
Cardiocondyla sp.1	X	
Hylomyrma balzani	X	
Hylomyrma reitteri	X	
Pheidole sp. 1	X	X
Pheidole sp. 2	X	X
Pheidole sp. 3	X	X
Pheidole sp. 4	X	X
Pheidole sp. 5	X	X
Pheidole sp. 6	X	X
Pheidole sp. 7		X
Pheidole sp. 8	X	X
Pheidole sp. 9	X	X
Pheidole sp. 10		X
Pheidole sp. 12	X	

Table 1. (Cont.) Species sampled in forest remnants and in matrix of grasslands in the region of Viçosa, MG, Brazil.

	Remnants	Matrix
Subfamily Myrmicinae (Cont.)		
Pheidole sp. 13	X	
Pheidole sp. 15	X	
Pheidole sp. 16	X	
Pheidole sp. 17	X	
Megalomyrmex goeldii	X	
Oxyepoecus reticulatus	X	
Solenopsis saevissima	X	X
Solenopsis sp. 2	X	
Solenopsis sp. 3	X	
Solenopsis sp. 4	X	
Solenopsis sp. 5	X	
Pogonomyrmex sp.1		X
Subfamília Ponerinae		
Ectatomma bruneum		X
Ectatomma edentatum	X	X
Ectatomma permagnum	X	X
Gnamptogenys horni	X	
Gnamptogenys striatula	X	
Heteroponera dentinodis	X	
Anochetus sp.1	X	
Anochetus sp.2		X
Hypoponera sp. 2	X	
Hypoponera sp. 3	X	
Hypoponera sp. 7	X	
Odontomachus chelifer	X	X
Odontomachus minutus	X	
Odontomachus haematodus		X
Pachycondyla striata	X	X
Pachycondyla metanotalis	X	
Pachycondyla magnifica	X	
Pachycondyla harpax	X	X
Pachycondyla lenis	X	
Pachycondyla obscuricanis		X
Pachycondyla marginata		X
Pachycondyla sp. 1	X	
Subfamily Pseudomyrmecinae		
Pseudomyrmex sp. 1	X	
Pseudomyrmex sp. 2	X	
Pseudomyrmex termitarius		X

There are more forest than generalist species inside the remnants, even in the small remnants, and the number of both categories increases with area (Table 2). However, generalist and forest species responded differently to remnant area (Fig. 3), evidenced by the significance of the interaction term in Table 2.

DISCUSSION

We found the expected species-area relationship (Fig. 1), showing that the fragmentation in the studied region led to species richness loss in smaller remnants. Such a loss occurred both during the fragmentation itself, and may continue to occur, with secondary extinction caused by, for instance, invasive species, changes in environmental condition, and increase in perimeter/ area ratio.

The pattern observed in Fig. 2 may be explained by four mechanisms, and the origin of matrix species is important to understand such mechanisms. There are two possible origins for the matrix ant species. They may have invaded the studied region after the fragmentation event, or they may be forest gap specialists that expanded their distribution after the fragmentation. Some of the species collected in the matrix were also sampled in "cerrado" vegetation, such as *Camponotus (Myrmaphaenus)* sp. 2 (Sandra M. Soares, personal communication) and *C. crassus* (Carla R. Ribas, personal communication). "Cerrados"

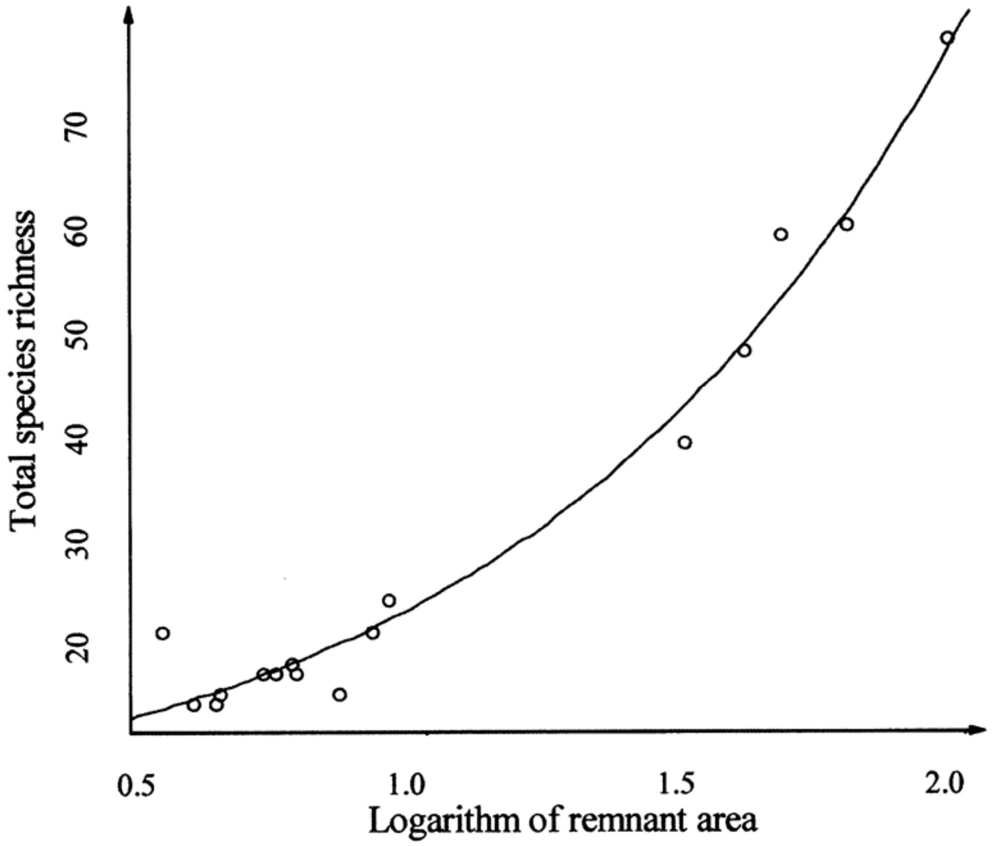

Fig. 1. Species-area relationship of total ant species sampled in the forest remnants in the region of Viçosa, MG, Brazil ($F_{1,15}$ = 408.30; p<0.0001; r^2 = 0.97).

Table 2. Deviance analysis resulting from the ANCOVA (Poisson errors corrected for overdispersion) of the variation of number of generalist and forest species with remnant area.

Source	df	SS	MS	F	p
Model	3	251.37	83.79	174.56	<0.0001
Area	1	184.69	184.69	384.77	<0.0001
Species category	1	46.92	46.92	97.75	<0.0001
Interaction	1	19.75	19.75	41.15	<0.0001
Error	30	14.53	0.48		
Total	33	265.89			

are savanna-like formations occurring in a distance of about 200km North of the studied region. In such cases, these species may be exotic in the region and they may exclude native species (Suarez *et al.* 1998) or may occupy vacant sites formerly occupied by the extinct native species. Disregarding the process involved, the substitution of several specialists species by one or a few generalists, leads to species richness

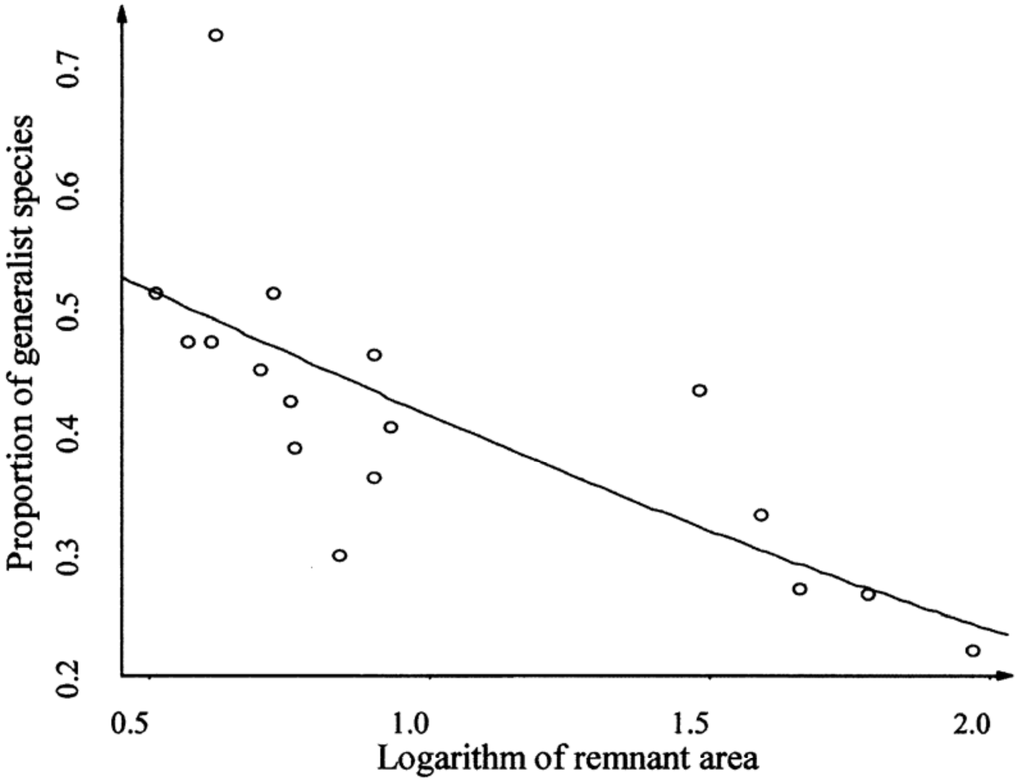

Fig. 2. Proportion of generalist ant species in relation to the logarithm of remnant area (binomial errors; $F_{1,15} = 19.41$; $p < 0.0001$; $r^2 = 0.70$).

decrease in the remnants. Smaller remnants suffer these effects more intensively because they tend to be more homogeneous, or to have their interior habitats more similar to the edge habitats (Murcia 1995 and references therein) and to the matrix. Species able to invade forest remnants should be more generalist because they have to survive in both environments. As small remnants are more homogeneous, generalist species may invade and occupy the entire remnant, instead of remaining only at its edge.

Firstly, if the matrix ant species have already been present in the pristine vegetation, for instance in open areas such as forest gaps, fragmentation benefited such species, which expanded their distribution in the region and occupied matrix habitats. These species would have occurred in higher proportion in small remnants because these are more disturbed, and their conditions resemble that of matrix and gaps. Gap habitat is considered similar to remnant edge. Similarities between matrix and edge communities in forest remnants, as well as a higher tolerance by matrix species to the edges, have been reported for several invertebrate groups (Martins 1989, Majer, Delabie & McKenzie

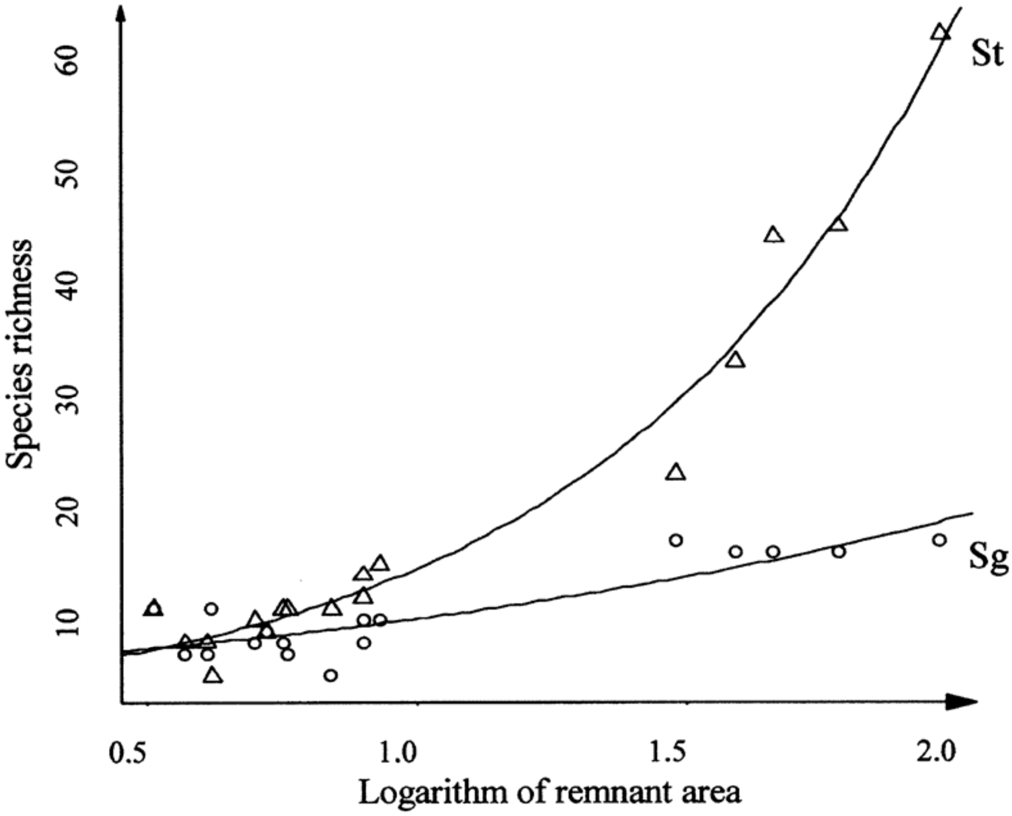

Fig. 3. Number of generalist species (Sg) and forest species (Sf) in relation to the logarithm of remnant area. The significance of regression analysis is summarized in Table 2.

1997, Didham *et al.* 1998a, Carvalho & Vasconcelos 1999, Vasconcelos 1999 Gascon *et al.* 1999). Therefore, in remnants having a larger relative edge, these species may invade them more easily and, depending on edge effect extension, they may spread inside the remnant.

The second mechanism to describe the observed pattern may be related to landscape design in Viçosa. This region is composed of several small remnants that are more isolated from each other and a few less isolated large remnants. Fragmentation has caused a primary species loss, and probably part of this loss was counterbalanced by immigration. The pool of species that may immigrate to small remnants is different from the pool of species able to enter large ones: small remnants are placed in a "sea" of matrix, whereas large remnants have forests nearby. There are species that cannot survive in the matrix, and others that tolerate this habitat (Martins 1989, Turner & Corlett 1996, Majer, Delabie & McKenzie 1997, Gascon *et al.* 1999). It was expected that smaller remnants receive proportionally more tolerant matrix species because they are distant from forest ant species sources.

The third mechanism considers that matrix ant species are exotic to the remnants, and did not occur in the pristine forest. Smaller remnants have two characteristics that facilitate the invasion and survival of invasive species: they have a higher perimeter/area ratio, and their conditions are more similar to matrix habitat (Suarez, Bolger & Case 1998). This mechanism is similar to the first one, diverging only in the origin of generalist species.

The fourth mechanism, tested in Fig. 3, results from the perimeter/area ratio. To understand such an effect we consider that fragmentation causes a species loss that is proportional to remnant area. Species invasion is dependent of remnant perimeter, which increases in larger remnants. Therefore, larger remnants receive more species from the matrix, producing the pattern observed in Fig. 3 (Sg). Area reduction is higher than perimeter reduction, and therefore smaller remnants would loose more forest species than larger ones (Fig. 3, Sf), but receive little less species from the matrix when compared with large remnants. The consequence may be the pattern observed in Fig. 2.

Due to the lack of historical sampling in the studied region, it is difficult to know whether generalist species are gap and edge specialists which expanded their distribution within the region after fragmentation, or invasive species which came from nearby regions with different habitats. The study of species composition of forest gaps may help to clarify such a question.

For several years the main focus of studies in forest fragmentation were the changes occurring in species richness after the fragmentation event (DeSouza & Brown 1994, Turner 1996, Davies & Margules 1998). However, changes in species richness may be less important to communities, because the main changes may occur in species composition. Even when no detectable effect is found in species richness with remnant area, a shift is species composition may occur (Davies & Margules 1998). A "rescue effect" may be occurring in the species richness because species lost due to fragmentation may be substituted by invading species, maintaining species richness. The species-area relationship found in fragmentation studies, therefore, may represent more than a sampling effect or a habitat loss, involving not only a species richness decrease but also a shift in species composition.

The observed shift in species composition in remnants may cause, by its turn, further effects, which are more pronounced in smaller remnants. In small remnants there are more species with simple life cycles, participating in less complex trophic webs and the absence of complex interactions such as herbivore parasitism by parasitoids (Kruess & Tscharntke 1994, Didham *et al.* 1998b, Fisher 1998, Terborgh *et al.* 2001). Smaller densities of predators in small remnants usually occur because these organisms cannot maintain a large population in such areas. The disappearance of predators leads to a pressure release of prey populations, which increase their population densities (Kruess & Tscharntke 1994, Terborgh *et al.* 2001). Pollinator and parasite population dynamics or requirements also may not match edge environments, causing also the disappearing of these species, which are substituted by species with simpler life cycles (Fisher 1998).

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Colonization and extinction of ant communities in a fragmented landscape

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Abstract In this paper we tested the assumption that smaller and more isolated remnants receive fewer ant colonizers and lose more species. We also tested hypotheses to explain such a pattern. We sampled ants in Brazil for 3 years in 18 forest remnants and in 10 grasslands between them. We tested the influence of remnant area and isolation on colonization rate, as well as the effect of remnant area on extinction rate. We tested the correlation between remnant area and isolation to verify the landscape design. Colonization rate was not affected by remnant area or isolation. Extinction rate, however, was smaller in larger remnants. Remnant area and isolation were negatively correlated. We tested two hypotheses related to the decrease in ant species extinction rate with increased remnant area: (i) small remnants support smaller and more extinction-prone populations; and (ii) small remnants are more often invaded by generalist species, which suffer higher extinction inside remnants. The density of ant populations significantly increased with area. Generalist species presented a lower colonization rate in larger remnants, contrary to the pattern observed in forest species. Generalist species suffered more extinction than expected inside remnants. The lack of response of colonization rate to remnant area can be explained by the differential colonization by generalist and forest species. The decrease of ant population density in smaller remnants could be related to loss of habitat quality or quantity. The higher colonization by generalist ant species in the smaller remnants could be related to landscape design, because smaller remnants are more similar to the matrix than larger ones. Our results have important implications for conservation strategies because small remnants seem to be more affected by secondary effects of fragmentation, losing more forest species and being invaded more often by generalist species. Studies that compare only species richness between remnants cannot detect such patterns in species composition.

Key words: fragmentation, island biogeography theory, matrix habitat, species–area relationship, species richness.

INTRODUCTION

Habitat fragmentation can arise from several human activities. Large, undisturbed habitat is divided into smaller areas, isolated from each other by urban areas, roads and agriculture. The disturbance generated by fragmentation can disrupt the original community in several ways, usually with effects on species richness (Wilcox & Murphy 1985; Turner 1996; DeSouza *et al.* 2001). The landscape created by the fragmentation process is seldom planned to consider remnant isolation, area, shape and edge effects, or other processes that could reduce species richness. Consequently, the resulting landscape is formed from several patches of original vegetation, with different areas, within a matrix of disturbed areas, and with different degrees of isolation among them.

Small vegetation remnants usually have fewer species than larger ones. This fact has been observed by several authors, working with different animal and plant taxa (Margules *et al.* 1982; Robinson & Quinn 1988; Rosenzweig 1995; Turner 1996; Ricklefs & Lovette 1999). Such a pattern is sometimes confounded by the species–area relationship, which is probably the most prevalent pattern in ecology (Ricklefs & Lovette 1999). The species-area relationship, however, does not consider processes that occur in a fragmented landscape. These processes, such as edge and shape effects (Carvalho & Vasconcelos 1999), isolation, and species invasions from the new environments created between the remnants of natural habitat (Sobrinho *et al.* 2003) can modify the pattern because they add new variables to the species–area relationship.

Immigration and extinction dynamics are important processes that alter species richness in remnants, and these processes depend on remnant area and isolation (Robinson & Quinn 1988; Turner 1996; Didham *et al.*

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1998; Boudjemadi *et al.* 1999). Remnant isolation can be fundamental in determining immigration rates, because it can directly influence the opportunity of species colonization or re-colonization of a given remnant (Schoener 1991; Turner 1996; Davies & Margules 1998; Huxel & Hastings 1998; Manne *et al.* 1998; Boudjemadi *et al.* 1999).

The effects of immigration and local extinction on island species richness were first formalized by MacArthur and Wilson (1967), and since then this has been the main theory to explain area and isolation effects, even though there are clear differences between true islands and vegetation remnants (Robinson & Quinn 1988; DeSouza *et al.* 2001). Predicted effects of area and isolation on immigration and extinction rates are not always observed in true islands (Manne *et al.* 1998; but see Simberloff & Wilson 1969; Ricklefs & Lovette 1999), or in vegetation remnants (Robinson & Quinn 1988; but see Turner 1996; Didham *et al.* 1998). Metapopulation theory (Schoener 1991; Verboom *et al.* 1991a,b; Nee & May 1992; Kindvall 1999) and source–sink models (Watkinson & Sutherland 1995; Thomas & Kunin 1999) provided further insight into the potential effects of immigration and extinction on remnant species richness.

In this context, the environment between remnants, usually called the matrix habitat, might also be important. The matrix can be formed by several different habitats – from artificial habitats, such as roads and urban environments, to crops, pastures and other monocultures (Gascon *et al.* 2000). Depending on the matrix type, it can be a source of species to habitat remnants, modifying their population dynamics, species composition and community structure (DeSouza *et al.* 2001). In addition to modifying species composition, the matrix type can prevent regeneration of remnant edges, causing small remnants to shrink as their edges recede (Gascon *et al.* 2000). Species invasion depends not only on matrix type, but also on remnant area and shape, or on their edge/area ratio. Smaller remnants might be invaded more often because they present more edge in relation to area (Kapos *et al.* 1997; Gascon & Lovejoy 1998; Carvalho & Vasconcelos 1999; Gascon *et al.* 1999).

Ants are easily collected, with a high abundance of individuals and species. Ant communities usually respond to fragmentation (Majer *et al.* 1997; Suarez *et al.* 1998; Carvalho & Vasconcelos 1999; Gascon *et al.* 1999; Sobrinho *et al.* 2003). Furthermore, some ant species from pasture matrix usually enter forest remnants (Suarez *et al.* 1998), which can alter species composition in smaller forest remnants (Sobrinho *et al.* 2003).

The aim of the present study was to examine the rates of colonization and local extinction of ant species in relation to remnant area in a fragmented landscape. We tested the hypothesis that smaller and more isolated remnants receive fewer colonizers (lower colonization rate) and lose more species (higher local extinction rate). We also tested some hypotheses to explain this pattern. DeSouza *et al.* (2001) suggested that smaller remnants receive fewer colonizers because they are more isolated and have shape characteristics that confer lower accessibility to potential colonizers.

Regarding the higher extinction rate in smaller remnants, species extinction might be caused by higher temporal variation in the density of small populations, making them more prone to stochastic extinction and demographic constraints (Davies & Margules 1998; Gascon & Lovejoy 1998; Suarez *et al.* 1998; Ricklefs & Lovette 1999).

The expected pattern for species extinction might also occur because smaller remnants are invaded more often by generalist species, whereas large remnants are occupied by 'deep forest' species (Didham *et al.* 1998). Furthermore, generalist species would suffer more extinction inside forest remnants because they would not be adapted to the forest environment.

METHODS

Study site

We carried out the study at Viçosa, south-eastern Brazil (20°45′S, 42°50′W), a region that was covered by forests until the twentieth century, when an accelerated process of fragmentation began. The pristine forest was fragmented by pastures and coffee plantations mainly in the 1930s and 1940s (Gomes 1975), and remaining secondary forests were usually restricted to a few remnants, particularly on hilltops. From the 1960s onwards, agriculture declined in the region and several forest areas have regenerated into secondary forests. Today the region comprises a mosaic of forest remnants varying from 3.2 to 298.0 ha, forming an excellent system to study the effects of fragmentation.

Sampling procedure

At Viçosa, we arbitrarily chose 18 remnants, with areas ranging from approximately 3–300 ha. We used digitalized aerial photographs of the region (CEMIG 1987) to determine the remnant area and estimate isolation. We estimated isolation by calculating the summed distance from the studied remnant to the nearest four remnants at the four cardinal points.

We sampled the remnants during the summer rainy season in three consecutive years (1994–1996), always at the same sites as the previous years. We collected the ants by pitfall traps, using human faeces, carrion and decomposing fruit as bait. We chose these baits because the traps were being used to attract ants (this study) and other insect groups (other studies). The pitfall traps were plastic containers (diameter 19 cm, height 11 cm) with an inner receptacle containing the bait; these were left in the field for 48 h. Ants attracted by the bait fell into a 5% detergent solution.

We set the pitfall traps in groups of three, each one containing a different bait type. Within groups, we set pitfall traps 2 m apart, and the minimum distance between groups was 30 m. The distance from forest edges was always larger than 50 m, thereby minimizing edge effects. We sampled each of the two larger remnants (93 and 298 ha) using 24 pitfall groups, each of the four medium-sized remnants (30 ha, 39 ha, 46 ha and 61 ha) using 12 pitfall groups and each of the 12 smaller remnants (ranging from 3.2 to 8.6 ha) using four pitfall groups. Sampling effort was therefore represented by three levels of sampling, depending on remnant area (Sobrinho *et al.* 2003).

In 1995, we also sampled 10 pasture sites in the matrix using a similar baited pitfall design. We set four groups of three pitfalls in each pasture at 60 m from the forest remnants.

We considered generalist ant species as those trapped both in the pasture and in the forest remnants. Pasture species can occur either only in the matrix (matrix species) or both in the matrix and in the forest remnants. We considered only the latter as generalists, because we were interested in the species that could occur in the remnants. Forest species were those collected only in forest remnants.

We sorted, mounted and identified the ants to genera with the help of identification keys (Hölldobler & Wilson 1990; Bolton 1994). Whenever possible, we identified the ants to species level. When species identification was not possible, we sorted ants according to their external morphology. We deposited voucher specimens in the reference collection of the Community Ecology Laboratory of the Department of General Biology of the Universidade Federal de Viçosa.

Effect of remnant area on colonization rate

We considered colonizers as those species that did not occur in one year and were sampled in the subsequent year in each remnant. We estimated absolute colonization rate as the average number of colonizers in both intervals (1994–1995 and 1995–1996) in each remnant. We estimated the relative colonization rate by dividing absolute colonization by the total number of species sampled in the remnant at the beginning of the interval.

Although Robinson and Quinn (1988) have suggested the use of the absolute colonization rate, the use of the relative colonization rate is justified because it shows the chance of colonization in relation to the species that were already present in the remnant. It also shows the importance that each colonizer might have in relation to the species richness of the remnant. Few species arriving in a species-poor remnant can increase their diversity more than the same number of species arriving in a species-rich remnant. This approach was also used by other authors (Didham *et al.* 1998; Manne *et al.* 1998).

We tested the influence of area and isolation (explanatory variables) on relative colonization rate (response variable) through analysis of covariance. Because we sampled remnants using different sampling efforts (4, 12 and 24 pitfall groups), we used the number of samples, a discrete variable, as another explanatory variable to allow the removal of possible sampling bias. This procedure was proposed by Schoereder *et al.* (in press). According to our working hypothesis, we expected that remnant area, disregarding the number of samples, would positively influence the colonization rate.

Landscape architecture can be important in the combined influence of area and isolation on colonization rate, because the studied areas are not experimental and therefore each of the effects cannot be set apart. For instance, one region might have large and less isolated remnants, whereas another region might have small and more isolated ones. To test the relationship between area and isolation, we carried out a linear correlation analysis.

Effect of remnant shape on colonization rate

If there was a positive relationship between colonization rate and remnant area, we predicted an increasing probability of an individual finding a forest remnant with increasing remnant perimeter (DeSouza *et al.* 2001). We tested the effect of remnant shape through linear regression analysis, using the perimeter/area ratio as an explanatory variable and relative colonization rate as a response variable.

Effect of remnant area on extinction rate

We considered locally extinct species as those that occurred in one year and were not sampled in the subsequent year. We estimated absolute extinction as the average number of species that became locally extinct in both intervals (1994–1995 and 1995–1996). We estimated the relative extinction rate by dividing the absolute extinction by the total number of species sampled in the remnant at the beginning of the interval. The same reasoning used for the choice of relative instead of absolute colonization rate is valid here.

We tested the influence of area (explanatory variable) on relative extinction rate (response variable) through linear regression. We also used the number of samples as an explanatory variable, allowing the removal of sampling bias. Some authors have also tested the effect of isolation on extinction rates (Schoener 1991; Verboom *et al.* 1991a; Manne *et al.* 1998; Boudjemadi *et al.* 1999). As isolation does not affect extinction rates directly, interfering only in rescue effects of extant populations, we did not include isolation in the extinction model in the present study. Furthermore, any possible effect of remnant isolation on species richness and in rescue effects would appear in the model used to explain colonization rates. We expected that extinction rate would decrease with increasing remnant area, and we tested the following hypotheses.

Effect of population density on extinction rate

Our working hypothesis was that small remnants have lower population densities. We estimated the population density of ant species from species frequency in pitfall traps, rather than absolute numbers in traps, because numbers can vary with recruitment ability among ant species (Hölldobler & Wilson 1990). Furthermore, the number of individuals collected depends on the distance between the pitfall trap and the colony. Therefore, we took the frequency of each species as a surrogate of population density – the frequency being the number of records of presence of each species in each remnant divided by the total number of pitfall groups in that remnant. We calculated in each remnant a frequency for each species, averaging these frequencies to estimate ant population densities. We tested the response of ant frequency to remnant area and number of samples by analysis of covariance.

If the hypothesis was true, a positive relationship between ant frequency and remnant area was expected, independent of the number of samples.

Effect of generalist species on extinction rate

This hypothesis has two steps: small remnants receive more colonizers from the matrix (generalist species) than from the forests nearby (forest species), and generalist species are more extinction-prone inside remnants than forest species.

We tested the first step using an analysis of covariance where the response variable was the number of colonizers in each category (generalist or forest species). Explanatory variables were remnant area, species category and the interaction between these two terms, with Poisson errors corrected for overdispersion (Crawley 2002).

To test the second step, we calculated the number of extinction events of generalist and forest species in each remnant. Because there were far more forest than generalist species inside the remnants, we estimated the number of expected extinction events in each category of ant species (forest and generalist) weighting the total number of extinction events by the number of species in each category. These numbers were tested by χ^2 test using Yates correction.

Analyses

We performed all analyses under R software (Ihaka & Gentleman 1996). In the analyses involving more than one explanatory variable, we fitted complete models and removed each variable in turn, verifying changes in deviance (Crawley 2002). We submitted all models to residual analysis to verify their suitability and the suitability of the error distribution.

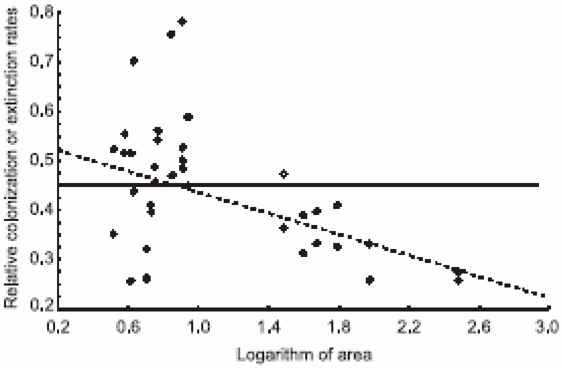

Fig. 1. Balance between relative colonization ($F_{1,15}$ = 2.17, P = 0.06) and extinction rates in remnants of different areas ($F_{1,16}$ = 14.27, P = 0.002). (—, ○), represents the average relative colonization, and (---, ●), the relative extinction.

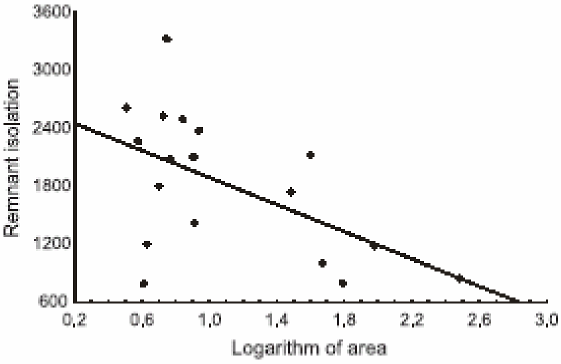

Fig. 2. Relationship between isolation and logarithm of area of the remnants (r^2 = 0.30, P = 0.019). Note that the landscape is composed of areas with small and isolated remnants and areas with large and less isolated ones.

RESULTS

We collected a total of 189 ant species. Of the 49 species found in the matrix, 26 also occurred in the remnants and were recognized as generalist species. One hundred and forty species were found only in the forest remnants.

Effect of remnant area on colonization and extinction rates

Colonization rate was not significantly affected by remnant area ($F_{1,15} = 2.17, P = 0.16$) (Fig. 1), isolation ($F_{1,16} = 1.88$, $P = 0.19$) or number of samples ($F_{2,13} = 0.40$, $P = 0.68$). Extinction rate, however, was significantly smaller in larger remnants ($F_{1,16} = 14.27$, $P = 0.002$) (Fig. 1), but was not affected by number of samples ($F_{2,14} = 3.66$, $P = 0.053$). This means that extinction rate decreased with increasing remnant area independent of the number of samples. Remnant area and isolation were negatively correlated ($r^2 = 0.30$, $P = 0.019$) (Fig. 2). Residual analyses confirmed the use of the models.

Because colonization rate was not affected by area, we did not test the hypotheses linked to this assumption, testing only the hypotheses linked to the relationship between extinction rate and area.

Effect of population density on extinction rate

The complete model was significant ($F_{5,12} = 8.56$, $P = 0.001$). Ant species frequency significantly increased with area ($F_{1,16} = 28.26$, $P = 0.0002$; Fig. 3) and with the number of samples ($F_{2,14} = 7.08$, $P = 0.009$). This means that larger remnants had higher population density and that this effect occurred even when correcting for the number of samples.

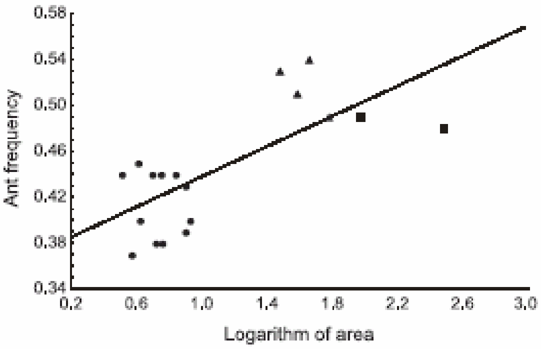

Fig. 3. Relationship between ant frequency and logarithm of remnant area. The data were analysed by linear regression ($F_{1,16} = 28.26$, $P = 0.0002$). (●) $n = 4$; (▲) $n = 12$; (■) $n = 24$.

Effect of generalist species on extinction rate

Colonization rate was influenced by species category (generalist or forest species) ($F_{1,33} = 188.88$, $P < 0.0001$), remnant area ($F_{1,34} = 12.75$, $P = 0.0004$) and by the interaction between species category and remnant area ($F_{1,32} = 7.55$, $P = 0.0006$; Fig. 4). The complete model was also significant ($F_{3,32} = 69.73$, $P < 0.0001$). The number of generalist colonizers decreased and forest colonizers increased with increasing remnant area.

In all remnants together, there were 123 generalist species extinction events and 471 forest species extinction events. The numbers of expected extinction events for generalist and forest species were 93.02 and 500.98, respectively. These numbers were significantly different from those observed ($\chi^2 = 11.18$, degrees of freedom = 1, $P = 0.0008$). Generalist species suffered more extinction and forest species suffered less extinction than random expectation.

DISCUSSION

Local extinction decreased with increasing remnant area, confirming our prediction. Nevertheless, colonization rate did not vary either with remnant area or isolation. Even though the balance between colonization and extinction could explain the species–area pattern observed by Sobrinho *et al.* (2003) in the same region, the absence of a relationship between colonization and remnant area deserves more explanation. Similar results have already been described by Ricklefs and Lovette (1999).

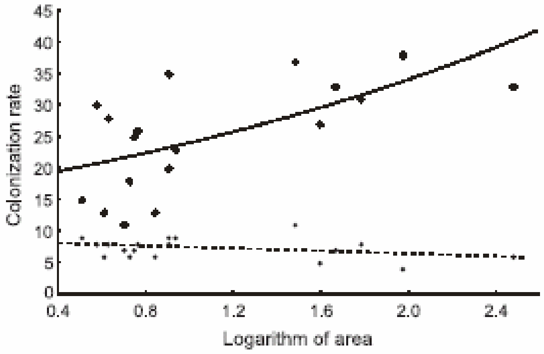

Fig. 4. Influence of remnant area on colonization rate ($F_{1,34} = 12.75$, $P = 0.0004$) of generalist and forest species ($F_{1,33} = 188.88$, $P < 0.0001$). (○) Forest species; (●) generalist species. The complete model ($F_{3,32} = 69.73$, $P < 0.0001$) and the interaction between area and species category were also significant ($F_{1,32} = 7.55$, $P = 0.0006$), meaning the curves are different.

Effect of remnant area on colonization rate

It was expected that larger areas would be easier to find by random colonizers than smaller ones (MacArthur & Wilson 1967; Ricklefs & Lovette 1999; DeSouza *et al.* 2001). Furthermore, in the study region, larger remnants were less isolated than smaller ones (Fig. 2). Why, then, did colonization rate not vary with remnant area?

The answer might be linked to species composition in the remnants. Contrary to true islands, the sea between the islands in this study (the matrix) might also be inhabited by species that could colonize the remnants. These species could invade the remnants, occupying empty niches or rescuing populations that were declining to local extinction (Wilcox & Murphy 1985; Ricklefs & Lovette 1999; DeSouza *et al.* 2001). Smaller remnants might be more accessible to generalist species than larger ones for several reasons. First, smaller remnants have more edge in relation to area, making them more prone to invasion (Turner 1996; Didham *et al.* 1998). Second, competition might be relaxed in smaller remnants (Nee & May 1992; Tilman *et al.* 1994; Huxel & Hastings 1998), which facilitates invasion by generalist species. Third, loss of primary species in smaller remnants might be greater than in larger ones, because of a loss of individuals and habitats, releasing resources to invaders (Turner 1996). Finally, and perhaps most importantly, the landscape in the present study was composed of areas with larger and less isolated remnants, and areas with smaller and more isolated ones; therefore, species composition in the pool of possible colonizers might vary. In the areas with larger and less isolated remnants there are probably more forest species ('deep forest species'; Didham *et al.* 1998) able to colonize the remnants. Conversely, in the areas with smaller and more isolated remnants, there will be more generalist species in the pool of colonizers.

Effect of remnant area on extinction rate

Various processes, that are not necessarily independent, could cause the pattern of lower extinction rate in larger remnant area: (i) small remnants cannot support larger population density and smaller populations are more prone to stochastic extinction; (ii) small remnants might be invaded more often by generalist species less adapted to living inside forest vegetation; (iii) disturbance might be higher in small remnants, decreasing native populations; (iv) remnants might have accumulated species from the neighbouring areas, and might then lose these species at a rate inversely proportional to their sizes (Robinson & Quinn 1988). From these four hypotheses, we tested only the first two.

Effect of population density on extinction rate

There was a sampling effect on ant population density, apart from the true effect of remnant area. Nevertheless, the effect of remnant area was also significant, suggesting that smaller remnants have lower population density. In the specific case of insect societies, such as ants, frequency of each species is related to the number of nests and/or the abundance of individuals. Lower nest densities can affect the net reproductive rate of each species by decreasing the probability of male/female encounters during the nuptial flight, the so-called Allee (1931) effect. Fewer individuals per colony can affect the production of reproductive castes, because a small colony has a weaker foraging effort and cannot produce the amount of energy needed to produce a large number of reproductives (Hölldobler & Wilson 1990; McGlynn *et al.* 2002). Furthermore, in smaller nests, the probability of stochastic extinction is higher than in nests with more individuals (Hölldobler & Wilson 1990). Similarly, an ant population with lower nest densities is more extinction-prone than one with high nest density. Thus, higher extinction rates in smaller remnants could be explained by the complex dynamics of nest density and/or individuals per nest in ant communities.

The decrease in ant frequency in smaller remnants was probably caused by habitat modifications related to changes in both resources and environmental conditions following fragmentation. Fragmentation events reduced habitat area and might have excluded some of the original microhabitats of the pristine forest. There was, then, a first wave of extinction of species related to the removed microhabitats. If only this had occurred, we would expect only an effect on species richness, because the remaining species would maintain their population density. However, we observed an effect on ant frequency probably linked to secondary effects of fragmentation that might have reduced the population densities of remaining species. Secondary effects included remnant isolation, demographic constraints and rescue effects (DeSouza *et al.* 2001).

Effect of generalist species on extinction rate

There is possibly a bias associated with matrix and remnant sampling efforts. The remnants were sampled over 3 years, whereas the matrix was sampled in only 1 year. Furthermore, the number of pitfalls set per year in the forest remnants (144) was higher than the number of pitfalls located in the matrix (120). Therefore, there are probably more generalist ant species than we collected. However, we have no reason to believe that the observed trend in the relationship would change with a higher sampling effort in the matrix.

The composition of colonizers in the forest remnants varied with remnant area: smaller remnants were invaded more often by generalist species and invaded less often by forest species than larger ones (Fig. 4). Two hypotheses could explain why generalist species colonized large remnants more rarely: (i) generalist ant species might recognize smaller remnants as being more similar to the matrix than larger ones; (ii) small remnants are immersed in a landscape with a higher proportion of matrix, facilitating colonization by generalist species. It is interesting to notice that, even though the colonization rate did not vary with remnant area, when we analysed colonization rates, each category (generalist or forest species) responded differently to remnant area. The opposite trend presented by each category could be responsible for the absence of any relationship between colonization rate and remnant area. Therefore, more important than the changes in the number of colonizers in relation to remnant area might be the habitat from which these species came.

Our hypothesis that generalist species suffer higher extinction inside the remnants was confirmed, meaning that smaller remnants presented a higher turnover of species. Generalist ant species colonized smaller remnants more frequently, but these species suffered more extinction inside the remnants. The same pattern has been observed by other authors (Majer *et al.* 1997; Gascon *et al.* 1999), who claimed that ant species inside the remnants were not affected by matrix species. In contrast, Suarez *et al.* (1998; and references therein) reported the exclusion of native ant species from remnant edges, and consequently from smaller remnants, by exotic ant species. We are not sure about the origin of the generalist ant species in the study region, and consequently, we do not know whether these species are exotic. Some ant species, however, occurred exclusively in the matrix and they are also found in other regions and habitats in Brazil. For instance, *Camponotus (Myrmaphaenus) genatus* (Sandra M. Soares, pers. comm.) and *Camponotus crassus* (Ribas *et al.* 2003) occur in fields and savannas in Minas Gerais and Bahia (Majer *et al.* 1997). Hence, there is evidence that these species might be exotic in this region, but it is difficult to ascertain with the present data which ant species are really exotic.

CONCLUSIONS

Even though no effect of area and isolation on colonization rate was found, the observed effect on extinction rate might indicate that small remnants lose proportionally more species, and consequently, that species turnover is higher in these remnants (Fig. 1). High turnover means that species composition changes more in small remnants than in large ones.

We hypothesized that the higher extinction rates occurring at smaller remnants were the result of the invasion of these remnants preferentially by generalist ant species and that these species would suffer more extinction. Higher extinction rates might also be produced because smaller remnants support lower population densities. Our hypotheses were confirmed: small remnants were invaded more often by generalist ant species than by forest species, and population densities in these remnants were smaller.

These results have an interesting implication in conservation, because it seems that secondary effects of fragmentation are higher in small remnants, where the effect of population reduction is more evident. Furthermore, in these remnants the species turnover is also more evident, which causes a change in species composition.

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TERCEIRO ARTIGO

Edge and shape effects on ants

Edge and shape effects on ant (Hymenoptera: Formicidae) species richness and composition in forest fragments

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Abstract. In this paper, we tested four hypotheses relative to edge and shape effects on ant communities: (i) forest edges have lower species richness than the remnant core; (ii) species richness increases with distance from the edge; (iii) irregularly shaped remnants have lower species richness than more regular remnants; (iv) there is a higher similarity of species composition between edge and core in irregular than in regular remnants. We sampled litter ant communities on the edge and core of ten remnants, in Viçosa, Minas Gerais, Brazil. Species richness was larger at the forest core than at the edges, although did not increase with distance from the edge. Species richness did not vary with shape complexity. The similarity of species composition between edge and core showed a decreasing trend with remnant area, and did not vary with shape complexity. The observed differences of species richness between forest core and edge may be due to higher harshness of edges, caused by environmental changes. The absence of relationship between species richness and distance from the edge might indicate the range of edge effects, which would be smaller than the smallest distance of core sampled. Therefore, edges would affect litter-dwelling ant species richness in a distance smaller than 50m. The observation of species composition allowed us to notice an effect of fragmentation that would not be noticed if we were considering only species richness. Edge may serve as step to generalist species, which may use it to colonise forest remnants. Furthermore, small remnants are more colonisation-prone by such species, and have a more homogeneous species composition than large remnants.

Key words: Edge effects; Formicidae; Habitat fragmentation; Shape effects; Species richness; Tropical rain forest.

Introduction

Habitat fragmentation consists in the reduction of continuous areas, resulting in the creation of one to several smaller and isolated remnants (Lovejoy et al. 1986; Murcia 1995; DeSouza et al. 2001) surrounded by matrix habitats (pastures, monocultures) (Turner 1996; Didham 1997). Fragmentation is considered one of the main processes responsible for the loss of biodiversity in tropical ecosystems (Turner and Corlett 1996; Didham et al. 1996; Majer et al. 1997; Davies and Margules 1998; Vasconcelos and Delabie 2000), and therefore has been frequently studied in the last decades.

Fragmentation may affect species composition and richness, as well as population abundance in the remnants. Several studies have reported alterations in species composition (Didham 1997; Brown and Hutchings 1997; Didham et al. 1998a; Didham et al. 1998b; Vasconcelos and Delabie 2000; Bruhl et al. 2003; Krauss et al. 2003; Sobrinho et al. 2003) and in species richness (DeSouza and Brown 1994; Vasconcelos 1999; Carvalho and Vasconcelos 1999; Sobrinho et al. 2003; Schoereder et al. 2004b) of different taxa due to fragmentation. Effects of fragmentation on species richness and composition may be both direct and indirect. Direct effects comprise those that occur at the moment of the disturbance, when species and habitats are lost. Indirect effects include secondary effects, such as edge and shape effects, extinction and colonization, and invasion by exotic species.

The processes originated by creation of edges between remnants and matrix, the so-called ‘edge effect’, have been considered to cause alterations on species number, population abundances and species composition (Murcia 1995; Zheng and Chen 2000). Fragmentation transforms pristine habitats on edges and increases the proximity between remnant core and exterior (DeSouza et al. 2001), consequently increasing the proportion of habitats exposed to other environments (Kapos et al. 1997). According to Murcia (1995), edge creation may cause three types of effects in the communities: (i) abiotic, characterized by climatic changes, (ii) direct biological effects, such as individual and/or populations loss due to environmental harshness, (iii) indirect biological effects, such as individuals loss due to alterations on interactions between species close to the edge. Edge creation cause microclimatic changes, increasing the incidence of winds and solar radiation in the portion that extends from the edge until approximately 100m to core (Lovejoy et al. 1986; Laurance and Yensen 1991; Murcia 1995; Laurance 1997; Turton and Freiburger 1997). Plant communities are affected by edge creation, with fall of trees and proliferation of pioneer vegetation (Laurance and Yensen 1991; Kapos et al. 1993; Laurance et al. 1998) and of exotic species (Laurance 1997). These changes in microclimate and in vegetation may cause alterations in communities of several taxa of animals, such as birds, mammals and invertebrates (Lovejoy et al. 1986; Fowler et al. 1993; Didham 1997; Brown and Hutchings 1997; Didham et al. 1998a).

The influence of edge creation in the communities depends on several factors, e. g., time elapsed after edge creation, orientation, isolation, shape and size of remnant, and on the studied biome (Kapos et al. 1997). Another important factor is the identity of studied species, because different organisms respond differently to the same level of fragmentation (Braschler and Baur 2003) and, at least to invertebrates, there is a consensus that the species do not respond uniformly to edge creation (Didham et al. 1998a). Some species of insects (mainly ants and beetles) behave as edge specialists (Majer et al. 1997, Didham et al. 1998a) and are positively affected by fragmentation, increasing their populations. Other species avoid edges and, depending on remnant size and on the extent of edge effects, may become extinct (Didham et al. 1998a; Zheng and Chen 2000).

Added to edge effects, the shape of remnants might also cause disruptions in community structure (DeSouza et al. 2001). Larger remnants usually have more core habitats in relation to edge habitats, or a lower edge/core ratio. This pattern is commonly reflected by a negative relationship between shape complexity and remnant area (McGarigal and Marks 1994). However, this negative relationship does not appear to be a consistent pattern, because both the absence of this pattern (Santos 2004) and a positive relationship between shape complexity and area (Ochoa-Gaona et al. 2004) have been found. Species diversity, nevertheless, may respond positively (Louzada 2000, Ochoa-Gaona et al. 2004) or negatively (Santos 2004) to shape complexity.

Studies on ants showed that these communities might respond to edge effects altering their species richness and/or composition. Apparently there is no defined pattern on how edges may affect ant communities, because the results obtained seem to be controversial. Ant abundance might maintain unaltered (Dauber and Wolters 2004) or increase (Vasconcelos 1999) at the edges. Similarly, species richness might increase (Majer et al. 1997) or decrease (Carvalho and Vasconcelos 1999, Kotze and Samways 2001) towards the core of remnants. Usually, patterns of increase or decrease of species richness are related to higher litter volume (Campos et al. 2003) and plant biomass Ribas et al. 2003). Even though there is controversy about ant abundance and species richness, there is a consensus that species composition change in habitat edges, when compared both to the matrix and to forest core (Didham 1998a).

In this paper we tested four hypotheses related to edge and shape effects on ant species richness and composition: (i) forest edges have lower species richness than the remnant core; (ii) species richness increases with distance from the edge; (iii) irregularly shaped remnants have lower species richness than more regular remnants; (iv) there is a higher similarity of species composition between edge and core in irregular than in regular remnants.

Methods

Study area

The study was carried in Viçosa, southeastern Brazil (20^{o} 45’ S, 42^{o} 50’ W). This region was covered by forest up to the last century, when an accelerated process of fragmentation began. The pristine forest was fragmented and intermingled with pastures and coffee plantations mainly in the 1930’s and 1940’s (Gomes 1975), and the remaining secondary vegetation has been restricted to few islands, particularly on hilltops. From the 1960’s onwards, the agriculture diminished in the region and several forest areas regenerated into secondary forests. Nowadays there is a mosaic of forest remnants in the region, with areas varying from three to 300 hectares, forming an ideal system to study the effects of fragmentation.

Sampling procedure

In the mosaic of forest remnants described above we choose arbitrarily 10 remnants with areas ranging from ca. 3ha to ca. 300ha. We sampled these remnants during summer (February-March 2001), which is the raining season in the region. In each remnant, we chose arbitrarily ten sampling points on the edge and ten in the core. Forest edges were always a transition zone between pasture matrix and remnants, consisting of a strip 1m maximum width inside the remnants. The cores were defined in an aerial photograph as the most central point in each remnant, and we calculated the distance from the edge using these photographs.

Remnant shape was estimated using the formula proposed by Ochoa-Gaona et al. (2004), which evaluates the irregularity of the fragment.

$$S = \frac{P}{2\sqrt{\pi . a}}$$

Where, S is the fragment shape, P is the perimeter (m) and a is the area (m^2) of the remnant. This index evaluates the irregularity of the remnant. Values near one correspond to circular shapes and as the value increases the edge/core ratio increases.

We sampled the litter ant fauna utilizing sifting and extraction with 'Winkler' extractors, according to the methodological approach proposed by Bestelmeyer et al. (2000). This technique consists in the removal of all litter and humus present under a $1m^2$ per sample (sampling point). The litter is sifted to remove and break branches and leaves. The extraction technique consists in placing each sample in a 'Winkler' extractor per 72 hours to extract ants and other invertebrates.

We sorted, mounted and identified ants to genera with help of identifications keys (Hölldobler and Wilson 1990; Bolton 1994). We identified ants to species level, whenever possible, but when this was not possible, we sorted ants according to their external morphology. Ivan C. Nascimento and Jacques H. C. Delabie confirmed species identification. We deposited voucher specimens in the reference collection of Laboratório de Ecologia de Comunidades of the Departamento de Biologia Geral of the Universidade Federal de Viçosa.

Statistical analyses

We did not intend to determinate total ant species richness, and therefore a uniform sampling effort was designed (Schoereder et al. 2004a). Nevertheless, because we sampled ants in remnants with varying areas, small remnants might be more exhaustively sampled than large remnants. To verify the sampling effort in the remnants studied, we performed species accumulation curves to all remnants, considering the total number of samples as 20 (edge and core). Species richness accumulated curves and their confidence intervals were estimated using the software EstimateS 7.5 (Colwell 2005).

We tested for differences between number of ant species collected on the edge and in the core of remnant with an analysis of variance (ANOVA). The response variable was the number of ant species and the explanatory variable was the local where the ants were collected (edge or core). To remove the effect of pseudoreplication, we used mixed effect models, in which the random term was remnants (Crawley 2002). To correct for nor-normality the response variable was log-transformed.

We tested the influence of distance from the edge on species richness through linear regression. To avoid pseudoreplication in the nested design, we used mixed effect models in data transformed to Poisson errors (Crawley 2002). In the fixed model, the response variable was species richness and the explanatory variable was distance from the edge. We included area and the interaction of area and shape complexity as explanatory variables, because both variables may be confounded to each other. The random term of the model was remnants.

We tested the shape effects on species richness using an analysis of covariance (ANCOVA). The response variable was species richness and the explanatory variables were category of ants (edge and core species), remnant shape and the interaction between these variables. To avoid pseudoreplication, we also used mixed effect models in data transformed to Poisson errors, considering category of ants in remnants as the random term.

To test the hypothesis that similarity of species composition between edge and core increases with shape complexity, we calculated a Jaccard similarity index between edge and core species to all remnants. We used the package "vegan" (Oksanen 2004) and the Jaccard index. We carried out a regression analysis between similarity indices and shape complexity. We included area and the interaction of area and shape complexity as explanatory variables, because both variables may be confounded to each other.

We carried out all analyses under R (R development Core Team 2004), followed by residual analyses to verify the suitability of the models and of the distributions of errors (Crawley 2002).

Results

We collected 117 ant species in all remnants, and 83 species were present on the edge and 99 species in the core of remnants (Table 1). From these, 34 species were sampled only in the forest cores, 18 were sampled only at their edges and 65 were found both at the edge an in the core. Even though the number of species sampled varied with remnants, none presented a trend of decrease of species accumulation (Fig. 1), and we assumed that remnants were equally sampled.

The number of species in the core was significantly larger than in the edge of remnants (mixed effect model; $p = 0.036$; Fig. 2).

Species richness did not vary with distance from the edge (mixed effect model; $p = 0.38$), remnant area ($p = 0.83$) and with the interaction area and distance ($p = 0.76$). Remnant shape did not influence the species richness of ants of both categories (mixed effect model; $p = 0.55$).

Shape complexity ($F_{1,7} = 0.56$; $p = 0.48$), remnant area ($F_{1,8} = 5.11$; $p = 0.06$; Fig. 3) and interaction between area and shape ($F_{1,6} = 2.33$; $p = 0.18$) did not influence similarity between species composition at the edge and core of the remnants.

Discussion

Although there is higher species richness in the remnant cores than at their edges, there was no trend of species richness increase towards the forest core, and such a result has already been found by other authors (Carvalho and Vasconcelos 1999; Kotze and Samways 2001; Braschler and Baur 2003). Our results seem to be inconsistent, because there was no trend of species richness increase with distance, but there are differences between edge and core. This might indicate the range of edge effects, which would be smaller than the smallest distance of core sampled. Therefore, edges would affect litter-dwelling ant species richness in a distance smaller than 50m. Edge habitats are considered to be harsher than forest core (Murcia 1995), and this harshness may affect ant species richness. Even thought there is a reported increase of litter accumulation at forest edges (Majer et al. 1997; Carvalho and Vasconcelos 1999), and Campos et al. (2003) reported an increase of ant species richness with litter abundance, this effect did not compensate the edge effects. At the edges there may be more influence of solar radiation and winds, making this habitat harsher than in the forest core.

There is no significant relationship between species richness and shape complexity. A higher shape complexity may provide more habitats to be invaded by opportunist species, which may come for instance from the matrix between remnants (Sobrinho et al. 2003). These invaders may (i) add species to former communities, therefore increasing the number of species, (ii) substitute resident species, thereby maintaining species richness, and (iii) exclude resident species, thereby decreasing species richness (DeSouza et al. 2001). Because forest cores were more speciose than edges, possibly the third process has occurred in the studied system.

Shape complexity did not influence species composition. Nevertheless, there is a weak and non significant trend of decrease of similarity between edge and core in larger remnants. This result would mean that smaller remnants present a more homogenous species composition between edge and core. However, this trend must be interpreted with caution, because it is actually non significant.

Small remnants have their cores more close to the edge than larger remnants. This characteristic may contribute to a higher susceptibility of small remnants to edge effects, in which edge species would disperse into remnants. We expected, thus, that a small remnant was composed virtually of edge habitats (Ochoa-Gaona et al. 2004), or at least with similar environmental conditions of that found in edge habitats. The environmental conditions in edges were harsher, because on the edge solar radiation, temperature and wind velocity are higher (Lovejoy et al. 1986, Laurance and Yensen 1991, Murcia 1995, Laurance 1997, Turton and Freiburger 1997). The higher solar radiation and temperature cause a decrease in moisture, while higher incidence of winds cause more tree falls or, at least, more branch and leaf falls on the edge than in the core of remnants. Thus, litter volume is higher on the edge than in the core, but this litter would be dryer than in the core, impairing ant colonisation and nesting by specialist species. However, opportunist species may benefit from these changes in microclimate, increasing their distribution inside remnants up to the distance influenced by the edge.

Furthermore, small remnants are more invaded by matrix ant species (Sobrinho et al. 2003), and if these remnants present homogenous environmental conditions, invader species tend to spread in the remnant and not to concentrate only on the edge. Schoereder et al. (2004a) noticed that ant population density decreased with decreasing remnant area in the same studied area. Invader species may be competitively superior (Suarez et al. 1998), and might exclude species that were present in the remnant. Such exclusion would occur more easily if original species have suffered a reduction in population size with fragmentation, as verified in the landscape studied.

In large remnants the above described process tends to occur less intensively. The invader species probably do not enter in the core of remnant, because the core conserves more effectively the characteristics of a pristine forest. We suppose that may occur a spatial segregation, i.e., the invader species, edge specialists, remain on the edge, while other species occur in the core. These invader species could exclude by competition some resident species on the edge of the remnants. However, other species, or at least those that were excluded on the edge, would remain intact in the core, where environmental conditions do not allow the establishment of invaders.

The habitat created between the remnants is a relatively new habitat, and species occurring there may be forest gap species that increased their distribution after fragmentation. *Camponotus crassus*, for instance, was not collected in intensive sampling in the same remnants, when this sampling deliberately avoided forest gaps and edges (Schoereder et al. 2004a). This species was frequently sampled, however, in matrices among the same remnants (Sobrinho et al. 2003), and also occurred in our sampling at the edge of six remnants. It has only occurred in the core of two small remnants, and Majer et al. (1997) consider this species a specialist of cleared lands. Even though this result occurred mainly with the cited species, this may be evidence that matrix species are invading small forest remnants, or that forest gap species are increasing their distribution in this region. The environmental harshness of edge habitats, therefore, may serve as a step to generalist species, which use the edge to enter the forest habitats.

Thus, it is important to study not only alterations in species richness due to edge creation, but also alterations in species composition. If we have considered only species richness, we would have concluded that edge creation did not cause changes in ant community. However, we verified that smaller remnants are more homogenous in relation to species composition, i.e., with similar faunas on the edge and in the core.

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Table 1. Ant species sampled on the edge and in the core of tropical rainforest remnants in the region of Viçosa, MG, Brazil.

	Edge	Core
Subfamily Cerapachyinae		
Cerapachys splendens	X	X
Subfamily Dolichoderinae		
Linepithema sp. 2	X	X
Linepithema sp. 5		X
Subfamily Ecitoninae		
Labidus sp.1	X	X
Labidus sp.2	X	
Subfamily Formicinae		
Brachymyrmex sp. 1	X	X
Brachymyrmex sp. 2	X	X
Brachymyrmex sp. 3	X	X
Brachymyrmex sp. 5	X	X
Brachymyrmex sp. 6		X
Brachymyrmex sp. 9	X	X
Camponotus sp. 1	X	
Camponotus sp. 3		X
Camponotus sp. 4	X	X
Camponotus (Myrmobrachys) sp. 1	X	X
Camponotus cingulatus	X	X
Camponotus crassus	X	X
Camponotus rufipes	X	X
Camponotus sericeiventris	X	
Camponotus trapezoideus	X	X
Camponotus vittatus		X
Myrmelachista sp. 1		X
Myrmelachista sp. 2	X	
Paratrechina sp. 1	X	X
Paratrechina sp. 2	X	
Subfamily Myrmicinae		
Acantognathus sp.1		X
Acromyrmex balzani	X	X
Acromyrmex rugosus	X	
Acromyrmex subterraneus	X	X
Atta sexdens rubropilosa	X	
Apterostigma sp. 1	X	X
Basiceros disciger	X	X

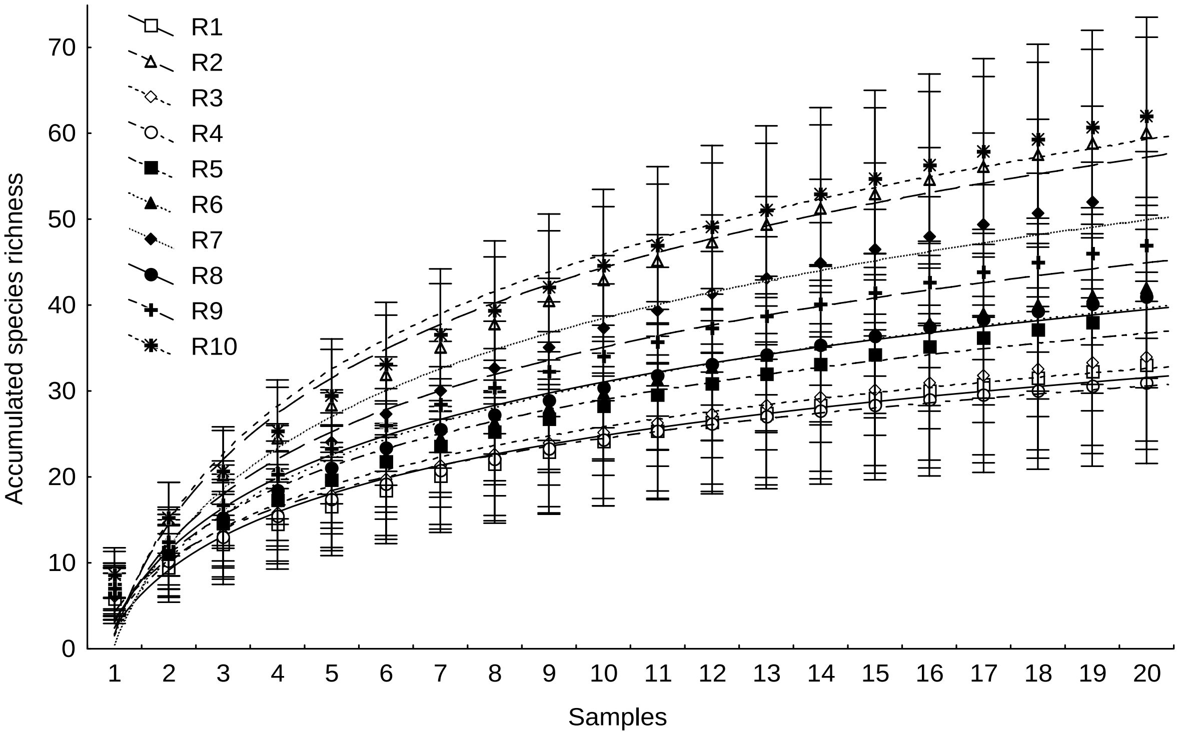
Cephalotes goeldii	X	
Cephalotes pusilus	X	X
Crematogaster sp. 1	X	X
Crematogaster sp. 2		X
Crematogaster sp. 3		X
Crematogaster sp. 4	X	
Cyphomyrmex sp. 1	X	X
Cyphomyrmex sp. 2	X	X
Glamyromyrmex sp. 1	X	X
Hylomyrma sp. 1	X	X
Leptothorax sp. 1	X	
Megalomyrmex sp. 1	X	X
Megalomyrmex sp. 2		X
Megalomyrmex sp. 3		X
Megalomyrmex sp.4		X
Monomorium floricula	X	X
Mycocepurus goeldi	X	X
Octostruma rugifera		X
Octostruma iheringi		X
Oligomyrmex urichi	X	
Oxypoecus sp. 1		X
Pheidole sp. 1	X	X
Pheidole sp. 2	X	X
Pheidole sp. 3		X
Pheidole sp. 4	X	X
Pheidole sp.5	X	X
Pheidole sp. 6	X	
Pheidole sp. 7		X
Pheidole sp.8	X	X
Pheidole sp.9	X	X
Pheidole sp.10	X	X
Pheidole sp.12	X	X
Pheidole sp.13	X	X
Procryptocerus sp.1	X	X
Procryptocerus sp. 2		X
Pyramica subedentata		X
Pyramica sp. 1	X	X
Rogeria sp. 1	X	X
Rogeria sp. 2		X
Rogeria sp. 3	X	
Sericomyrmex sp. 1	X	X
Sericomyrmex sp.2	X	X
Solenopsis saevissima	X	
Solenopsis sp. 1	X	X
Solenopsis sp. 3	X	X
Solenopsis sp. 4		X
Solenopsis sp. 5	X	X
Solenopsis sp. 16	X	

Solenopsis sp. 17		X
Solenopsis sp. 18	X	X
Solenopsis sp. 19		X
Strumigenis perpava	X	X
Strumigenys sp. 1	X	X
Strumigenys sp. 2		X
Strumigenys sp. 3		X
Wasmannia auropunctata	X	X
Wasmannia sp. 3		X
Subfamily Ponerinae		
Amblyopone lurilabes	X	X
Anochetus diengensis	X	X
Anochetus sp.1	X	X
Ectatomma edentatum	X	X
Ectatomma permagnum	X	
Gnamptogenys acuminata	X	X
Gnamptogenys minuta		X
Gnamptogenys striatula	X	X
Gnamptogenys sp. 1	X	X
Gnamptogenys sp. 3		X
Heteroponera dentinotalis		X
Heteroponera sp.1		X
Heteroponera sp.2		X
Hypoponera sp.1	X	X
Hypoponera sp.7	X	X
Hypoponera sp.8		X
Hypoponera sp.9	X	X
Hypoponera sp.10		X
Hypoponera sp.11	X	X
Odontomachus chelifer	X	X
Odontomachus meinerti	X	X
Pachycondyla sp.1		X
Pachycondyla prox. venusta		X
Pachycondyla striata	X	X
Pachycondyla ahruaca	X	
Pachycondyla harpax	X	X
Subfamily Pseudomyrmecinae		
Pseudomyrmex gracilis	X	
Pseudomyrmex tenuis	X	X

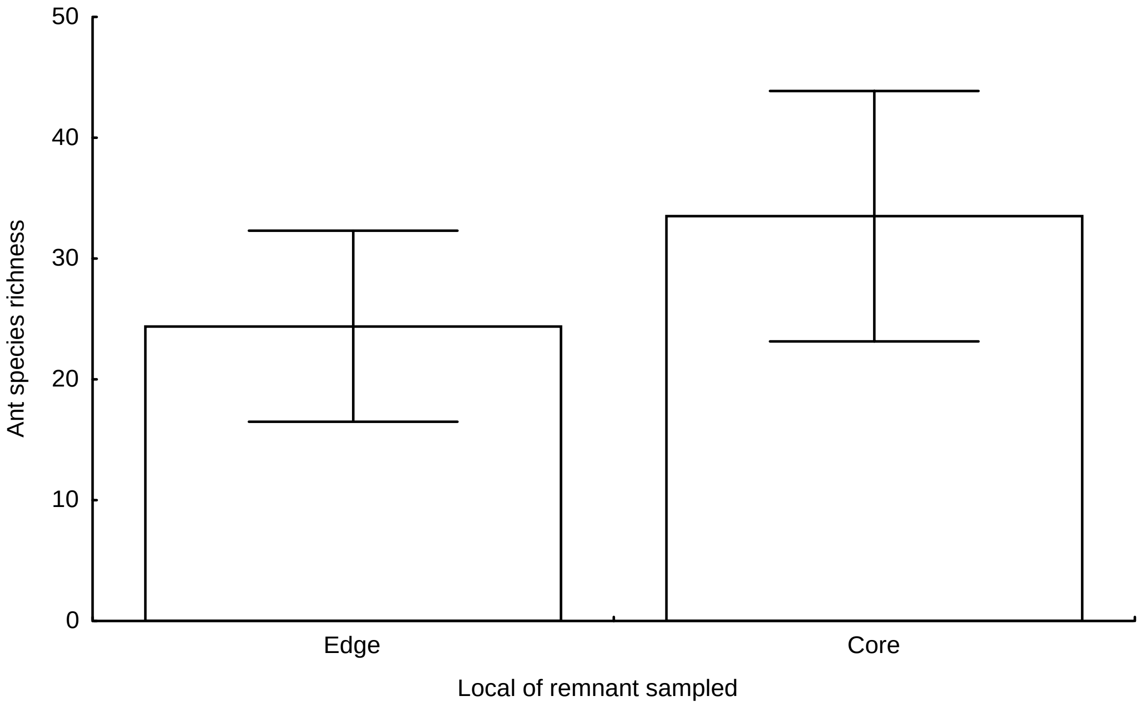
Figure 1 – Species accumulation curves for the ants sampled in the ten remnants studied (R1 to R10). Points are observed accumulated species richness and vertical bars are confidence intervals.

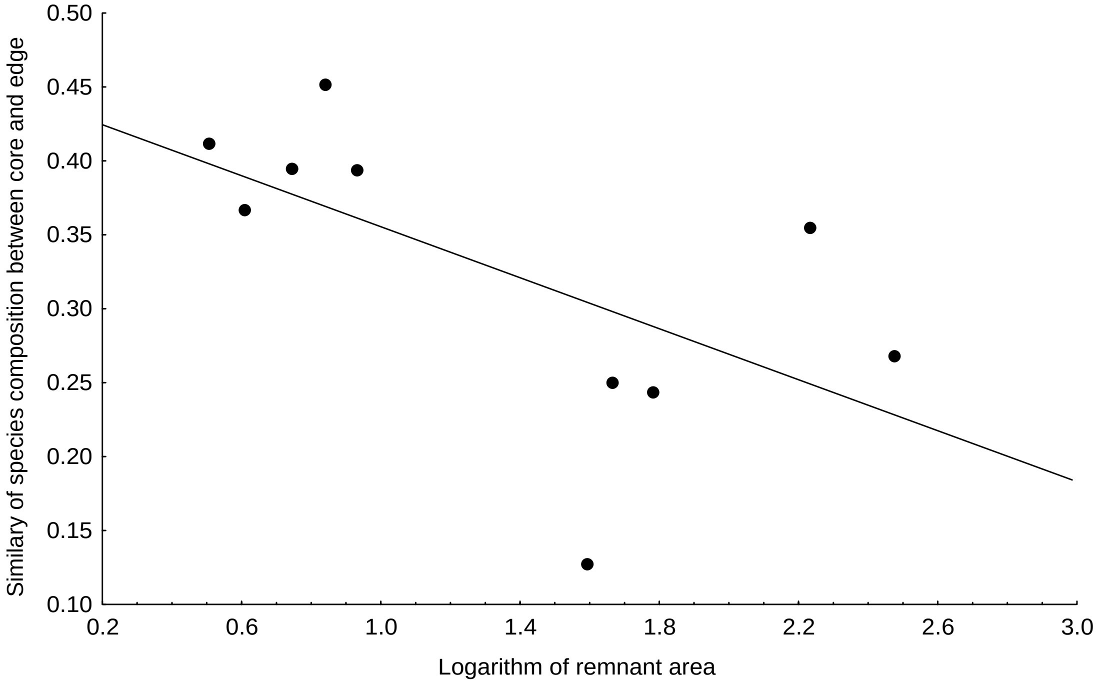
Figure 2 – Ant species richness at forest core and edge. Forest cores presented higher species richness than edges (mixed effect model; $p = 0.036$).

Figure 3 – Relationship between similarity of species composition between forest cores and edges and the logarithm of remnant area. There was a non significant trend of decrease of similarity with area ($F_{1,8} = 5.11$; $p = 0.06$).



R1
R2
R3
R4
R5
R6
R7
R8
R9
R10
Accumulated species richness
0
10
20
30
40
50
60
70
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
Samples


50
40
30
20
10
0
Ant species richness
Edge
Core
Local of remnant sampled


0.50
0.45
0.40
0.35
0.30
0.25
0.20
0.15
0.10
Similary of species composition between core and edge
0.2
0.6
1.0
1.4
1.8
2.2
2.6
3.0
Logarithm of remnant area

CONCLUSÕES GERAIS

Independentemente da relação espécie-área ser considerada uma das poucas "leis" em Ecologia (Rosenzweig 1995, Ricklefs & Lovette 1999), os resultados sugerem que mecanismos ecológicos parecem atuar nas comunidades de formigas que vivem em fragmentos florestais, causando principalmente alterações na composição de espécies. Dentre esses mecanismos pode-se destacar a importância dos processos de colonização e extinção, bem como os efeitos de borda e de forma sobre as comunidades de formigas.

Fragmentos menores parecem sofrer maior invasão de espécies das áreas de matriz, uma vez que os mesmos se mostram mais similares em termos de composição específica com estas. Este padrão provavelmente é devido a uma maior similaridade das áreas de borda com o ambiente da matriz (Martins 1989, Gascon *et al.* 1999), visto que os fragmentos menores apresentam uma maior borda relativa (Murcia 1995). Além disso, o interior dos fragmentos menores está mais próximo da borda, sendo por isso mais parecido com a mesma e, conseqüentemente com a matriz circundante. As espécies de matriz, sendo generalistas e competitivamente superiores (Suarez *et al.* 1998), podem levar à extinção de espécies especialistas em florestas nos fragmentos pequenos, já que nestes as populações são menores (freqüência diminui com a diminuição da área do remanescente) e mais próximas de um tamanho crítico.

Sendo assim, pelo menos para a comunidade de formigas, fragmentos menores parecem estar realmente mais susceptíveis a processos ecológicos gerados pela fragmentação que causam alterações na riqueza e composição de espécies. Era de se esperar que áreas menos isoladas apresentassem maior colonização (Robison e Quinn 1988) e dessa forma populações residentes em pequenos fragmentos poderiam ter as chances de extinção diminuídas pela constante recolonização de espécies extintas localmente ("efeito resgate") vindas de áreas vizinhas, se estas fossem próximas.

Entretanto, a taxa de colonização não variou com o grau de isolamento do fragmento e, além disso, ocorreu uma maior taxa de extinção nos fragmentos menores. Estes dados já são bastante interessantes, mas o mais interessante é que neste estudo verificou-se que estes mecanismos que agem em escala regional (colonização e extinção) não são gerais, variando de acordo com a identidade da espécie estudada. Espécies generalistas (aquelas que ocorrem tanto na matriz quanto na floresta) comportam-se de forma diferente das especialistas (presentes apenas nas florestas). Formigas generalistas colonizam mais freqüentemente os fragmentos pequenos, enquanto as especialistas de florestas colonizam mais os fragmentos grandes. Há também diferenças na taxa de extinção, sendo as formigas generalistas mais susceptíveis à extinção dentro dos fragmentos do que as especialistas, independentemente da área do fragmento. Estes resultados ajudam a fortalecer uma tendência cada vez mais forte de se estudar não apenas as áreas remanescentes que restaram do processo de fragmentação, mas a paisagem como um todo, pois mostra que as espécies que habitam as áreas de matriz contribuem para os padrões observados nos fragmentos. Algumas espécies ocorrem apenas em áreas de matriz (neste caso, pastagens) não estando presentes em áreas de floresta. Embora difícil de testar, uma vez que não há dados da composição de espécies de formigas nas florestas originais antes da fragmentação, é necessário saber a origem destas espécies de matriz, as quais podem ser inclusive exóticas.

Species richness did not vary with distance from the edge (mixed effect model; $p = 0.38$), remnant area ($p = 0.83$) and with the interaction area and distance ($p = 0.76$). Remnant shape did not influence the species richness of ants of both categories (mixed effect model; $p = 0.55$).

Shape complexity ($F_{1,7} = 0.56$; $p = 0.48$), remnant area ($F_{1,8} = 5.11$; $p = 0.06$; Fig. 3) and interaction between area and shape ($F_{1,6} = 2.33$; $p = 0.18$) did not influence similarity between species composition at the edge and core of the remnants. A riqueza de espécies de formigas foi maior no centro do que na borda dos fragmentos de diferentes áreas, confirmando as tendências apontadas quando estes foram examinados com relação às espécies de matriz, ou seja de que o ambiente de borda pode representar um habitat mais hostil. Isto pode ser explicado pelo fato de que embora a complexidade de forma não influencie a similaridade na composição de espécies entre borda e centro, os menores possuem uma maior borda relativa. Sendo assim, estes tendem a ser mais homogêneos em termos de condições ambientais, o que acarreta também maior homogeneidade em termos de composição de espécies.

Nos três capítulos fica claro que a fragmentação altera a composição de espécies de formigas e que estas alterações são mais pronunciadas em áreas menores, mesmo que os mecanismos testados em cada um deles sejam diferentes. Dessa forma, algumas conclusões gerais podem ser tiradas e merecem atenção, como por exemplo, o fato de diferentes grupos responderem de forma dissimilar a fragmentação. No caso das formigas, pode-se perceber que existem espécies que são especialistas em matriz de pastagem, outras que são especialistas em habitas de florestas, e que outras são generalistas. A modificação na composição específica reflete estas diferenças e a tendência parece ser de diminuição de espécies especialistas de florestas em áreas menores e mais perturbadas, nas quais as generalistas se tornam cada vez mais abundantes.

Durante muitas décadas os estudos de fragmentação focaram seus interesses na relação espécie-área e na Teoria de Biogeografia de Ilhas (MacArthur & Wilson 1967). Entretanto, nem todas as espécies respondem da mesma maneira ao mesmo grau de fragmentação e um estudo focado na identidade das espécies pode ser mais informativo do ponto de vista conservacionista. Além disso, um estudo da totalidade da paisagem fragmentada deve ser feito a fim de se entender como agem os processos locais e regionais na estruturação das comunidades em ambientes fragmentados.

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