CARLA RODRIGUES RIBAS

GRADIENTE LATITUDINAL DE RIQUEZA DE ESPÉCIES DE FORMIGAS EM CERRADO: REGRA DE RAPOPORT E EFEITOS DA PRODUTIVIDADE E HETEROGENEIDADE

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

VIÇOSA
MINAS GERAIS - BRASIL
2006

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APROVADA: 23 de fevereiro de 2006

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“Somos do tamanho dos nossos sonhos.”

Fernando Pessoa

À Eduarda que me ensina todos os dias o que é o amor,

dedico...

AGRADECIMENTOS

Ao Zhé por ter sido meu exemplo todos esses anos e por tudo que passamos juntos.

Ao Carlos por ter sido fonte de inspiração ou de piração, sempre.

Aos meus dois melhores amigos, Rogério e Renata, que sempre estão prontos pra me dar colo, mesmo longe.

À Duda por existir.

Aos meus pais, minha tia e a minha avó por serem sempre meu exemplo e todo apoio necessário.

À D. Maria que virou minha mãe em Viçosa.

À Carina e ao Marco que são pessoas sempre presentes, sempre companheiras e que se tornaram meus grandes amigos.

Ao João por ter concordado em realizar meu pedido e por ter se tornado tão companheiro.

Aos amigos que me ajudaram com o trabalho de campo, Carla, Marcelo, Rogério, Zhé e Renata.

Ao pessoal do IBAMA, aos diretores dos parques, estações e floretas nacionais por terem permitido e colaborado com a realização desse trabalho sem o qual não seria possível a realização dessa tese.

Aos amigos que sempre estiveram dispostos a ler mais uma versão dos artigos e sem cara feia, principalmente para o Leandro e Renata.

Ao Arne por ter ajudado na redação dos artigos e na discussão da minha tese como um todo.

Ao pessoal do laboratório por ter me ajudado com as infinitas dúvidas nesses quatro anos.

Ao Og e ao Ronaldo por terem ajudado com as análises “eRradas”.

Ao Adrian por ter me ajudado com o segundo artigo e principalmente por ter se tornado meu amigo.

Ao Crodoaldo pela companhia sempre que preciso, as 18:00h no Moreira’s.

Ao Hildo por trazer sempre a mais gelada.

Ao Carlinhos e a Ritinha por fazerem o trailer ser tão bom.

Aos estagiários do laboratório que sempre (ou quase sempre) me fazem ficar de bom humor, principalmente ao João Vítor, Washington, Ricardo e Clarice.

À D. Paula, à Mirian e todos os professores e colegas da pós-graduação pelo apoio durante o doutorado.

À Universidade Federal de Viçosa e à CAPES sem as quais não seria possível a realização dessa tese.

À British Ecological Society e à The Nature Conservancy do Brasil pelo apoio financeiro sem o qual não seria possível a realização dessa tese.

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RESUMO

RIBAS, Carla Rodrigues, D.S., Universidade Federal de Viçosa, fevereiro de 2006. **Gradiente latitudinal de riqueza de espécies de formigas em cerrado: regra de Rapoport e efeitos da produtividade e heterogeneidade.** Orientador: Carlos Frankl Sperber. Conselheiros: José Henrique Schoereder e Og Francisco Fonseca de Souza.

O gradiente latitudinal de riqueza de espécies (GLRE) é um padrão bem documentado para diversos grupos de organismos. Apesar de várias hipóteses terem sido levantadas para explicar o gradiente algumas são tidas como mais promissoras, tais como as relacionadas à energia, a heterogeneidade ambiental, ao tempo evolutivo e ao efeito do domínio mediano. O objetivo dessa tese é testar a existência do gradiente latitudinal de riqueza de espécies de formigas arborícolas em cerrado, assim como testar hipóteses explicativas para o padrão encontrado. No primeiro capítulo propusemos um método que permite testar o efeito Rapoport em gradientes altitudinais, latitudinais e em distribuições que são restritas arbitrariamente pela área amostrada pelo pesquisador. Re-analisamos 55 distribuições publicadas em 39 artigos e observamos diversos padrões de correlação entre a extensão de ocorrência das espécies e seu ponto médio de distribuição, poucos evidenciando o efeito Rapoport. A maioria dos métodos utilizados até hoje para testar o efeito Rapoport não são capazes de distinguir entre padrões determinísticos e aqueles gerados pelo acaso e o efeito Rapoport não deve ser considerado como um padrão em macroecologia. No segundo capítulo, o objetivo foi testar a existência do GLRE de formigas no Cerrado e a hipótese de que o gradiente é correlacionado com a produtividade e heterogeneidade do habitat em diferentes escalas espaciais. Observamos um aumento da riqueza de espécies com a latitude, um gradiente latitudinal oposto ao encontrado na literatura. As variáveis ambientais analisadas não explicaram a variação da riqueza de espécies. Provavelmente, processos importantes em escalas espaciais locais não levam a variação da riqueza de espécies em escalas globais. No terceiro capítulo testamos a existência do efeito do domínio mediano e do efeito Rapoport usando modelos nulos. Encontramos uma riqueza de espécies maior do que esperado pelo efeito do domínio mediano em locais de maior latitude e ao invés do efeito Rapoport, as extensões de ocorrência das espécies são maiores do que o esperado pelo acaso somente nos limites do domínio. Outras hipóteses como a distribuição geográfica do Cerrado e a história evolutiva das espécies de formigas devem ser investigadas como causadoras do gradiente latitudinal reverso de riqueza de espécies de formigas arborícolas em Cerrado.

ABSTRACT

RIBAS, Carla Rodrigues, D.S., Universidade Federal de Viçosa, February 2006. **Latitudinal pattern of arboreal ant species richness: testing Rapoport's effect and the effect of productivity and heterogeneity.** Advisor: Carlos Frankl Sperber. Committee members: José Henrique Schoereder and Og Francisco Fonseca de Souza.

The latitudinal gradient in species richness is a well recognized pattern for several taxa. Although many hypotheses have been proposed to explain this gradient some of them are described as more relevant, such as those related to ambient energy, habitat heterogeneity, evolutionary time and mid-domain effect. The aim of this thesis was to test the existence of the latitudinal gradient in arboreal ant species richness at Cerrado, as well as to test explanatory hypothesis for the pattern found. In the first chapter we proposed a method that allowed testing the Rapoport effect in altitudinal and latitudinal distributions and in distributions that are restricted by the sampled area. We re-analysed 55 distributions published in 39 scientific papers and observed several patterns of correlation between range size and midpoint, few of them showing a Rapoport effect. Most statistical methods used up to now to test the Rapoport effect were not able to distinguish between stochastically and deterministically generated patterns, therefore the Rapoport effect should not be considered as a pattern in global ecology. In the second chapter the aim was to test the existence of the latitudinal gradient in arboreal ant species richness at Cerrado and the hypotheses that this gradient was correlated to habitat productivity and heterogeneity at different spatial scales. We observed an increase in species richness with latitude, a reverse latitudinal gradient from that observed in the scientific literature. The environmental variables analysed in this study did not explain the variation in species richness. Probably, processes acting at local spatial scales did not scale up to larger scales. In the third chapter we tested the existence of the mid-domain effect and the Rapoport effect using null models. We found a larger species richness than expected by the mid-domain effect at higher latitudes and instead of the Rapoport effect we observed larger ranges sizes than expected by null assumptions at the boundaries of the domain. Other hypotheses, such as the Cerrado geographical distribution and the evolutionary history of ant species, should be tested as the cause of the reverse latitudinal gradient in arboreal ant species richness at Cerrado.

INTRODUÇÃO GERAL

O gradiente latitudinal de riqueza de espécies (GLRE) é um padrão encontrado para vários grupos de organismos e já foram levantadas mais de 30 hipóteses para explicá-lo (Willig et al. 2003; Hawkins and Agrawal 2005). Ultimamente existem algumas hipóteses que são tidas como mais promissoras, tais como as relacionadas à energia, à heterogeneidade ambiental, ao tempo evolutivo e ao efeito do domínio mediano (Turner 2004; Bjorholm et al. 2005; Brayard et al. 2005; Mora and Robertson 2005; Rex et al. 2005).

As hipóteses relacionadas à energia e a hipótese da heterogeneidade ambiental são na verdade fatores correlacionados à latitude e não mecanismos que poderiam explicar o aumento do número de espécies em direção ao equador (Hawkins and Diniz-Filho 2004). Mesmo assim esses dois fatores estão freqüentemente correlacionados à riqueza de espécies em vários grupos (Tews et al. 2004; Evans et al. 2005).

A hipótese do efeito do domínio mediano (EDM) prevê que a alocação aleatória de espécies com diferentes tamanhos de distribuição dentro de um domínio com limites geográficos produz um pico de riqueza de espécies no meio desse domínio (Colwell and Hurtt 1994; Colwell and Lees 2000). Apesar de existir bastante controvérsia sobre o uso do EDM como um modelo nulo para explicar o GLRE (Colwell et al. 2005; Hawkins et al. 2005; Zapata et al. 2005), Colwell et al. (2004) revisaram diversos trabalhos que testaram esse efeito chegando à conclusão de que esse é um efeito importante na explicação de gradientes de riqueza de espécies.

Outro padrão que algumas vezes é relatado como sendo um mecanismo que poderia causar o GLRE é a regra de Rapoport (Stevens 1989), que prevê uma relação positiva entre o tamanho da distribuição das espécies e a latitude. Apesar dos problemas com diversas metodologias que são utilizadas para se testar essa relação (Gaston et al. 1998), recentemente tem sido encontrada em alguns grupos (e.g. Fortes and Absalão 2004; Arita et al. 2005; Folgarait et al. 2005). Gaston et al. (1998) criticaram a visão de que esse padrão seja considerado uma regra, uma vez que é um fenômeno local e não se aplica ao hemisfério sul, sugerindo o termo efeito Rapoport como mais plausível. Os resultados de trabalhos que testam o efeito Rapoport como causa do GLRE são conflitantes (Rohde 1996; Fleishman et al. 1998; Kolasa et al. 1998; Taylor and Gaines 1999; Smith and Gaines 2003).

O objetivo dessa tese é testar a existência do gradiente latitudinal de riqueza de espécies de formigas arborícolas em cerrado, assim como testar hipóteses explicativas para o padrão encontrado. A tese encontra-se dividida em três capítulos, cada um correspondendo a um artigo científico.

No primeiro capítulo propusemos um método modificando um modelo nulo anteriormente proposto por Lyons and Willig (1997), que permite testar o efeito Rapoport tanto em gradientes altitudinais quanto em gradientes latitudinais. Esse método permite também testar o efeito em distribuições que são restritas arbitrariamente pela área amostrada pelo pesquisador. Para isso, levantamos a hipótese de que a extensão de ocorrência das espécies é similar àquela esperada pela simples imposição de limites a essas extensões (distribuição nula). Quando as distribuições são diferentes da esperada pelo acaso, deve-se testar a hipótese de que as distribuições correspondem àquelas esperadas pelo efeito Rapoport. Nesse capítulo utilizamos esse novo método para re-analisar 55 distribuições publicadas em 39 artigos.

No segundo capítulo, o objetivo foi testar a existência do gradiente latitudinal de riqueza de espécies de formigas arborícolas no Cerrado. Testamos também se o gradiente é correlacionado com a produtividade do habitat, a heterogeneidade de recursos e a heterogeneidade estrutural do ambiente e qual a influência das diferentes escalas espaciais no gradiente e nos fatores correlacionados. Esse trabalho foi realizado com dados coletados em 11 unidades de conservação no cerrado em três escalas espaciais, abrangendo um gradiente latitudinal de 14°.

No terceiro capítulo testamos a existência do efeito do domínio mediano e do efeito Rapoport na comunidade de formigas arborícolas em Cerrado, usando modelos nulos. Esses modelos excluem o efeito de gradientes espaciais causados por variáveis ambientais incluindo somente limitações geográficas na distribuição das extensões de ocorrência das espécies. Se os padrões observados são diferentes do esperado pelo acaso, pode-se deduzir que mecanismos biológicos podem ser responsáveis pelos gradientes observados. Esse trabalho também foi realizado com dados coletados em 11 unidades de conservação no cerrado.

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Running Title: Rapoport effect revisited

Is the Rapoport effect widespread? Null models revisited

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Artigo aceito em Global Ecology and Biogeography

Abstract.

1. Aim To test the Rapoport effect using null models and data sets taken from literature. We proposed an improvement on an existing method, testing Rapoport effect in elevational and latitudinal distributions when the sampled distributions are restricted by the latitudinal/elevational variation sampled.

2. Location Global.

3. Methods First, we hypothesized that real range size distributions were similar to those expected by imposing boundaries or limits to species distributions (null distribution). When these distributions were different from those expected under the null assumptions, we tested the hypothesis that these distributions corresponded to those expected when a Rapoport effect would occur. We used two simulation methods, random and pseudo-random, which differed only in that the latter one assumes fixed species midpoints, coinciding with real midpoints. The observed correlations were compared with the frequency distribution of 1,000 simulations, using both simulation methods. We compared the parameters of the correlation curves generated by 1,000 simulations with those of the observed distributions, testing whether correlations indicated a Rapoport effect.

4. Results Several significant patterns of correlations between range size and midpoint were observed in the data sets when compared to random and pseudo-random simulations. Nevertheless, few results indicated a Rapoport effect and correlations between range size and midpoint were frequently similar to that expected under the null assumptions.

5. Main conclusions Using null models and midpoint as a distribution parameter we were unable to confirm the Rapoport effect in many data sets studied. Even though some recent studies have supporting this effect, our results suggest that the Rapoport effect is not widespread as a pattern in global ecology.

6. Keywords: Altitude; Biogeography; Distribution; Latitude; Meta-analysis; Mid-Domain Effect; Null models; Range size.

Introduction

The term Rapoport's rule has been proposed by Stevens (1989) to describe a pattern of global species distribution. The rule suggests that a latitudinal increase in the size of species distributions (hereafter, range size) occurs when one moves from the equator to the poles. Following the same reasoning, Stevens (1992) extended Rapoport’s rule to elevational gradients in which there would be a positive relationship between range size and altitude. There are many mechanisms proposed to account for this controversial pattern and the possible explanations of the Rapoport's rule are beyond the scope of this paper (more details can be found in Folgarait *et al.*, 2005; Hernández Fernández & Vrba, 2005a; Parmesan *et al.*, 2005).

Several authors have noticed the coincident patterns of Rapoport’s rule and the gradient in species richness and some of them tested for a causal relationship between these patterns, but results are still inconclusive (Rohde, 1996; Rohde & Heap, 1996; Fleishman et al., 1998; Kolasa et al., 1998; Taylor & Gaines, 1999; Smith & Gaines, 2003). Willig et al. (2003) reported that some taxa exhibited a marked latitudinal gradient without showing Rapoport's rule, concluding that this hypothesis did not explain well the gradient of species richness.

Disregarding the relationship between Rapoport's rule and gradients of species richness, several papers have documented the rule in studies of spatial distribution of species (e.g., Stevens, 1992; Fleishman et al., 1998; Harcourt, 2000; Cardillo, 2002; Sanders, 2002; Fortes & Absalão, 2004, and see Gaston, 2003, for an extensive review of the groups that have been studied). However, Blackburn & Gaston (1996) reported that Rapoport’s rule might not be so widespread, because it has been described mostly in the northern hemisphere, and they suggested the term Rapoport effect as more suitable.

Different methodologies were used to test the relationship between range size and latitude or altitude. Stevens' method (1989) consists of dividing the area considered in latitudinal bands, calculating and regressing the average latitudinal range size of all species occurring in each band against latitude. This method creates a statistical difficulty because it includes the same species several times, generating non-independent data (Rohde et al., 1993). In Rohde's midpoint method (following Rohde et al., 1993), for each species the mean range extent (midpoint) is calculated and then regressed against range extent. Pagel et al. (1991) suggested the most-distal point method, which categorizes a species by the latitude within its range that is farthest from the equator, and then range size is regressed against most-distal latitude within that range.

The use of different methodologies to test the Rapoport effect and the lack of such relationships in the southern hemisphere (Gaston et al., 1998; Reed, 2003; Hernández et al., 2005) and in some taxa (Rohde et al., 1993) has prevented clarification of the importance of Rapoport rule as a general pattern of species distribution. Nathan & Werner (1999) suggested that a more critical and formal method, which does not suffer from statistical biases, is currently needed. Ashton (2001) recommended that meta-analytical techniques would be particularly useful to assess the generality of ecological patterns, such as the Rapoport effect.

Lyons & Willig (1997) suggested a method to test the Rapoport effect based on range size distributions limited by geographic boundaries. Colwell & Hurtt (1994) had already predicted that range extents should increase towards the centre of domains, and that small ranges could be located closer to domain boundaries. The Lyons & Willig's (1997) method is able to distinguish stochastically produced patterns from those affected by biological mechanisms using null models.

Recently, a new perspective to test for gradients in species richness came from the mid-domain effect (Colwell & Hurtt, 1994; Colwell et al., 2004; Mora & Robertson, 2005; Arita, 2005, but see Zapata et al., 2003), in which there is a peak in species richness in the centre of a domain, caused only by imposing physical or ecological boundaries to the limits of this domain. The random placement of ranges within these boundaries generates a species richness peak, independently of biological mechanisms. Mid-domain models predict that not only more ranges will pile up in the centre of a domain, but that range sizes will be larger in the centre of a domain as a function of geometric constraints.

In this paper, we proposed an improvement to the method of Lyons & Willig (1997), allowing the test for Rapoport effects both in elevational and latitudinal distributions, even when described distributions are restricted by the latitudinal range sampled. First, we hypothesized that range size distributions were similar to those expected by imposing boundaries to these distributions (null distribution). When these distributions were different from those expected under null assumptions, we tested the hypothesis that these distributions corresponded to those expected under a Rapoport effect.

Material and Methods

Data sets

We used distributional data from 39 studies (see Appendix S1 in Supplementary Material). Some papers contained data about more than one taxa distribution, totalling 55 data sets. We selected the papers using the keywords "Rapoport", "distribution", "latitude", "altitude", and "range size" in the ISI Web of Knowledge (http://isi02.isiknowledge.com/portal.cgi). We chose the studies selecting those that contained species distributions per latitude or altitude. This group of papers describes the distribution of several taxa, in northern and southern hemispheres or both, independent of including tests of the Rapoport effect.

Latitudinal distributions – expected null correlations

Following Lyons & Willig (1997), the first step to analyze latitudinal distributions was to describe the expected correlation between range size and mid-latitude. Stevens (1989) and Rohde et al. (1993) expected a positive correlation between range size and a latitudinal descriptor, but Lyons & Willig (1997) demonstrated an inverse correlation among these variables because the end of northern and southern continents (hard boundaries) impose a constraint such that ranges become smaller when one moves to higher latitudes in both directions (see Fig. 1 in Lyons & Willig, 1997). In lower latitudes, larger ranges might occur due to the lack of boundaries that restrict the extent of the ranges. We used midpoint instead of the most distal point because its use eases the detection of deterministic patterns in range sizes (Lyons & Willig, 1997).

We expected a negative correlation between range size and mid-latitude, when there are hard boundaries in the northern and southern limits of range distributions, and when ranges encompass an entire continent, including zero latitude and extending to north and south latitudes. In our data, these criteria are matched by the data from Rohde (1999) and Harcourt (2000).

Lyons & Willig (1997), however, did not account for distributions that are limited because sampling was carried out in a latitudinal extent smaller than real distributions of species studied. In that case, there are no true hard boundaries present. The boundaries define an arbitrary domain (sensu Colwell et al., 2004) and they are the highest and the lowest latitudes in which sampling was carried out (Fig. 1). In these cases, using midpoint as a latitudinal descriptor, we expected smaller ranges close to the limits of the sampled area and larger ranges in the centre of the sampled area independent of latitude. The expected null correlation between range size and midpoint in these data, considering only sampling boundaries, was quadratic with a peak in range sizes at intermediate sampling latitudes. All data sets of latitudinal distributions, except for Rohde (1999) and Harcourt (2000), were descriptions of latitudes ranging in a smaller scale than the entire continent and they were analyzed using this expected quadratic correlation.

Latitudinal distributions – linear correlation analysis

We calculated range size and mid-latitude for each species distribution in each data set as a function of latitude, for test the linear correlation between range size and mid-latitude. Subsequently we calculated the correlation between range size and mid-latitude, using Pearson product-moment coefficient.

We randomized range size and mid-latitude using the two models proposed by Lyons & Willig (1997) both assuming hard boundaries: random and pseudo-random simulations, for create a random distribution. Random simulation randomized range size and mid-latitude, and pseudo-random simulation randomized only range sizes, with the midpoints having exactly the same distribution as in the real data. Pseudo-random simulations, therefore, were not completely stochastic because they maintained the empirical midpoints of species distributions.

In each model, we randomized the variables 1,000 times and calculated the correlation between range size and mid-latitude for each simulation using Pearson coefficient. As a result, we obtained a frequency distribution of simulated Pearson coefficients (1,000) and a single observed coefficient value for each data set. If the real coefficient was within the 95% limits of frequency distribution of the simulated coefficients, we accepted the null hypothesis that the correlation between range size and midpoint was the same as expected by chance alone (null assumptions assuming hard boundaries). Because this test is two-tailed, we accepted null hypothesis with $p > 0.025$.

If the observed correlation coefficient was different from that produced by the simulation, we investigated why this difference occurred. There are two possible results: a positive or a negative correlation. If we observed a positive correlation between range size and mid-latitude, this represents smaller range sizes in lower latitudes and larger range sizes in higher latitudes than expected by chance, i.e. the expected Rapoport effect. However, even if we found a negative correlation, we had to test for the Rapoport effect, because a lower slope than expected by chance means smaller range sizes at lower latitudes and larger range sizes at higher latitudes, i.e. the expected Rapoport effect. We calculated the slope of correlation for the observed data sets, and for each simulated distribution, generating a frequency distribution of 1,000 simulated values. We then compared the observed slope with the frequency distribution of 1,000 simulated ones. If the observed slope was below the 95% limits of frequency distribution, we rejected the null hypothesis and accepted the existence of a Rapoport effect.

Latitudinal distributions – quadratic correlation analysis

To test if the correlation between range size and mid-latitude was different from that expected under the inclusion of sampling boundaries when the data did not include latitudinal variation extending to north and south latitudes of the equator (Fig. 1), we calculated the correlation coefficient (r) of the following quadratic correlation for each latitudinal distribution data,

$$y = a + bx + cx^2$$

where y is range size, a, is the intercept, b, and c are equation parameters, and x is the mid-latitude.

The expected correlation follows a triangular distribution of points because the upper corners represent combinations of midpoints and range that are geometrically impossible (Colwell & Hurtt, 1994). The quadratic model was chosen because it was the simplest model describing a unimodal distribution.

We calculated r and a, b, and c parameters for all data sets with restricted latitudinal sampled areas (Sokal & Rohlf, 1981). We then simulated 1,000 random and 1,000 pseudo-random distributions and for each simulation we calculated the correlation coefficient, obtaining a frequency distribution of 1,000 coefficients, comparing each observed correlation coefficient with the 95% frequency distribution. If the observed coefficient was outside the 95% limits of the simulated frequency distribution coefficients, we rejected the null hypothesis that the correlation between range size and midpoint was the same as the one expected by chance alone (null assumptions assuming sampling boundaries) and we would investigate why these differences appeared.

If there was a Rapoport effect, we would expect range sizes smaller than expected by chance in low latitudes and higher than expected by chance in high latitudes (Fig. 2). Therefore, to check for the Rapoport effect, we calculated a, b, and c parameters (Sokal & Rohlf, 1981) for each of the 1,000 simulations in each simulation model (random and pseudo-random) and compared the frequency distribution of 1,000 simulated values with that calculated for observed distributions.

Elevational distributions – expected null correlations and analysis

Stevens (1992) also expected a positive correlation between range size and mid-altitude, but if we consider that the base and the top of mountains are hard boundaries (Colwell & Hurtt, 1994; Rahbek, 1997; Colwell & Lees, 2000; Sanders, 2002), the expected null correlation would also be quadratic with a peak in range sizes at intermediate altitudes (Fig. 3). At higher and lower altitudes, we expected smaller range sizes. This is the expected correlation for all our data of elevational distributions.

We used the same procedure as the one to test the quadratic correlation in latitudinal distributions to test if the correlation between range size and mid-altitude is different from that expected under the inclusion of hard boundaries.

Results

Latitudinal distributions

The coefficients of linear correlation between range size and mid-latitude were smaller than expected by chance in the two data distributions analyzed (Rohde, 1999; Harcourt, 2000), using the two methods of simulation (random and pseudo-random) (see Appendices S2 and S3 in Supplementary Material). However, the correlations showed range sizes larger than expected by chance at small latitudes and smaller than expected by chance at high latitudes (see Appendices S2 and S3 in Supplementary Material; Fig. 4). Because this pattern seems the opposite of the expected by the Rapoport effect, we called hereafter a reverse Rapoport, even though we have to consider that the real reverse Rapoport would be based on the average range size distributions (Stevens 1989)

In the analysis of the quadratic correlation between range size and mid-latitude, five correlations were significantly different from that expected by chance in the random simulations and one in the pseudo-random simulations. From these, three results were observed: smaller range sizes at the boundaries, a reverse Rapoport and one Rapoport effect (see Appendices S2 and S3 in Supplementary Material; Fig. 5abc).

Elevational distributions

In the random simulations, 34 correlations were different from expected by chance (see Appendix S2 in Supplementary Material) and 10 were similar to that expected by chance. Among the 34 significant correlations, four supported a Rapoport effect (see Appendix S2 in Supplementary Material; Fig. 5c). Other results observed were: (i) parameters of the observed curves significantly equal to that obtained in the simulations (Fig. 5d); (ii) larger range sizes in all altitudes (Fig. 5e); (iii) smaller range sizes at the boundaries (Fig. 5a); and (iv) reverse Rapoport (Fig. 5b) (see Appendix S2 in Supplementary Material).

In the pseudo-random simulations, 25 correlations were different from that expected under null assumptions and 17 were similar to that expected by chance (see Appendix S3 in Supplementary Material). One was indicative of a Rapoport effect (Fig. 5c), and other results observed were: (i) parameters of the observed curves significantly equal to that obtained in the simulations (Fig. 5d); (ii) larger range sizes in all altitudes (Fig. 5e); (iii) smaller range sizes in all altitudes (Fig. 5f); (iv) smaller range sizes at the boundaries (Fig. 5a); (v) larger range sizes at the boundaries (Fig. 5g); and (vi) reverse Rapoport (Fig. 5b) (see Appendix S3 in Supplementary Material).

The results obtained using random and pseudo-random simulations to all data sets analysed were summarized in Figure 6.

Discussion

Our results showed a weak evidence of a Rapoport effect because few of them were different from that expected under null assumptions. The five distributions showing Rapoport effect did not present any coincidence of gradient studied (latitude or altitude), hemisphere (South and North) and taxa. Therefore, even though some distributions did show a Rapoport effect, such an effect cannot be viewed as a general pattern in ecology. The idea that the Rapoport effect is not so spread is corroborated by the 10 distributions that showed a reverse Rapoport effect, with larger range sizes than expected by chance in lower midpoints, and smaller range sizes than expected by chance in higher midpoints. Some authors (Gaston *et al.*, 1998; Gaston, 2003) already reported that geographic ranges of tropical species might, on average, be larger than in adjacent temperate regions.

The patterns found in distributions that were significantly different from the simulations could be explained by different biological mechanisms. The midpoint of species distributions may represent optimal conditions or the geographical centre of its evolutionary origin (Lyons & Willig, 1997), assuming non-directional dispersal movements. If range sizes were smaller than expected under the null assumptions, specialization may be a mechanism restricting species distributions, independent of latitude or altitude. By specialization here we mean every adaptation of the individuals that restricts their distribution that can be resources, environmental conditions or biological interactions, such as the presence of predators or competitors. Conversely, observed range sizes larger than expected by chance may indicate an absence of specific requirements of resources and environmental conditions.

Distributions in which range sizes are smaller than expected by chance only in the boundaries may be explained by truncated species ranges. If species ranges are truncated, the quadratic relationship between midpoint and range size will not hold, especially if ranges are truncated more often at one end of the domain. For example, studies that examine range size in South Hemisphere are biased unless they eliminate the species whose ranges cross into the North Hemisphere. In those cases, ranges are more likely to be truncated in the north and ranges will pile up at the northern edge of the domain (*sensu* soft boundaries of Colwell & Hurtt, 1994). In this example, there will be significant deviations from the null model provided here, which are more related with a biased data sets than with biology. These significant deviations will always occur when a soft boundary is produced by the arbitrarily defined domain.

The data from Sklená & Jørgensen (1999) produced an interesting result, which is shown in Fig. 5h. The data show a monotonic decrease of range sizes with mid-altitude, instead of the usual triangular distribution. This may happen due to the presence of few species occurring only at low altitudes, which caused the loss of the left hand side of the triangle. Interestingly, the model we proposed captures this linear correlation even when we were expecting a quadratic relationship, changing the signals of the parameters a, b and c.

The Rapoport effect has been analyzed before comparing the observed pattern with that one generated by chance firstly by Lyons & Willig (1997), and then by other authors (Koleff & Gaston 2001; Diniz-Filho & Tôrres, 2002; Arita *et al.*, 2005; Folgarait *et al.*, 2005; Mora & Robertson, 2005). However, the above authors, except for Mora & Robertson (2005), assumed that the expected distribution considering geometric constraints was the same as in Lyons & Willig (1997). The latter authors analyzed the entire American continent from south to north, passing by 0^{o} latitude and, therefore, the expected pattern was a negative correlation between range size and mid-latitude (see Fig. 1 in Lyons & Willig, 1997). The other authors, however, sampled only in one hemisphere and, therefore, the geometric constraints in this case were not the borders of the continent but actually the limits of latitudes in which they sampled (see the differences of approaches in Fig. 1). Following this reasoning, the expected correlation between range size and mid-latitude would be quadratic with larger range sizes in the middle latitudes of the sampled area and smaller range sizes close to the boundaries of the sampled area.

The large number of observed results in the random and pseudo-random simulations suggests the inexistence of a single pattern in the distribution of range sizes (Fig. 6). Results of random simulations changing to that expected by chance in pseudo-random simulations might evidence that several different environmental variables (such as climate or biome distribution) may influence the distribution of organisms (Hernández Fernández & Vrba 2005a, b). The absence of a single pattern in pseudo-random simulations may be a result of the inclusion of the specific geographic location of each species in the simulation. Randomness generated by the pseudo-random simulation would be more similar to real distributions, which increases the chance of finding results similar to that expected by chance alone. This may explain the higher proportion of results in which correlations were not significantly different from that expected under null assumptions in pseudo-random simulations (from 16 in random simulations to 27 in pseudo-random, compare Appendices S2 and S3 in Supplementary Material). Added to this change, we observed more distribution patterns in pseudo-random (six) than in random (four) simulations (Fig. 6).

Because we observed a high proportion of results in which correlations were not significantly different that obtained under null assumptions (Fig. 6), there would be no need to evaluate biological mechanisms causing the observed patterns in these distributions analyzed. However, it is necessary to remember that the action of several biological mechanisms acting on a parameter, for instance range size, may result in a pattern that resembles that one expected by chance (Colwell *et al.*, 2004), which is usually called a deterministic chaos (Bascompte & Solé, 1995). A different approach, with models incorporating such biological mechanisms and testing the responses of species distributions, is necessary to test such hypothesis.

The random simulations in the present study are identical to mid-domain effect (MDE) models, with a theoretical range size frequency distribution as discussed in Colwell *et al.* (2004) and Arita (2005). The pseudo-random simulations are essentially MDE midpoint re-sampling models, even though we used them for a different purpose here. MDE models have been initially suggested to study only one-dimensional distributions, such as those analyzed in the present study. However, more recent studies incorporated longitude in the models (Bokma & Mönkkönen, 2000; Bokma *et al.*, 2001; Hawkins & Diniz-Filho 2002; Brayard *et al.* 2005) because species distributions are at least two-dimensional structures. We did not use two-dimensional distributions because the Rapoport effect is usually analyzed in one dimension (latitude, elevation or depth).

The fact that the simulations of Lyons & Willig (1997) are mid-domain models applied to range size data is not entirely clear in their paper. This is, in part, because their domain crossed the equator and the equator is roughly in the centre of the domain for bats and marsupials. Consequently they could approximate this to a linear relationship by taking the absolute value of latitude. Here, we make the expected parabolic relationship clear and provide a way to evaluate it when the domain does not cross the equator. A parabolic relationship is always expected but it can be more easily modelled as linear if the equator falls in the centre of the domain. However, there are no fundamental differences among the null model predictions. One case is just more mathematically tractable.

We concluded that most statistical methods used up to now to test for the Rapoport effect were not able to distinguish between stochastically and deterministically generated patterns. One of the most important parts of hypothesis testing in science is to make this distinction and to describe expected patterns under null assumptions. In our work, the Rapoport effect was found in few gradients analyzed. Furthermore, correlation between range size and midpoint was frequently similar to that expected under the null assumptions and, for that reason, there was no need to search for biological mechanisms in these specific correlations. Even though some recent studies have found a Rapoport effect (Fortes & Absalão, 2004; Arita *et al.*, 2005; Folgarait *et al.*, 2005), others authors (Rohde *et al.*, 1993; Blackburn & Gaston, 1996; Rohde, 1996; Rohde & Heap, 1996; Ruggiero & Lawton, 1998; Gaston & Chown, 1999; Samyn & Tallon, 2005) claim that Rapoport's rule is not widespread to be considered as a pattern in global ecology.

Acknowledgments. We thank of Sandra M. Soares for the initial ideas of this paper and for selecting and computing several data. The authors are grateful for the suggestions and comments by Carlos F. Sperber, Bruno G. Madeira, Frederico S. Neves, Renata B. F. Campos, Tathiana G. Sobrinho, Leandro S. Souto, Julio N. C. Louzada, Paulo De Marco Jr., Ronaldo Reis Jr. and Arne Janssen (Visiting Teacher, Scholarship Professor Visitante Estrangeiro from CAPES, Brazil). Tom Romdal, Nicholas Gotelli and four anonymous referees made critical contributions to the first draft. Celia and Charles Lancaster and João A.M. Ferreira revised and corrected the English. Carla R. Ribas is supported by a CAPES grant and José H. Schoereder is supported by a CNPq grant. British Ecological Society (SEPG), The Nature Conservancy of Brazil, and FAPEMIG supported this work.

Supplementary Material

The following material is available online at www.blackwell-synergy.com/loi/geb

Appendix S1 Articles used in the analyses of the Rapoport effect

Appendix S2 Results of random simulations of the Rapoport effect

Appendix S3 Results of pseudo-random simulations of the Rapoport effect

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Biosketches

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Figure 1 – Lower drawings represent the expected relationship between range sizes (lines) and mid-latitude (circles) in two possible cases of species distribution (upper drawings). On the left side, a distribution that does not cross the equator (0º) produces a unimodal expected relationship between the variables, because increasing or decreasing the latitude from the midpoint of the distribution decreases range sizes. On the right side, a linear correlation is expected because the distribution crosses the equator, and the increase in latitude corresponds to a decrease in range sizes.

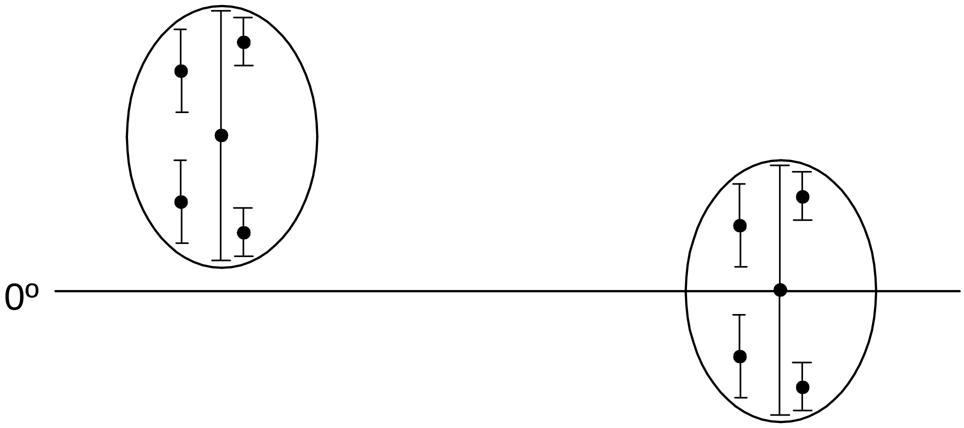
Figure 2 – Representation of correlation between range size and midpoint. The solid line represents the expected correlation (EXP) considering the null assumptions. The dashed line represents the correlation under the Rapoport effect (OBS): smaller range sizes in small latitudes/altitudes and larger range sizes in high latitudes/altitudes.

Figure 3 – Representation of range sizes (lines) and mid-altitude (circles). In elevational distributions, defined by two hard boundaries (the base and the top of mountains), range sizes should be smaller close to these boundaries and larger in the centre of the domain, by chance alone. These constraints produce a unimodal relationship between range size and mid-altitude (right hand side).

Figure 4 – Representation of the correlation between range sizes and mid-latitude expected (EXP) under geometric constraints and that observed (OBS) in actual data analyzed (Rohde, 1999; Harcourt, 2000), showing a reverse Rapoport effect. The observed correlation produced larger range sizes in lower latitudes and smaller range sizes in high latitudes than expected by chance.

Figure 5 – Examples of results found of correlations between range size and midpoint. Dashed lines represent the expected correlations considering the null assumptions. Solid lines represent the observed correlations. a) Smaller range sizes at the boundaries of distribution (Adolfo & Navarro, 1992); b) Reverse Rapoport effect (Samson *et al.*, 1997); c) Rapoport effect (Gotelli & Ellison, 2002 – forest); d) Parameters of the observed curves significantly equal to that obtained in the simulations (Fisher, 1996); e) Larger range sizes (Nathan & Werner, 1999 - reptiles); f) Smaller range sizes (Wolf, 1993 – lichens); g) Larger range sizes at the boundaries of the distribution (Wolf, 1993 - bryophytes); h) Linear correlation (Sklená & Jørgensen, 1999).

Figure 6 – Frequency of results obtained in the random (white bars) and pseudo-random (black bars) simulations, including the 55 data sets used. a) Smaller range sizes at the boundaries of distribution; b) Reverse Rapoport effect; c) Rapoport effect; d) Parameters of the observed curves significantly equal to that obtained in the simulations; e) Larger range sizes; f) Smaller range sizes; g) Larger range sizes at the boundaries of the distribution; h) Non-significant correlations. These results are further detailed in Appendices S2 and S3.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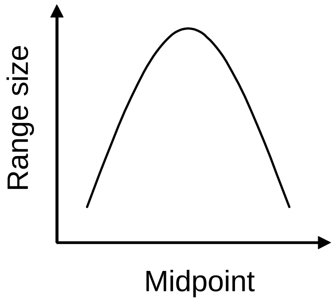
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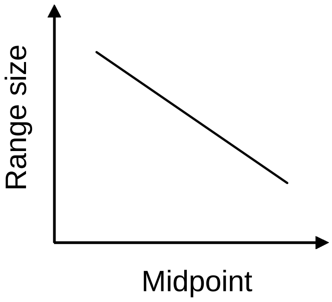
Midpoint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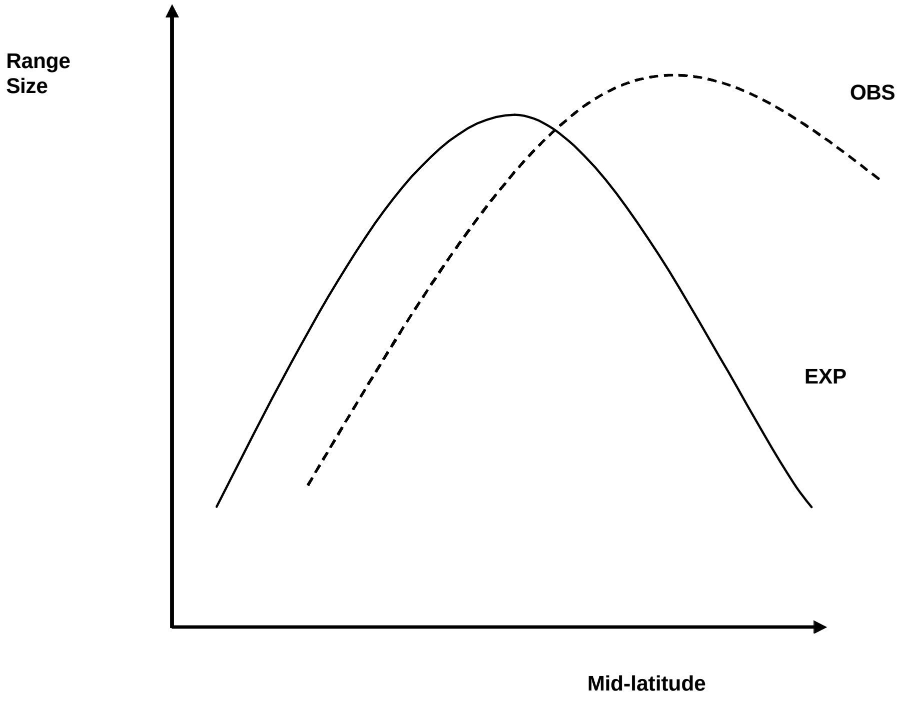
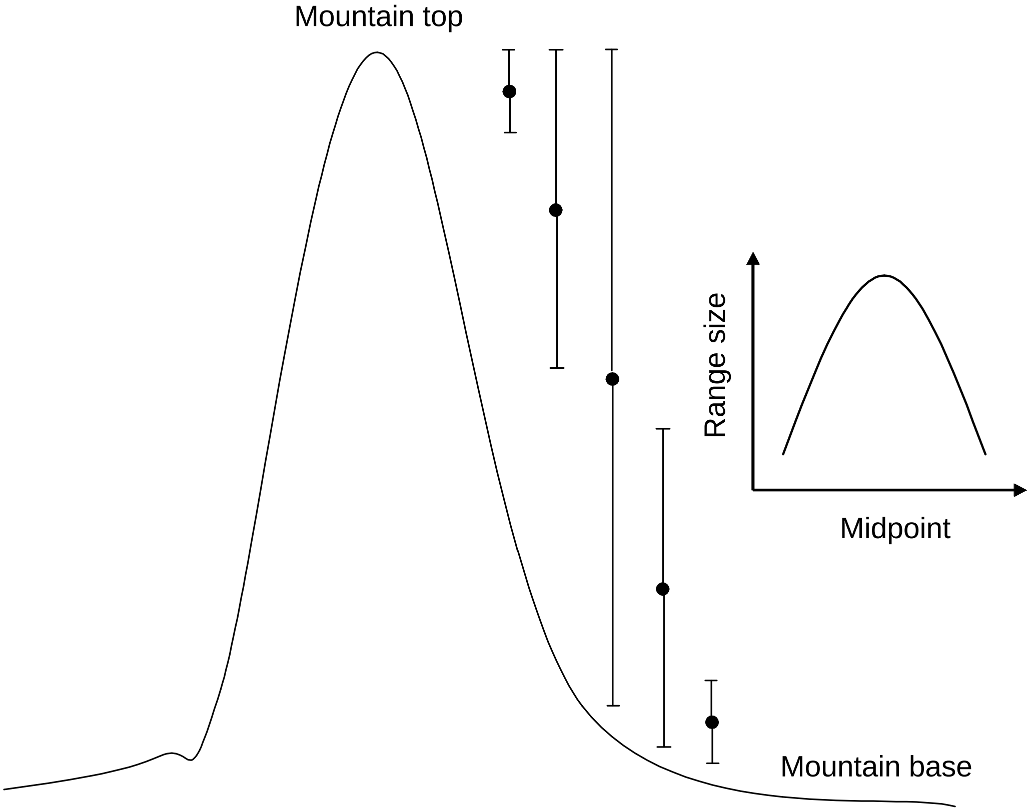
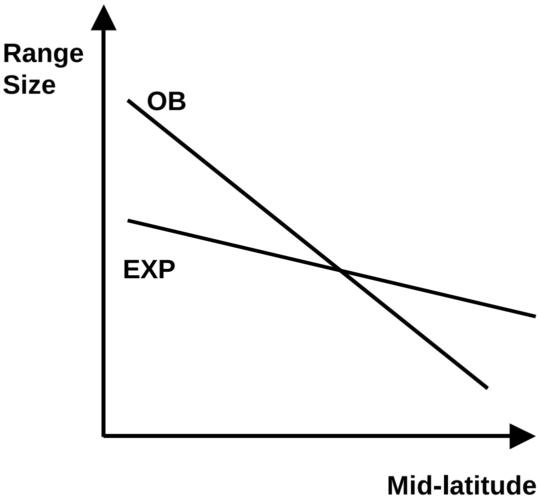
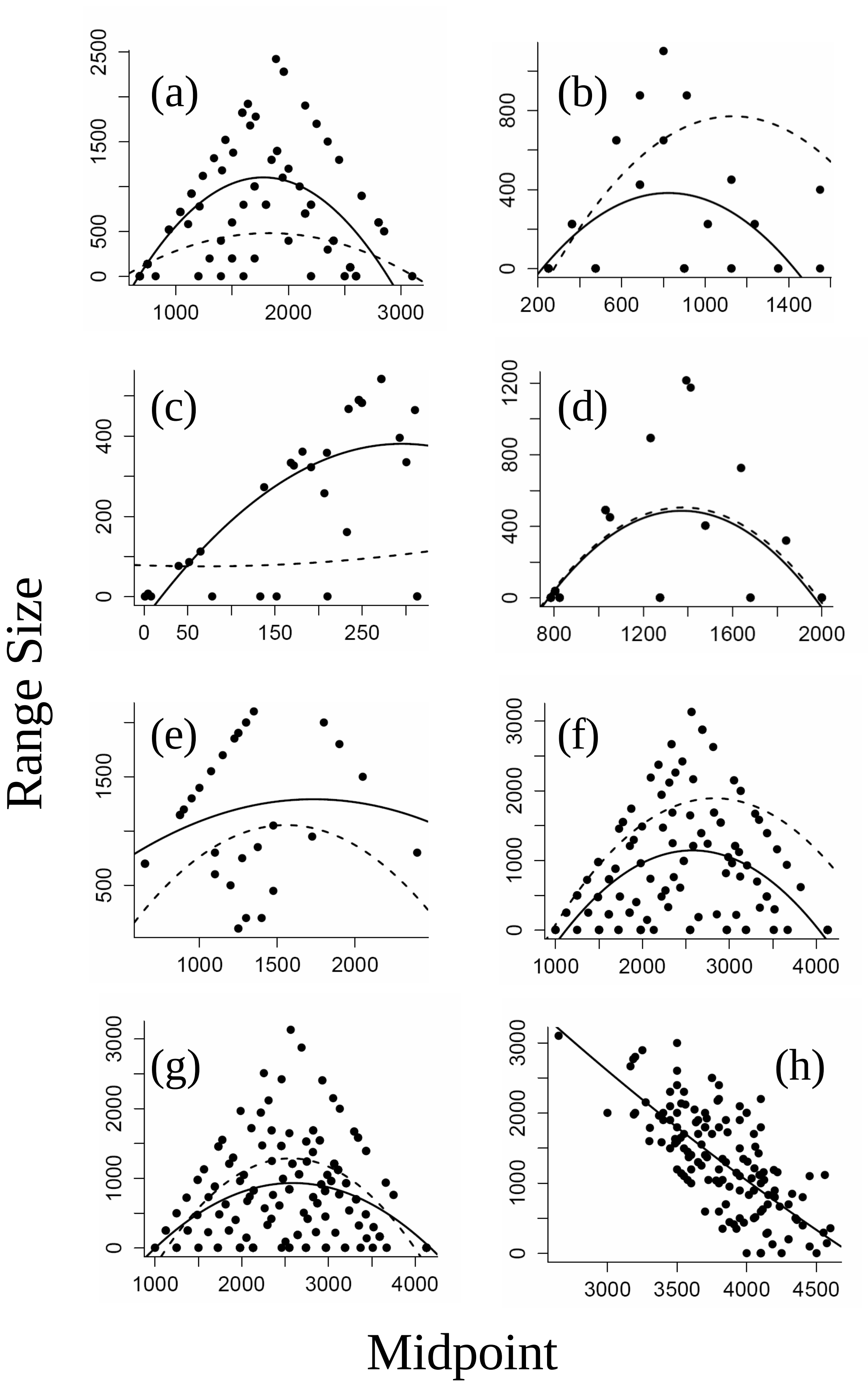

Range
Size
OBS
EXP
Mid-latitude


Mountain top
Range size
Midpoint
Mountain base


Range Size
OB
EXP
Mid-latitude


(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
Range Size
Midpoint
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500
1500
2500
1000
2000
3000
0
400
800
200
600
1000
1400
0
200
400
0
50
150
250
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400
800
1200
800
1200
1600
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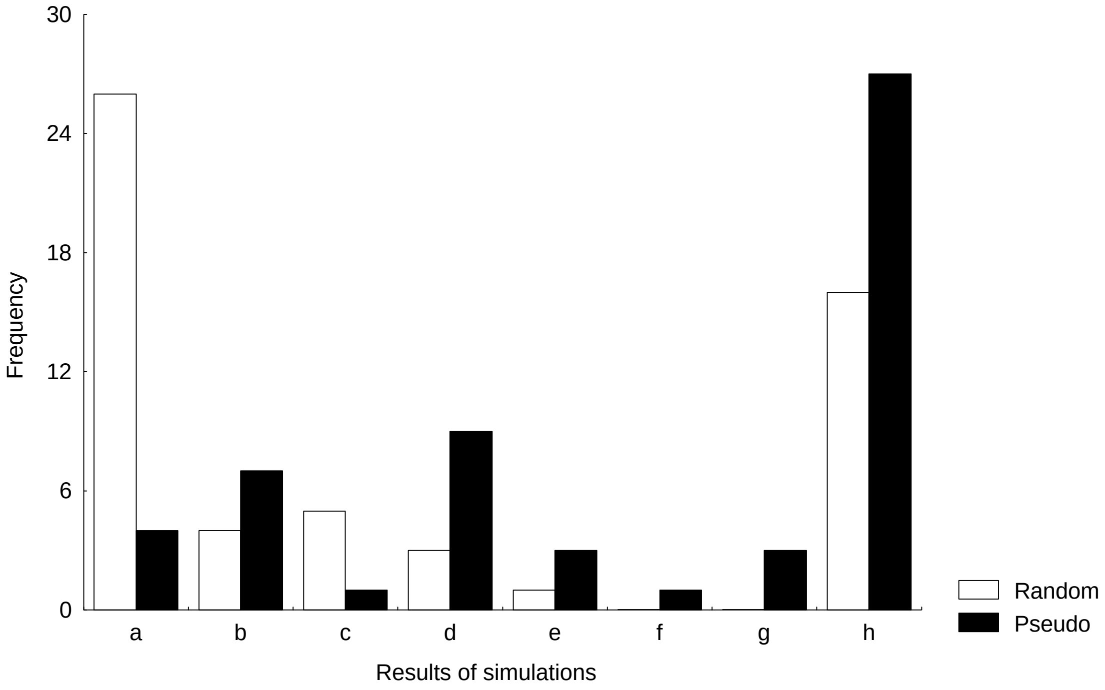
30
24
18
12
6
0
Frequency
a
b
c
d
e
f
g
h
Results of simulations
Random
Pseudo

Appendix S1 – Data used in the analyses of the Rapoport effect, and number of taxa distributions described (Distributions used). Some authors have analysed the Rapoport effect (Fleishman *et al.*, 1998; Rohde, 1999; Harcourt, 2000; McCain, 2003). From these, McCain (2003) did not find a Rapoport effect, Rohde (1999) found a reverse Rapoport effect, and the other two papers described Rapoport effects.

Authors	**Gradient**	*Taxa*	**Distributions used**	**Range limits**
Adolfo & Navarro (1992)	Altitude	Birds	1	680-3100 m
Alexander & Hilliard Jr. (1969)	Altitude	Orthoptera	1	1530-4265 m
Araújo & Fernandes (2003)	Altitude	Ants	1	800-1500 m
Beaumont & Hughes (2002)	Latitude	Butterflies	1	9.6-43.6 degrees
Clausnitzer & Kityo (2001)	Altitude	Rodents	1	2875-4120 m
Fisher (1996)	Altitude	Ants	1	785-2000 m
Fisher (1998)	Altitude	Ants	2	25-1015 m 875-1985 m
Fisher (1999)	Altitude	Ants	1	430-1250 m
Fleishman *et al.* (1998)	Altitude	Butterflies	1	1900-3260 m
Gagné (1979)	Altitude	Arthropods	1	15-2400 m
Gathorne-Hardy *et al.* (2001)	Altitude	Termites	1	20-1400 m
Gotelli & Ellison (2002)	Altitude Latitude	Ants	4	1-543 m 42-44.95 degrees
Harcourt (2000)	Latitude	Primates	1	21 S - 41 N degrees
Hawkins (1999)	Altitude	Birds	1	20-2200 m
Heaney (2001)	Altitude	Mammals	3	1100-2700 m 475-1750 m 300-950 m
Hofer *et al.* (1999)	Altitude	Amphibians and Reptiles	2	900-2000 m

Hortal-Muñoz *et al.* (2000)	Altitude	Beetles	1	75-1200 m
Hosoda (1999)	Altitude	Beetles	1	1100-1720 m
Kikuta *et al.* (1997)	Altitude	Beetles	1	550-1950 m
Lees *et al.* (1999)	Altitude Latitude	Butterflies	2	0-2050 m 12.5-25 degrees
Lobo & Halffter (2000)	Altitude	Beetles	1	1900-3300 m
McCain (2003)	Latitude	Rodents	1	19-45 degrees
McCain (2004)	Altitude	Mammals	1	0-1800 m
MD. Nor (2001)	Altitude	Mammals	1	700-3200 m
Moles & Westoby (2003)	Latitude	Plants	4	10.7-43.07 degrees 27-63.27 degrees 25-51 degrees 37.53-46.43 degrees
Nathan & Werner (1999)	Altitude	Reptiles and Birds	2	100-2800 m 300-2800 m
Ochocińska & Taylor (2003)	Latitude	Shrews	1	44.12-69.47 degrees
Poulsen & Lambert (2000)	Altitude	Birds	1	0-2060 m
Rickart (2001)	Altitude	Mammals	1	1220-3745 m
Robertson (2002)	Altitude	Ants	1	300-1850 m
Rohde (1999)	Latitude	Scombrids	1	45 S-45.8 N degrees
Samson *et al.* (1997)	Altitude	Ants	1	250-1750 m
Sánchez-Cordero (2001)	Altitude	Rodents and Bats	2 1 1	720-2450 m 750-2950 m 750-2650 m
Sanders *et al.* (2003)	Altitude	Ants	1	900-2500 m
Sfenthourakis (1992)	Altitude	Oniscidea	1	500-2900 m
Shepherd & Kelt (1999)	Altitude	Mammals	1	66-2667 m
Sklenář & Jørgensen (1999)	Altitude	Plants	1	1100-5200 m

Stephenson *et al.* (2000)	Latitude	Myxomycetes	1	34.43-77 degrees
Wolf (1993)	Altitude	Bryophytes and Lichens	2	1000-4130 m

Appendix S2 – Results of random simulations of the Rapoport effect. The *Non-significant correlations* are those in which the results of comparisons between the observed correlation coefficient and that expected under null assumptions were non-significant. The *Parameter analysis* columns show the results of comparisons between the parameters of the observed curves with that expected under null assumptions. Studies are ordered first by type of gradients (latitude or altitude), correlations (linear and quadratic), then alphabetically by author.

Authors	Non-significant correlations	Parameter analysis				
		Chance	**Larger ranges**	**Smaller ranges at boundaries**	**Reverse Rapoport**	**Rapoport**
Latitudinal distributions – linear correlations						
Harcourt (2000)					X	
Rohde (1999)					X	
Latitudinal distributions – quadratic correlations						
Beaumont & Hughes (2002)					X	
Gotelli & Ellison (2002) – bog distribution						X
Gotelli & Ellison (2002) – forest distribution				X		
Lees *et al.* (1999)				X		
McCain (2003)				X		
Moles & Westoby (2003) – Australia	X					
Moles & Westoby (2003) - Eastern North America	X					
Moles & Westoby (2003) - New Zealand	X					
Moles & Westoby (2003) - North America	X					
Ochocińska & Taylor (2003)	X					
Stephenson *et al.* (2000)	X					
Elevational distributions – quadratic correlations						
Adolfo & Navarro (1992)				X		
Alexander & Hilliard Jr. (1969)			X			
Araújo & Fernandes (2003)				X		

Clausnitzer & Kityo (2001)	X				
Fisher (1996)			X		
Fisher (1998) – Masoala Peninsula distribution			X		
Fisher (1998) – RS d’ Anjanaharibe-Sud distribution			X		
Fisher (1999)			X		
Fleishman *et al.* (1998)					X
Gagné (1979)			X		
Gathorne-Hardy *et al.* (2001)			X		
Gotelli & Ellison (2002) – bog distribution	X				
Gotelli & Ellison (2002) – forest distribution					X
Hawkins (1999)					X
Heaney (2001) – Mt. Isarog distribution		X			
Heaney (2001) – Mt. Kitanglad distribution	X				
Heaney (2001) – Mt. Pangasugan distribution		X			
Hofer *et al.* (1999) – amphibians distribution			X		
Hofer *et al.* (1999) – reptiles distribution	X				
Hortal-Muñoz *et al.* (2000)			X		
Hosoda (1999)	X				
Kikuta *et al.* (1997)	X				
Lees *et al.* (1999)				X	
Lobo & Halffter (2000)	X				
McCain (2004)	X				
MD. Nor (2001)	X				
Nathan & Werner (1999) – birds distribution			X		
Nathan & Werner (1999) – reptiles distribution	X				
Poulsen & Lambert (2000)			X		
Rickart (2001)					X
Robertson (2002)			X		
Samson *et al.* (1997)			X		
Sánchez-Cordero (2001) – Sierra Mazateca bats			X		

distribution		
Sánchez-Cordero (2001) – Sierra Mazateca rodents distribution		X
Sánchez-Cordero (2001) – Sierra Mixteca bats distribution		X
Sánchez-Cordero (2001) – Sierra Mixteca rodents distribution		X
Sanders *et al.* (2003)		X
Sfenthourakis (1992)		X
Shepherd & Kelt (1999)		X
Sklená & Jørgensen (1999)	X	
Wolf (1993) – bryophytes distribution		X
Wolf (1993) – lichens distribution		X

Appendix S3 –Results of pseudo-random simulations of the Rapoport effect. The *Non-significant correlations* are those in which the results of comparisons between the observed correlation coefficient and that expected under null assumptions were non-significant. The *Parameter analysis* columns show the results of comparisons between the parameters of the observed curves with that expected under null assumptions. Studies are ordered first by type of gradients (latitude or altitude), correlations (linear and quadratic), then alphabetically by author.

		Parameter analysis						
Authors	**Non-significant correlations**	**Chance**	**Smaller ranges at boundaries**	**Larger ranges at boundaries**	**Smaller ranges**	**Larger ranges**	**Reverse Rapoport**	**Rapoport**
Latitudinal distributions – linear correlations								
Harcourt (2000)							X	
Rohde (1999)							X	
Latitudinal distributions – quadratic correlations								
Beaumont & Hughes (2002)	X							
Gotelli & Ellison (2002) – bog distribution	X							
Gotelli & Ellison (2002) – forest distribution			X					
Lees *et al.* (1999)	X							
McCain (2003)	X							
Moles & Westoby (2003) – Australia	X							
Moles & Westoby (2003) - Eastern North America	X							
Moles & Westoby (2003) - New Zealand	X							
Moles & Westoby (2003) - North America	X							
Ochocińska & Taylor (2003)	X							
Stephenson *et al.* (2000)	X							

Elevational distributions – quadratic correlations							
Adolfo & Navarro (1992)	X						
Alexander & Hilliard Jr. (1969)				X			
Araújo & Fernandes (2003)	X						
Clausnitzer & Kityo (2001)	X						
Fisher (1996)		X					
Fisher (1998) – Masoala Peninsula distribution						X	
Fisher (1998) – RS d’ Anjanaharibe-Sud distribution						X	
Fisher (1999)					X		
Fleishman *et al.* (1998)		X					
Gagné (1979)		X					
Gathorne-Hardy *et al.* (2001)			X				
Gotelli & Ellison (2002) – bog distribution	X						
Gotelli & Ellison (2002) – forest distribution	X						
Hawkins (1999)					X		
Heaney (2001) – Mt. Isarog distribution		X					
Heaney (2001) – Mt. Kitanglad distribution	X						
Heaney (2001) – Mt. Pangasugan distribution		X					
Hofer *et al.* (1999) – amphibians distribution			X				
Hofer *et al.* (1999) – reptiles distribution	X						
Hortal-Muñoz *et al.* (2000)							X
Hosoda (1999)	X						
Kikuta *et al.* (1997)	X						
Lees *et al.* (1999)				X			
Lobo & Halffter (2000)		X					
McCain (2004)	X						
MD. Nor (2001)	X						

Nathan & Werner (1999) – birds distribution	X						
Nathan & Werner (1999) – reptiles distribution						X	
Poulsen & Lambert (2000)							X
Rickart (2001)		X					
Robertson (2002)		X					
Samson *et al.* (1997)							X
Sánchez-Cordero (2001) – Sierra Mazateca bats distribution							X
Sánchez-Cordero (2001) – Sierra Mazateca rodents distribution	X						
Sánchez-Cordero (2001) – Sierra Mixteca bats distribution	X						
Sánchez-Cordero (2001) – Sierra Mixteca rodents distribution	X						
Sanders *et al.* (2003)	X						
Sfenthourakis (1992)			X				
Shepherd & Kelt (1999)	X						
Sklená & Jørgensen (1999)		X					
Wolf (1993) – bryophytes distribution				X			
Wolf (1993) – lichens distribution					X		

Spatial scale dependence of a reverse latitudinal gradient in arboreal ant species richness

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Artigo submetido à Oecologia

Abstract

In this study, we do not attempt to answer the question why there are more species in the tropics, but to test the existence of a latitudinal gradient in ant species richness, and test factors responsible for it. We sampled ants and measured environmental variables (habitat productivity and heterogeneity) in the Cerrado (Brazilian savannah) at three spatial scales: trees, plots and sites. Contrary to expectation, ant species richness (alpha diversity) increased with latitude at the spatial scales of trees and plots. Beta diversity, measured as the difference in species composition among trees within plots and among plots within sites, did not vary with latitude or with environmental variables. Habitat productivity (estimated as tree biomass), resource heterogeneity (estimated as tree species richness), and structural heterogeneity (estimated as the coefficient of variation of distances among trees) did not correlate significantly with alpha or beta diversity at any spatial scale. Different patterns of gradients in species richness were possibly linked to the spatial scale studied. The reverse latitudinal gradient in alpha species richness was possibly caused by the Cerrado geographical distribution or by the evolutionary history of ant species. At the larger spatial scale sites, the absence of correlation between alpha diversity and latitude might have been caused by the small number of samples. Unsaturated communities may account for the absence of correlation between beta diversity and latitude. We demonstrate that latitudinal gradients can be found even with small latitudinal variation, but these gradients may be the reverse of global gradients. We conclude that processes acting at local spatial scales can lead to local variations in species richness that do not scale up to global patterns. Thus, studies performed at a global scale may overlook important regional variation in determinants of diversity.

Keywords - Alpha diversity; Beta diversity; Cerrado; Heterogeneity; Productivity

Introduction

The astonishing species diversity of the tropics is widely recognized, but its causes remain controversial (Hawkins and Agrawal 2005). Willig et al. (2003) reviewed more than 30 hypotheses on the processes that could explain this latitudinal gradient in species richness (LGSR). Among these hypotheses, they considered habitat productivity or ambient energy as potential factors to explain the LGSR, and some recent studies have considered this hypothesis (Turner 2004; Bjorholm et al. 2005; Brayard et al. 2005; Mora and Robertson 2005; Rex et al. 2005).

Although habitat productivity or ambient energy is often presented as a hypothesis, it is actually not a mechanism that explains the latitudinal gradient, but a factor that correlates with latitude (Hawkins and Diniz-Filho 2004). The most commonly used estimates for productivity are plant biomass (Braschler et al. 2004; Grughy et al. 2005), evapotranspiration (Rangel and Diniz-Filho 2005), net primary productivity (Cleland et al. 2004), the normalized difference of vegetation index (Bailey et al. 2004), and temperature (Brayard et al. 2005). A positive correlation between species richness and energy estimates has been reported for different taxa (Mittelbach et al. 2001; Evans et al. 2005), independent of which estimate of energy is used. Some factors, such as increased population size, niche position and diversification rate, may appear to contribute frequently to the correlation between species richness and energy estimates at macro-scale (for further discussion of these mechanisms, see Evans et al. 2005).

Another latitudinal correlate that is often presented as a hypothesis that could explain the LGSR is habitat heterogeneity (Kerr and Packer 1997; Davidowitz and Rosenzweig 1998; Rahbek and Graves 2001). At least two types of heterogeneity can be found: structural heterogeneity and resource heterogeneity (Brose 2003). Structural heterogeneity usually concerns variation in the environmental conditions in which the organisms live, associated to abiotic characteristics of their habitat. Resource heterogeneity refers to variations in resource types available to the organisms, and can be associated to abiotic or biotic characteristics of the habitat. An increase in habitat heterogeneity might allow a higher number of species to coexist (Tilman and Pacala 1993), and this correlation can be found repeatedly in the ecological literature (Roth 1976; Reed 1978; Bell et al. 2000; Bestelmeyer and Wiens 2001; Ribas et al. 2003; Sperber et al. 2004; Tews et al. 2004). Additional to the fact that habitat heterogeneity is also a latitudinal correlate, it is left unexplained why there is more heterogeneity in the tropics (Rohde 1999).

Until recently, most studies of species richness patterns implicitly assumed that they are scale invariant, although some authors have shown how large-scale species richness patterns can vary with spatial scale (Hillebrand 2004; Rahbek 2005). This approach has only recently been used in studies of latitudinal gradients (Lyons and Willig 2002; Rodríguez and Arita 2004) and of altitudinal gradients (Sanders et al. 2003; Aubry et al. 2005) in species richness, demonstrating the scale-sensitivity of these gradients (but see Lyons and Willig 1999; Bjorholm et al. 2005). Species richness is a consequence of processes acting at different spatial scales (Kneitel and Chase 2004), and the study of species richness at different spatial scales may therefore contribute to the identification of processes that are important determinants of species richness (Ricklefs 2004). The partition of species richness in alpha and beta diversities is a tool that can be used to evaluate the relative importance of processes acting at different spatial scales (Willis and Whittaker 2002). Significant correlations of alpha diversity with variables tested are usually interpreted as evidence of processes acting at smaller spatial scales being more important than those acting at regional and global scales.

Invertebrates have been recognized as better habitat indicators than vertebrates for evaluation of conservation priorities and for monitoring biodiversity, because they are abundant, relatively easy to sample, and respond relatively fast to habitat modifications (Lewinsohn et al. 2005). Ants are described as particularly suitable organisms for these purposes because they are affected by habitat characteristics such as resource diversity (Armbrecht et al. 2004), climatic variables (Folgarait et al. 2005), vegetation structure (Crist and Wiens 1994), habitat productivity (Kaspari 2005), habitat diversity and complexity (Armbrecht et al. 2005). Although ants show the LGSR in some habitats, there are few studies, to our knowledge, (Farji-Brener and Ruggiero 1994; Majer et al. 2001; Johnson and Ward 2002; Kaspari et al. 2004) on the Southern hemisphere that tested hypotheses to explain this pattern.

Our specific aim was to test: (i) the existence of a latitudinal gradient in species richness in arboreal ants in the Cerrado, (ii) whether the gradient is correlated with habitat productivity, resource heterogeneity and structural heterogeneity, and (iii) what is the influence of spatial scale on the LGSR and its correlates.

Material and methods

Study sites

The Cerrado biome, savannah-like ecosystem from Brazil, is one of the World's biodiversity hotspots (Klink and Machado 2005; Marris 2005), with a very rich flora, and high levels of endemism compared to other savannas. Deforestation rates have transformed several parts of this biome into pasture and agricultural lands, which needs urgent conservation practices. The Cerrado is a plant community composed of several physiognomies (Coutinho 1978; Ribeiro and Walter 1998), varying from grassland to forest formations with tree densities from less than 1000 trees/ha to over 3000 trees/ha

(Goodland 1971). In Central Brazil, the Cerrado covers an area of about 1.800.000 km^2 (Ratter 1992; Câmara 1993). The rainy season is from September to April with around 1500 mm of rainfall, and the dry season is during the coldest months of the year (May to August) (Goodland 1971). We carried out the fieldwork at 11 sites consisting of conservation units in the Cerrado biome in Brazil between 8º and 22ºS latitude (Table 1).

Sampling design- latitudinal gradient and spatial scales

We sampled arboreal ants using pitfall traps baited with sardine and honey. The pitfall traps were plastic containers (diameter 19 cm, height 11 cm) with an inner receptacle containing the bait. Ants attracted by the bait fell into a 5% detergent plus salt solution. Traps were tied to tree stems at a height of ca. 1.3 m and remained in the field for 48h. Samplings were always carried out during the rainy season (December, January and February in three consecutive years 2003, 2004 and 2005) (Table 1), because ants are more abundant in this season. Ants were identified to genera according to Bolton (1994; 2003). Whenever possible, we identified the ants to species level by comparison to the reference collection of the Community Ecology Lab of the Federal University of Viçosa. When species identification was not possible, we sorted ants according to their external morphology. Voucher specimens are deposited in the above reference collection.

The sites were the largest spatial scale studied (11 replicates). Within each site, we delimited three plots (15 x 15m) (33 replicates) and within each plot, we sampled 10 trees (330 replicates). Hence, we sampled at three spatial scales. We delimited all three plots in the same Cerrado physiognomy (between 2000-3000 trees/ha). When possible, we chose three sites with different tree densities, but all of them inside the physiognomy above, to obtain data from sites with as high habitat heterogeneity as possible. Within each plot, we selected the 10 trees that were most distant from each other.

We assessed alpha diversity at the three spatial scales and beta diversity at the two larger scales. Alpha diversity, or point diversity, is species richness of local communities (Cornell and Lawton 1992; Loreau 2000), hence, we measured alpha diversity as the total number of ant species at each spatial scale. Beta diversity, or species turnover, is the difference in species composition among local communities (Cornell and Lawton 1992; Loreau 2000). We estimated beta diversity as the difference in presence/absence of species (Mountford dissimilarity index) between each pair of trees within plots and between each pair of plots within sites, averaging all values obtained in each spatial scale. To calculate beta diversity we used the Mountford dissimilarity index because this index is based on presence/absence of species. We calculated all beta estimates using R (The R Development Core Team 2005) with the vegan package (Oksanen 2004).

Habitat productivity

We measured plant biomass as a stand-in measure for productivity. Plant biomass is a direct estimate of available energy (Mittelbach et al. 2001). We measured the basal perimeters of all trees inside the plots. From all trees with a basal perimeter larger than 15 cm (adult trees in the Cerrado), we also measured the two largest dimensions of their crown. To estimate the basal area, we used the following formula (Krebs 1989): basal area = $(BC)^2/4*$ where, BC is the tree basal circumference. To estimate the area of the crown, we used the following formula (Portela and Santos 2003): crown area = $A*B*(/4)$ where, A and B are the two largest widhts of the crown. We summed basal and crown area of all trees in each plot to obtain the plant biomass per plot. The plant biomass per site was obtained by summing the plant biomass of the three plots.

Resource heterogeneity and structural heterogeneity

We used plant species richness as a stand-in measure for resource heterogeneity (Ribas et al. 2003). To this aim, all the trees in the plots were sorted according to their morphology. Samples of leaves, branches, flowers and fruits of each plant species were collected in each plot, and then compared to determine species richness per site.

We used the coefficient of variation (CV) of distance among trees as a stand-in measure for structural heterogeneity, because CV is expected to be positively proportional to environmental heterogeneity (Lundholm and Larson 2003). We estimated the CV of the distance among trees using the point quadrant method (Krebs 1989). This method consists of measuring the distance to the nearest tree in the four quadrants, and calculating the standard deviation divided by the mean of these distances. We repeated this measurement three times around each tree sampled for ants, thus obtaining 12 distances per tree.

Statistical analyses

We carried out an independent analysis for each spatial scale to test the relationship between alpha diversity and latitudinal correlates. The response variable was alpha diversity at each spatial scale and the explanatory variables for the scale of trees were latitude and structural heterogeneity. For the plot and site scales, we used latitude, productivity, resource heterogeneity, and structural heterogeneity. We used Poisson error distributions.

We carried out two independent analyses for plots and sites to test the relationship between beta diversity and latitudinal correlates. Beta diversities were the response variables and the explanatory variables were latitude, productivity, resource heterogeneity, and structural heterogeneity. We used normal error distributions.

We used generalized linear mixed models (glmm) because our sampling design was nested (Crawley 2002). All models were composed of a fixed effect and of a random effect, both different at each spatial scale. The fixed effect was composed of the different explanatory variables: latitude, productivity, resource heterogeneity and structural heterogeneity, depending on spatial scale analysed. The random effect was trees nested in plots nested in sites at the tree scale, and plots nested in sites at the plot scale. All the analyses were carried out using the R software (The R Development Core Team 2005), followed by residual analyses to check for the suitability of the models and error distribution.

Results

Ant species richness

We collected 147 ant species, belonging to eight subfamilies - Dolichoderinae, Formicinae, Ecitoninae, Ectatomminae, Myrmicinae, Paraponerinae, Pseudomyrmecinae and Ponerinae. Ant species richness varied from zero to 10 at the spatial scale of trees, from 10 to 29 at the spatial scale of plots and from 20 to 43 per site.

Latitudinal gradient and spatial scales

At the spatial scales of trees and plots, the alpha diversity increased with latitude (t = 2.80; d.f. = 9; p = 0.02; Fig. 1 and t = 2.63; d.f. = 9; p = 0.03; Fig. 2, respectively).

At the spatial scale of sites, alpha diversity did not vary with latitude (t = 1.37; d.f. = 6; p = 0.22; Fig. 3).

Beta diversity did not vary with latitude at the scale of plots (t = 0.87; d.f. = 9; p = 0.41; Fig. 4), nor at the scale of sites (t = 0.50; d.f. = 6; p = 0.63; Fig. 5).

Habitat productivity

Alpha diversity was not significantly affected by productivity at the spatial scale of plots (t = 0.68; d.f. = 19; p = 0.51) and sites (t = 1.21; d.f. = 6; p = 0.27). Likewise, beta diversity did not vary with productivity at the scale of plots (t = 0.99; d.f. = 19; p = 0.33), or of sites (t = -1.01; d.f. = 6; p = 0.35).

Resource heterogeneity and structural heterogeneity

The effect of resource heterogeneity on alpha diversity was not significant at the spatial scale of plots (t = 0.87; d.f. = 19; p = 0.40) and of sites (t = 0.59; d.f. = 6; p = 0.58). Neither was the effect of resource heterogeneity on beta diversity at the scale of plots (t = -0.49; d.f. = 19; p = 0.63) and of sites (t = 1.42; d.f. = 6; p = 0.21).

Alpha diversity did not vary with structural heterogeneity at any scale (trees: t = -1.35; d.f. = 296; p = 0.18; plots: t = -0.97; d.f. = 19; p = 0.34; sites: t = 0.01; d.f. = 6; p = 0.99). Structural heterogeneity did not have a significant effect on beta diversity at the scale of plots (t = -1.02; d.f. = 19; p = 0.32), or at the scale of sites (t = 0.81; d.f. = 6; p = 0.45).

Discussion

Latitudinal gradient

A reverse latitudinal gradient, or absence of a normal latitudinal gradient, were reported before (Janzen 1981; Rohde 1999). Willig et al. (2003) suggested that such a pattern is more frequent in studies of small latitudinal variation, because such studies cover a small variation of habitats, and local mechanisms therefore would be more important in determination of species richness, obscuring the effects of mechanisms acting at larger spatial scales. Recently, Hillebrand (2004) reviewed nearly 600 studies, and did not find any evidence of effects of the latitudinal variation studied on the latitudinal gradients in species richness.

There are some studies on latitudinal gradients of ant species richness (Farji-Brener and Ruggiero 1994; Majer et al. 2001; Gotelli and Ellison 2002; Johnson and Ward 2002; Pfeiffer et al. 2003; Kaspari et al. 2004). These studies reveal various patterns possibly due to the spatial scale analysed. Studies at regional scales did not produce the expected latitudinal gradient (Johnson and Ward 2002; Pfeiffer et al. 2003; this study), whereas studies at global scales found an increase in species richness towards the equator (Majer et al. 2001; Kaspari et al. 2004). Gotelli and Ellison (2002) studied ant species diversity at a small latitudinal range (3 degrees), in the Northern Hemisphere and detected the expected species richness gradient. This last result might indicate that local mechanisms may be less important than global mechanisms, or that local mechanisms coincidentally produce the same pattern as expected from global mechanisms. Contrary to the other studies, Farji-Brener and Ruggiero (1994) analysed only leaf-cutting ants, of which the origin of distribution is probably the Amazon Basin (Fowler and Claver 1991).

Alpha and beta diversities and spatial scales

We found no evidence of the expected latitudinal gradient in ant species richness at any spatial scale, but, rather, a reverse latitudinal gradient in alpha species richness at the two smaller spatial scales studied. Alpha diversity at the two smaller spatial scales (trees and plots) was positively correlated with latitude, i.e., we collected more ant species per tree and plot at higher latitudes. One explanation for this pattern may be linked to the geographical distribution of cerrado vegetation in Brazil. Cerrado occurs mainly in the central region of Brazil, being more scattered at smaller latitudes, and interrupted in the north by the Caatinga and the Amazon forest.

A hypothesis that has gained substantial attention at explaining the LGSR is the mid-domain effect (Colwell et al. 2004). Colwell and Hurt (1994) propose that species richness gradients can arise through simple geometric constraints on species ranges. According to this hypothesis, the random placement of species ranges within the boundaries of a domain produces a peak of species richness in the centre of the domain, the mid-domain effect (Colwell and Lees 2000). This hypothesis, although controversial both in concept and in applications, is considered as an adequate null model to evaluate species richness patterns (Colwell et al. 2004; Arita 2005). The Cerrado geographical distribution may cause species distribution patterns as expected by mid-domain effects, and this pattern could be coincident with our data. The existence of the mid-domain effect in our latitudinal gradient will be analysed elsewhere.

Another explanation for the correlation between alpha diversity and latitude is associated with the evolutionary origin of ant species. It has been shown that phylogeny or evolutionary history may explain the latitudinal gradient in species richness (Wiens and Donoghue 2004; Cardillo et al. 2005; Rex et al. 2005). Difficulties in evaluating this hypothesis for the data collected here are the lack of information on phylogeny of tropical ant species and of data on ant biology. Information on the existence of endemism of ants in Cerrado biome could be used as evidence of the evolutionary origin of these species to allow for a test of this hypothesis in tropical ants.

At the largest spatial scale studied here (site), we did not detect an effect of latitude on alpha diversity. If alpha diversity increased with latitude at the two smaller scales, and these two were nested within the scale of sites, why was alpha diversity at the scale of sites not affected by latitude? One reason for this may be the small number of samples (eleven) at this spatial scale (compare Figs. 1, 2 and 3), reducing the power of our analysis and preventing us from unravelling an eventual increase of diversity with latitude. An evidence for the importance of reducing the number of samples in the absence of relationship between alpha diversity and latitude at the scale of sites was the absence of correlation between beta diversity and latitude (Fig. 5). Since at smaller spatial scales the correlation between alpha diversity and latitude was positive, the expected correlation between beta diversity and latitude would be a negative correlation, because to obtain a measurement of alpha diversity at the spatial scale of sites we summed the total species richness of the two other spatial scales.

Beta diversity was not affected by latitude, i.e. species turnover did not change with latitude at any spatial scale. An explanation for this may be that ant communities are unsaturated. If ant communities are saturated, we could expect that increasing the regional pool of species would cause an increase in beta diversity because alpha diversity (local diversity) is limited (Srivastava 1999; 2005).

Habitat productivity and habitat heterogeneity

We found no evidence for habitat productivity, resource heterogeneity, and structural heterogeneity as causing the reverse latitudinal gradient in ant species richness, because there were no correlations among these latitudinal correlates and ant species richness at any spatial scale. Few papers explicitly tested hypotheses to explain latitudinal gradients in ant species richness (but see Pfeiffer et al. 2003; Kaspari et al. 2004). Although the mechanisms involved in an increase of species richness with productivity and energy remain controversial (Currie et al. 2004; Evans et al. 2005), there are several taxa that show positive correlations between species richness and productivity and other measurements of energy (Francis and Currie 2003; Hawkins et al. 2003a; b). For example, gradients of energy, measured as gradients in mean monthly temperature and net primary productivity, are correlated with global variation in ant worker mass and number (Kaspari 2005). Resource heterogeneity and structural heterogeneity are also reported as positively correlated to species richness of several taxa (Tews et al. 2004). Concerning ants, some hypotheses could help to explain this relationship, such as an increase in the variation of resources and habitat conditions, an increase in the amount of resources, and other factors such as habitat productivity, that may influence both ants and the measure of heterogeneity used (Ribas et al. 2003; Armbrecht et al. 2004; Armbrecht et al. 2005).

Even if a factor correlates with species richness at smaller scales, this does not imply that it is responsible for generating gradients in species richness (Turner 2004). It has been shown that processes acting at local spatial scales can lead only to local variation in species richness, whereas they do not scale up to global patterns (Turner 2004; Srivastava 2005). Several authors have argued that relationships of species richness with environmental variables, such as habitat productivity and heterogeneity, may depend on the spatial scale studied (Kotliar and Wiens 1990; Whittaker et al. 2001; Williams et al. 2002; Bailey et al. 2004; Braschler et al. 2004). Possibly, we could not find correlations between species richness and environmental variables because our study was carried out at a larger spatial scale than the scale at which these factors act.

Conclusions

Our study evaluated latitudinal patterns of species richness at a regional scale in South America. Studies of latitudinal correlates of gradients in species richness at regional scales such as the present one can highlight important aspects of factors determining species richness at smaller scales (Mora and Robertson 2005). Studies carried out only at larger scales could miss important regional variation in determinants of diversity gradients.

Our main result is that there might be latitudinal gradients at regional scales, but such gradients may be opposite to global gradients. This suggests that regional and global trends in species diversity are caused by different factors. Understanding the spatial scale at which species richness patterns occur is essential for a better understanding of species richness patterns. We propose that further studies might be carried out to test why there is a reverse latitudinal gradient of ant species richness in this biome.

Acknowledgements – We gratefully acknowledge Arne Janssen (Visiting Teacher, Scholarship Professor Visitante Estrangeiro from CAPES, Brazil) for critical contributions to writing the manuscript and assistance with the English. The authors thank IBAMA for permission to collect in the conservation units, and IBAMA, Carla Galbiati, Marcelo S. Madureira, Rogério F. Ribas, Renata B.F. Campos for field assistance. The authors are indebted to João A.M. Ferreira and Adrian J. Molina for suggestions and comments. Carla R. Ribas is supported by a CAPES grant, José H. Schoereder is supported by a CNPq grant and Carlos F. Sperber was an invited researcher at the Max-Planck-Institute for Limnology, Ploen, Germany, during part of this work, supported by a CAPES grant. The British Ecological Society (SEPG), The Nature Conservancy of Brazil and FAPEMIG supported this work. Samplings carried out comply with the current laws of Brazil.

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Table 1 – Sampled Cerrado sites in conservation units in Brazil, geographic coordinates and dates in which fieldwork has been carried out.

Site	Coordinates (S) (W)	Date sampled
Estação Ecológica Uruçuí-Una	8^{o}52’, 44^{o}58’	January 2005
Parque Nacional da Chapada dos Veadeiros	14^{o}07’, 47^{o}30’	February 2003
Parque Nacional da Chapada dos Guimarães	15^{o}27’, 55^{o}44’	January 2004
Parque Nacional de Brasília	15^{o}46’, 47^{o}55’	February 2003
Estação Ecológica da Serra das Araras	16^{o}04’, 57^{o}40’	January 2004
Parque Nacional Cavernas do Peruaçu	15^{o}02’, 44^{o}11’	December 2004
Parque Nacional das Emas	17^{o}34’, 52^{o}33’	December 2003
Floresta Nacional de Paraopeba	19^{o}16’, 44^{o}24’	January 2003
Parque Nacional da Serra do Cipó	19^{o}30’, 43^{o}44’	January 2003
Near Parque Nacional da Serra da Canastra	20^{o}14’, 46^{o}21’	December 2003
Fazenda Campininha	22^{o}18’, 47^{o}11’	February 2003

Figure 1 – Correlation between ant alpha diversity and latitude at the spatial scale of trees. Alpha diversity was estimated as arboreal ant species richness on 330 trees in the Brazilian Cerrado. The fitted line was obtained from a generalized linear mixed model ($y = e^{(0.628 + 0.049x)}$).

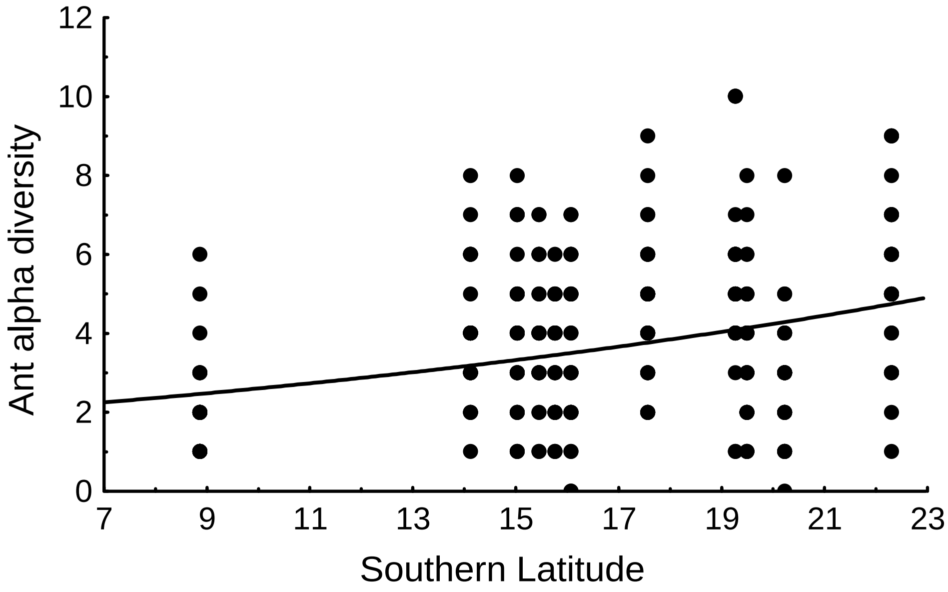
Figure 2 – Correlation between ant alpha diversity and latitude at the spatial scale of plots. Alpha diversity was estimated as arboreal ant species richness on 33 (15 x 15m) plots in the Brazilian Cerrado. The fitted line was obtained from a generalized linear mixed model ($y = e^{(2.371 + 0.035x)}$).

Figure 3 – Correlation between ant alpha diversity and latitude at the spatial scale of sites. Alpha diversity was estimated as arboreal ant species richness on 11 sites in the Brazilian Cerrado. The relationship was not significant ($p = 0.22$).

Figure 4 – Correlation between ant beta diversity and latitude at the spatial scale of plots. Beta diversity was calculated as the difference in presence/absence of species between each pair of tree within plots, averaging all values obtained. The relationship was not significant ($p = 0.407$).

Figure 5 - Correlation between ant beta diversity and latitude at the spatial scale of sites. Beta diversity was calculated as the difference in presence/absence of species between each pair of plots within sites, averaging all values obtained. The relationship was not significant ($p = 0.633$).

Figure 1


Ant alpha diversity
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4
6
8
10
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7
9
11
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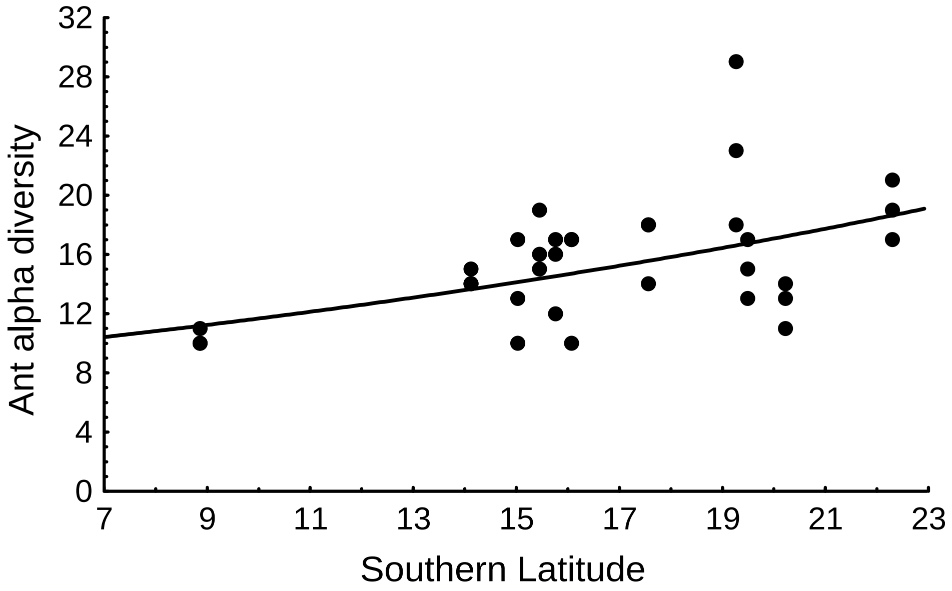
15
17
19
21
23
Southern Latitude

Figure 2


32
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Ant alpha diversity
7
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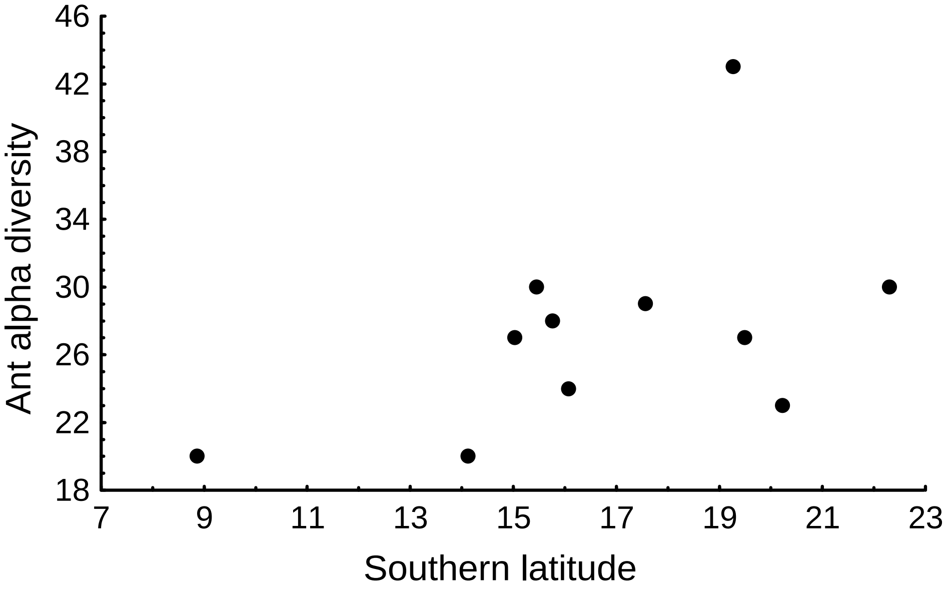
23
Southern Latitude

Figure 3



Ant alpha diversity
46
42
38
34
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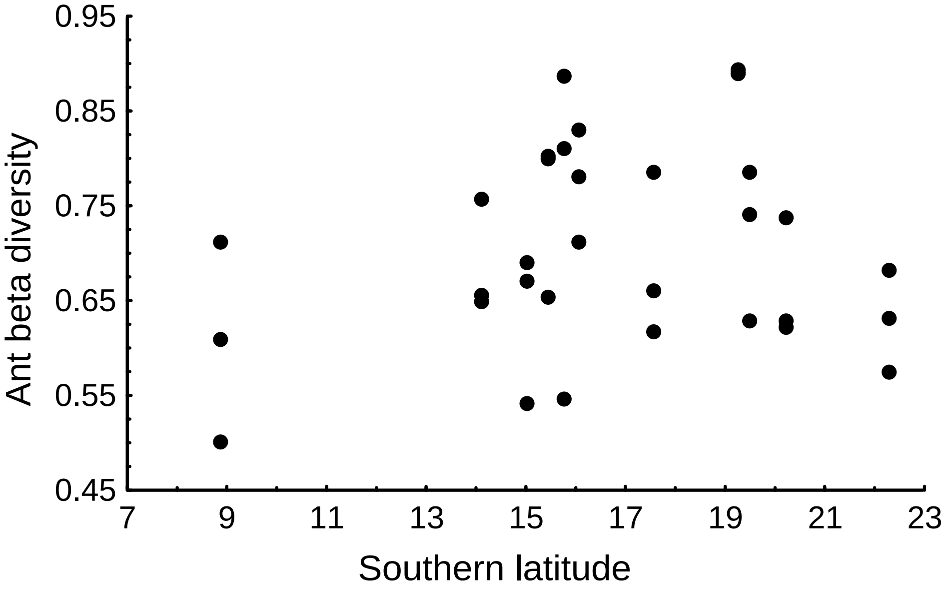
23
Southern latitude

Figure 4


0.95
0.85
0.75
0.65
0.55
0.45
Ant beta diversity
7
9
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17
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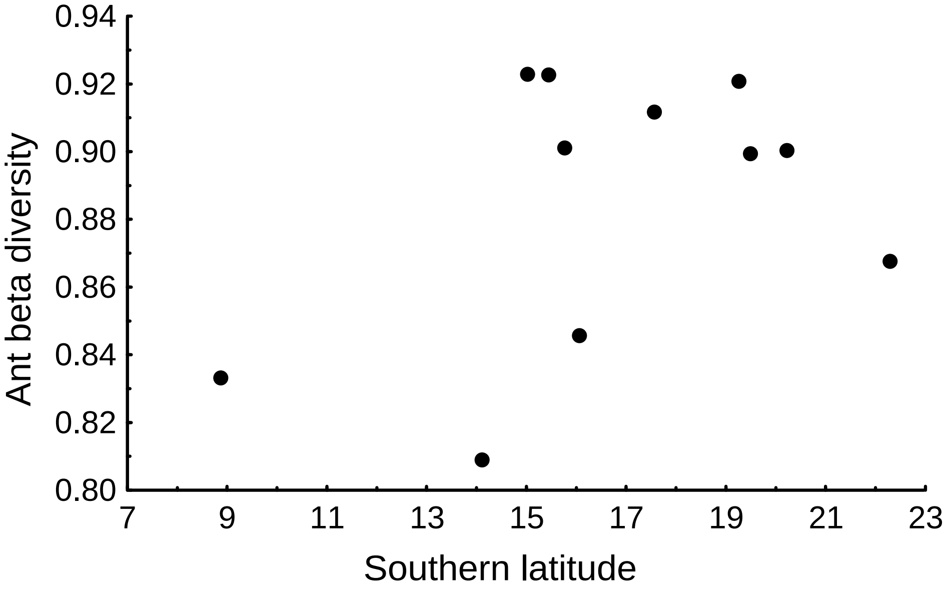
21
23
Southern latitude

Figure 5


0.94
0.92
0.90
0.88
0.86
0.84
0.82
0.80
Ant beta diversity
7
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21
23
Southern latitude

Mid-domain and Rapoport effects - Null models for testing latitudinal gradients in ant species richness

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Artigo a ser submetido à Ecology Letters

Abstract

There is a great deal of controversy about whether the mid-domain effect (MDE) is really a null model for diversity gradients. The Rapoport effect also has been analysed at the light of MDE effects. In this article we aimed to test for MDE and the Rapoport effect using null models in the arboreal ant community at Cerrado biome (Brazilian savanna). These null models exclude effects of spatial gradients on the distribution of species ranges locations within a geographical domain. If observed patterns were different from that expected under the null assumptions of these models, we could deduce that biological mechanisms may be responsible for the observed gradients. We sampled arboreal ants using pitfall traps in 30 trees at each one of eleven sites at Cerrado. We tested for the existence of geometric constraints comparing empirical species richness with MDE (null model) predictions, using 1,000 simulations to obtain mean species richness and 95% confidence intervals. We also tested for MDE effects deleting a percentage of the species richness of the simulated distributions to control for spatial patchiness of species distribution. We tested if the correlation between range size and mid-latitude (Rapoport effect) was different from that expected under null assumptions. The empirical species richness showed a weak MDE effect since only 27% of the empirical species richness points occurred within the predicted species richness expected under MDE effect. When we removed 36% of the species from the null samples to include the spatial patchiness in the model, empirical species richness also did not show a MDE effect. We did not observe a Rapoport effect, observing instead larger range sizes than expected by chance at the boundaries of the domain. This result may indicate an absence of specific requirements of resources and environmental conditions of ant species occurring at the boundaries of the Cerrado distribution. Our results showed a higher species richness than expected by the MDE effect mainly at the higher latitude sampling points. The results in this study demonstrated that MDE effect should not be responsible for the reverse latitudinal gradient found in other study performed at the same sites. Process-based models offer a way to advance MDE classic models, allowing formulation of null models as well as alternatives that incorporate biological and environmental variables. Besides advancing in testing the MDE hypothesis to explain the gradient found we could also conclude that the Rapoport effect may not be responsible for the latitudinal gradient.

Keywords – Cerrado; Geometric constraints; Geographic ranges; Range size; Macroecology

Introduction

Many explanations have been attributed to latitudinal gradients in species richness (Willig *et al.* 2003). Attention has focused on a small number of these explanations, such as those related to variations in area, energy availability and habitat heterogeneity. Other potential hypotheses are the mid-domain effect (MDE) or geometric constraints hypothesis (Colwell & Hurtt 1994; Colwell & Lees 2000) that have been proposed as null models for the observed gradients.

The MDE hypothesis states that the random placement of species ranges within a domain delimited by boundaries produces a peak in species richness in the middle of the domain. In a recent article, Colwell *et al.* (2004) reviewed all studies of the mid-domain effect responding to several critiques of MDE (Koleff & Gaston 2001; Whittaker *et al.* 2001; Grytnes & Vetaas 2002; Hawkins & Diniz-Filho 2002; Laurie & Silander 2002; Vetaas & Grytnes 2002; Zapata *et al.* 2003). The discussion is far away from settled, since there is no agreement regarding the utility of MDE as a null model to explain gradients in species richness (Colwell *et al.* 2005; Hawkins *et al.* 2005; Zapata *et al.* 2005). The debate focuses on the definition of the domain limits, whether MDE are actually null models, in the predictions of MDE regarding the range size frequency distribution (RSFD), and in their statistical assessment (see Colwell *et al.* 2005; Zapata *et al.* 2005 for a comprehensive discussion of each critique).

Another recent approach of null models is their use to test for gradients of the size of species ranges, the so-called Rapoport rule (Stevens 1989). Gaston (2003) reviewed the groups that have been studied and although this “rule” has been shown in several taxa (e.g., Stevens 1992; Fleishman *et al.* 1998; Harcourt 2000; Cardillo 2002; Fortes & Absalão 2004), exceptions are numerous (e.g., Rohde *et al.* 1993; Gaston *et al.* 1998; Reed 2003; Hernández *et al.* 2005; Ribas & Schoereder in press) and its generality has been questioned making the use of the term Rapoport effect more plausible (Blackburn & Gaston 1996; Rohde 1996; Rohde & Heap 1996; Ruggiero & Lawton 1998; Gaston & Chown 1999; Samyn & Tallon 2005). Several authors have tested for the Rapoport effect using different null models, but results are contradictory (Lyons & Willig 1997; Koleff & Gaston 2001; Diniz-Filho & Tôrres 2002; Arita *et al.* 2005; Folgarait *et al.* 2005; Mora & Robertson 2005; Ribas & Schoereder in press).

In this article we aimed to test for MDE and the Rapoport effects using null models in the arboreal ant community at Cerrado biome (Brazilian savanna). These null models exclude effects of spatial gradients on the distribution of species ranges locations within a geographical domain. If observed patterns were different from that expected under the null assumptions of these models, we could deduce that biological mechanisms may be responsible for the observed gradients.

Material and methods

Study sites

The Cerrado biome, savannah-like ecosystem from Brazil, is one of the World's biodiversity hotspots (Klink & Machado 2005; Marris 2005), with a very rich flora, and high levels of endemism, compared to other savannas. Deforestation rates have transformed several parts of this biome into pasture and agricultural lands, which needs urgent conservation practices. In Central Brazil, the Cerrado covers an area of about 1.800.000 km^2 (Ratter 1992; Câmara 1993). The Cerrado is a plant community composed of several physiognomies (Coutinho 1978; Ribeiro & Walter 1998), varying from grassland to forest formations with tree densities from less than 1000 trees/ha to over 3000 trees/ha (Goodland 1971). The rainy season is from September to April with around 1500 mm of rainfall, and the dry season is during the coldest months of the year

(May to August) (Goodland 1971). We carried out the fieldwork at 11 sites consisting of conservation units in the Cerrado biome in Brazil between 8º and 22ºS latitude (Table 1).

Sampling design

In each site we delimited three plots (15 x 15m) in similar Cerrado physiognomies (between 2000-3000 trees/ha). When possible, we chose plots with different tree densities, but all of them inside the above physiognomy, to obtain data from sites with as high habitat heterogeneity as possible. Within each plot, we selected the 10 trees that were most distant from each other.

In each tree we sampled arboreal ants using pitfall traps baited with sardine and honey. The pitfall traps were plastic containers (diameter 19 cm, height 11 cm) with an inner receptacle containing the bait. Ants attracted by the bait fell into a 5% detergent plus salt solution. Traps were tied to tree stems at a height of ca. 1.3 m and remained in the field for 48h. Samplings were always carried out during the rainy season (February and December 2003 and January 2004) (Table 1), because ants are more abundant in this season. Ants were identified to genera according to Bolton (1994; 2003). Whenever possible, we identified the ants to species level by comparison to the reference collection of the Community Ecology Lab of the Federal University of Viçosa. When species identification was not possible, we sorted ants according to their external morphology. Voucher specimens are deposited in the above reference collection.

MDE effect

We tested for the existence of geometric constraints comparing empirical species richness with MDE (null models) predictions, using 1,000 simulations to obtain mean species richness and 95% confidence intervals. These simulations were computed using the RangeModel program (Version 4, R. K. Colwell, http://viceroy.eeb.uconn.edu/rangemodel, Colwell 2005). If there is a MDE effect, we would expect empirical species richness similar to that expected under a MDE effect.

Tests of the mid-domain effect assumed that a species occurs everywhere along its range. Many species have patchy distributions and when this patchiness is ignored null models overestimate diversity. Some authors (Pineda & Caswell 1998; Grytnes & Vetaas 2002; McClain & Etter 2005) have already controlled for this patchiness with different methodologies. We chose to incorporate the patchiness into the null model similarly to Grytnes & Vetaas (2002) and McClain & Etter (2005). We deleted a percentage of species (patchiness factor) of the simulated distributions. This factor was calculated by verifying the mean percentage of species missing from our sampling points relative to empirical species richness calculated by the program, which assumes that a species is continuously distributed between the extreme sampling points.

Rapoport effect

We calculated the range size of each ant species as the difference between the maximum and minimum latitude in which they were sampled. To calculate midpoint we calculated the average latitude between the maximum and minimum in which each species was sampled.

The expected null correlation between range size and midpoint considering only sampling boundaries, was a quadratic with a peak in range sizes at intermediate sampling latitudes (Ribas & Schoereder in press). This correlation is expected since the distributions are limited by the sampling extent that was carried out in a latitudinal range smaller than real distributions of the studied species. In this case, there are no true hard boundaries present. The boundaries define an arbitrary domain (*sensu* Colwell *et al.* 2004) and they are the highest and the lowest latitudes in which sampling was carried out (Fig. 1). The null expectation, using midpoint as a latitudinal descriptor, was that there were smaller ranges close to the limits of the sampled area and larger ranges in the centre of the sampled area independent of latitude.

We used the method proposed in Ribas & Schoereder (in press) to test if the correlation between range size and mid-latitude was different from that expected under null assumptions. We simulated 1,000 random and 1,000 pseudo-random distributions and for each simulation we calculated the correlation coefficient, obtaining a frequency distribution of 1,000 coefficients, comparing each observed correlation coefficient with the 95% frequency distribution. If the observed coefficient was outside the 95% limits of the simulated frequency distribution coefficients, we rejected the null hypothesis that the correlation between range size and midpoint was the same as the one expected under null assumptions and we would investigate why these differences appeared.

If there was a Rapoport effect, we would expect range sizes smaller than expected by chance in low latitudes and higher than expected by chance in high latitudes (Fig. 2). We calculated a, b, and c parameters (Sokal & Rohlf 1981) of the quadratic model fitted to the correlation between range size and mid-latitude for each of the 1,000 simulations in each model (random and pseudo-random). Therefore, to check for the Rapoport effect we compared the frequency distribution of 1,000 simulated values with that calculated for observed distributions.

Results

Ant species richness

We collected 147 ant species, belonging to eight subfamilies - Dolichoderinae, Formicinae, Ecitoninae, Ectatomminae, Myrmicinae, Paraponerinae, Pseudomyrmecinae and Ponerinae. Ant species richness varied from 20 to 43 per site.

MDE effect

The empirical species richness showed a weak MDE effect (Fig. 3). From 11 empirical species richness points only three (27%) occurred within the predicted species richness expected under MDE effect. These points include higher latitudes (17^{o}34'S, 19^{o}30'S and 20^{o}14'S). The other points have smaller species richness (five sampling points) or higher species richness (three sampling points) than expected by MDE effects.

When we removed 36% of the species from the null samples to include the spatial patchiness in the model, we observed lower expected diversity values (Fig. 4). Although our main result was maintained, empirical species richness did not show a MDE effect. In this case, at only four sampling points (36%) we could accept the MDE effect. These points were different from that found when we did not remove any species, being in this case (14^{o}07'S, 15^{o}27'S, 16^{o}04'S and 15^{o}02'S). All other sampling points have higher species richness than expected by MDE effects.

Rapoport effect

In the random simulation, correlation between range size and midpoint was similar to that expected by chance ($p=0.38$) and therefore we did not have to test for significance of equation parameters. In the pseudo-random simulation correlation was significantly higher than expected by chance ($p<0.001$) and the parameters of the observed curves indicated significantly larger range sizes at the boundaries (Fig. 5).

Discussion

MDE effect

Studies testing MDE effects have reached different results independent of the kind of gradient in which they were performed (latitudinal, altitudinal and depth gradients). Several authors concluded that MDE effects are determinants of the observed gradients (e.g. Willig & Lyons 1998; Lees *et al.* 1999; Falster *et al.* 2001; Krystufek & Griffiths 2002; McCain 2003; Bellwood *et al.* 2005), while others found a weak relationship between the predicted and observed gradients (e.g. Bokma *et al.* 2001; Jetz & Rahbek 2001; Diniz-Filho *et al.* 2002; Hawkins & Diniz-Filho 2002; Grytnes 2003; Rangel & Diniz-Filho 2003; 2004; Aliabadian *et al.* 2005; Hernández *et al.* 2005).The absence of MDE effects found in some studies (Jetz & Rahbek 2002; Smith & Brown 2002; Connolly *et al.* 2003; Carpenter 2005; Ferrer-Castán & Vetaas 2005; McClain & Etter 2005) has been attributed to a variety of factors including the generating algorithms, the distribution of range sizes, patchiness of species and the mis-dentification of hard boundaries (McClain & Etter 2005). Colwell *et al.* (2004) reviewed several studies about MDE effects concluding that there is not a general pattern in the studies accepting or rejecting MDE effects, in respect of location of study, taxa, gradient, and one or two dimensional studies (but see Bokma *et al.* 2001; Koleff & Gaston 2001; Hawkins & Diniz-Filho 2002; Laurie & Silander 2002; Rangel & Diniz-Filho 2003; Zapata *et al.* 2003). To our knowledge there are only two papers testing MDE effects in ant communities: Sanders (2002) detected a MDE effect in an altitudinal gradient, while Kaspari *et al.* (2003), studying different spatial scales, failed to support MDE predictions. Although Romdal *et al*. (2005) concluded that we should expect stronger effects of MDE gradients for small study regions or geographically small-scale gradients, our study detected no MDE effects in these circumstances.

Our results showed a higher species richness than expected by the MDE effect when we incorporate the spatial patchiness in the null model. There is a trend showing a higher species richness mainly at the higher latitude sampling points (Fig. 4). In a previous study in these same sites, Ribas *et al.* (submitted) have found a reverse latitudinal gradient. These authors have tested for correlations between these gradient and habitat variables such as heterogeneity and productivity, and rejected these variables as explanation for the latitudinal gradient in ant species richness. They suggested that Cerrado geographical distribution, the evolutionary history of ant species or MDE effects may be responsible for the pattern found. The results in this study rejected MDE effect as an explanation for the observed latitudinal gradient.

Rapoport effect

Other authors already found an absence of the Rapoport effect when comparing the real range size pattern with that generated by chance (Lyons & Willig 1997; Koleff & Gaston 2001; Diniz-Filho & Tôrres 2002; Arita *et al.* 2005; Folgarait *et al.* 2005; Mora & Robertson 2005). Although the majority of these studies have found a Rapoport effect even when using null models (Lyons & Willig 1997; Diniz-Filho & Tôrres 2002; Arita *et al.* 2005; Folgarait *et al.* 2005; Mora & Robertson 2005), Ribas & Schoereder (in press), in a meta-analytical approach analysing 55 data sets, showed that there is a higher number of studies where there is no evidence of this effect.

The result of the random simulation changing to different from expected by chance in the pseudo-random simulation may be a result of the inclusion of the specific geographic location of each species in the latter simulation. Randomness generated by the pseudo-random simulation would be more similar to the real distribution. Although there is not a Rapoport effect, the pattern found in the real distribution should be explained by a biological mechanism. The midpoint of species distributions may represent optimal conditions or the geographical centre of its evolutionary origin (Lyons & Willig 1997), assuming non-directional dispersal movements. The observed range sizes larger than expected by chance in the distribution boundaries may indicate an absence of specific requirements of resources and environmental conditions presented by ant species located closer to Cerrado boundaries.

Conclusions

One of our main results is the coincidence between a previous study performed at the same site and this study. The other study (Ribas *et al.* submitted) showed a reverse latitudinal gradient in ant species richness and this study besides demonstrating that there is not a MDE effect evidenced higher species richness at higher latitudes. In the history of MDE null models a recent and elegant approach is the use of process-based models (Bellwood *et al.* 2005; Brayard *et al.* 2005; Connolly *et al.* 2005; Davies *et al.* 2005; Mora & Robertson 2005; Rangel & Diniz-Filho 2005a; b; Romdal *et al.* 2005). These models mechanistically integrate geometric constraints with environmental variables or evolutionary processes within a bounded domain. We agree with these authors that process-based models offer a way to advance MDE classic models, allowing the formulation of null models as well as alternatives that incorporate biological and environmental variables.

Instead of finding a Rapoport effect, we found larger range sizes at extreme latitudes, which could indicate species being more generalists. Other authors already have claimed that the Rapoport effect is not widespread to be considered as a pattern in global ecology (Rohde *et al.* 1993; Blackburn & Gaston 1996; Rohde 1996; Rohde & Heap 1996; Ruggiero & Lawton 1998; Gaston & Chown 1999; Hernández *et al.* 2005;

Samyn & Tallon 2005; Ribas & Schoereder in press). Besides advancing in testing a hypothesis to explain the gradient found we showed that the Rapoport effect was not responsible for the observed latitudinal gradient. Although some authors (Rohde 1996; 1999; Rohde & Heap 1996, but see Smith & Gaines 2003) have considered the coincident patterns of Rapoport's rule and the gradient in species richness as indicating that Rapoport's rule could generate the species richness gradients, the studies that test for a causal relationship between Rapoport's rule and species richness gradients, the results are conflicting (Kolasa *et al.* 1998; Taylor & Gaines 1999; Addo-Bediako *et al.* 2000).

Acknowledgements – We gratefully acknowledge IBAMA for permission to collect in the conservation units, and IBAMA, Carla Galbiati, Marcelo S. Madureira, Rogério F. Ribas, Renata B.F. Campos for field assistance. The authors are indebted to Robert K. Colwell for support with the program. Carla R. Ribas is supported by a CAPES grant and José H. Schoereder is supported by a CNPq grant. The British Ecological Society (SEPG), The Nature Conservancy of Brazil and FAPEMIG supported this work. Samplings carried out comply with the current laws of Brazil.

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Table 1 – Sampled Cerrado sites in conservation units in Brazil, geographic coordinates and dates in which fieldwork has been carried out.

Site	Coordinates (S) (W)	Date sampled
Estação Ecológica Uruçuí-Una	8°52’, 44°58’	January 2005
Parque Nacional da Chapada dos Veadeiros	14°07’, 47°30’	February 2003
Parque Nacional da Chapada dos Guimarães	15°27’, 55°44’	January 2004
Parque Nacional de Brasília	15°46’, 47°55’	February 2003
Estação Ecológica da Serra das Araras	16°04’, 57°40’	January 2004
Parque Nacional Cavernas do Peruaçu	15°02’, 44°11’	December 2004
Parque Nacional das Emas	17°34’, 52°33’	December 2003
Floresta Nacional de Paraopeba	19°16’, 44°24’	January 2003
Parque Nacional da Serra do Cipó	19°30’, 43°44’	January 2003
Near Parque Nacional da Serra da Canastra	20°14’, 46°21’	December 2003
Fazenda Campininha	22°18’, 47°11’	February 2003

Figure 1 – Lower drawings represent the expected relationship between range sizes (lines) and mid-latitude (circles) in two possible cases of species distribution (upper drawings). On the left side, a distribution that does not cross the equator (0º) produces a unimodal expected relationship between the variables, because increasing or decreasing the latitude from the midpoint of the distribution decreases range sizes. On the right side, a linear correlation is expected because the distribution crosses the equator, and the increase in latitude corresponds to a decrease in range sizes.

Figure 2 – Representation of correlation between range size and midpoint. The solid line represents the expected correlation (EXP) considering the null assumptions. The dashed line represents the correlation under the Rapoport effect (OBS): smaller range sizes in small latitudes/altitudes and larger range sizes in high latitudes/altitudes.

Figure 3 – Correlation between ant species richness and latitude. Circles represent real species richness sampled at Cerrado sites. Bars represent 95% confidence intervals after 1,000 simulations.

Figure 4 – Correlation between ant species richness and latitude after controlling for spatial patchiness. Circles represent real species richness sampled at Cerrado sites. Bars represent 95% confidence intervals after 1,000 simulations.

Figure 5 - Correlation between range size and mid latitude - larger range sizes at the boundaries of the distribution. Dashed line represents the expected correlation considering the null assumptions. Solid line represents the observed correlation.

Figure 1

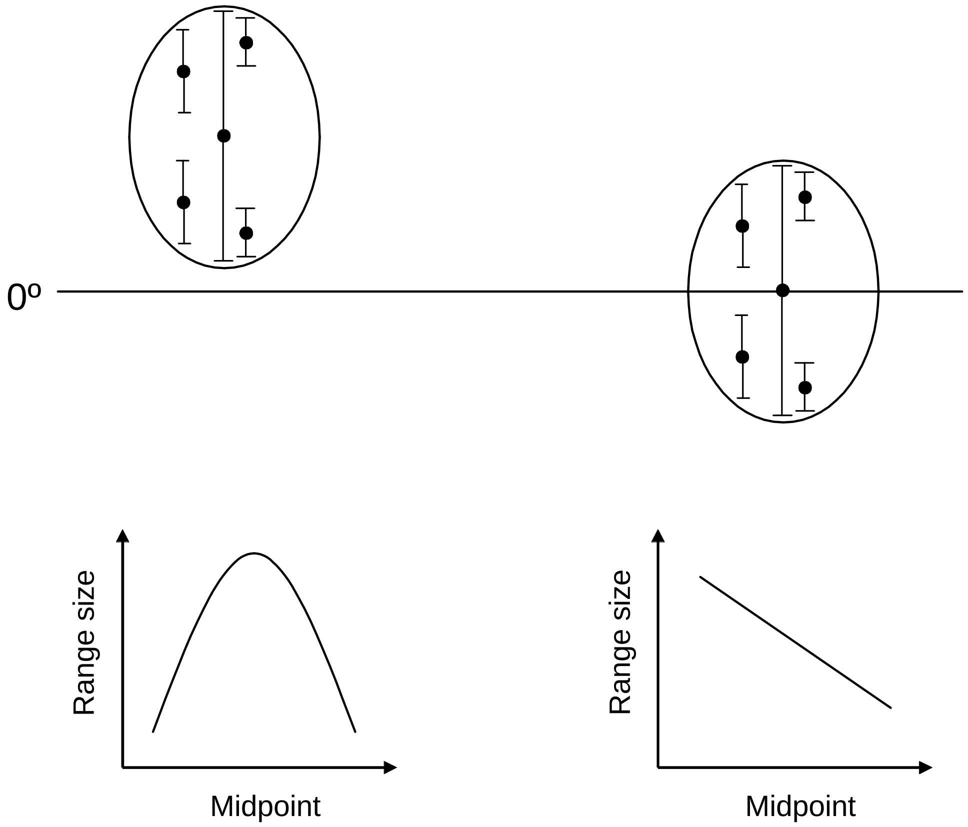


Figure 2

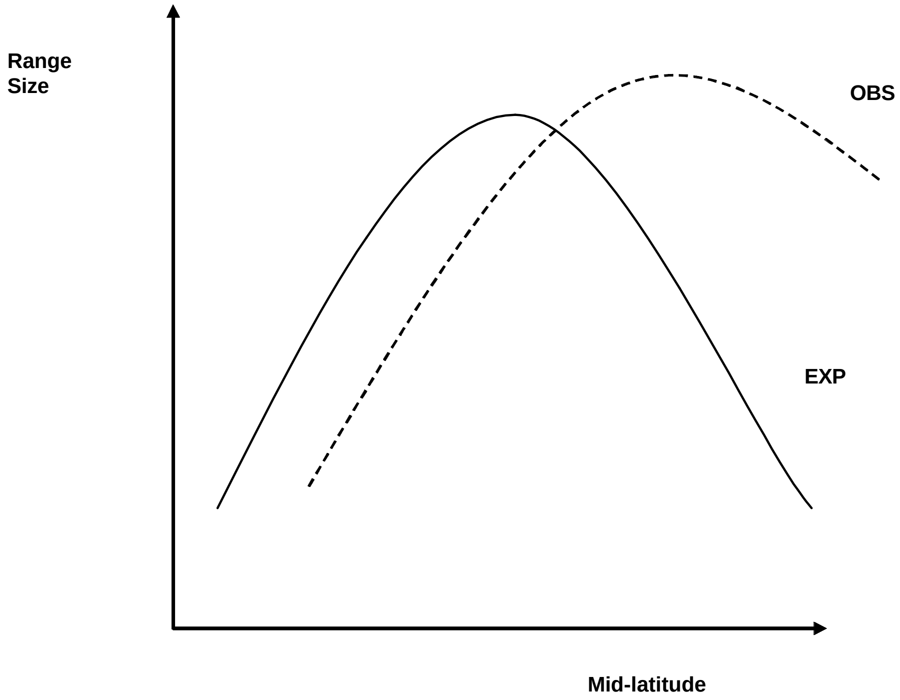


Figure 3

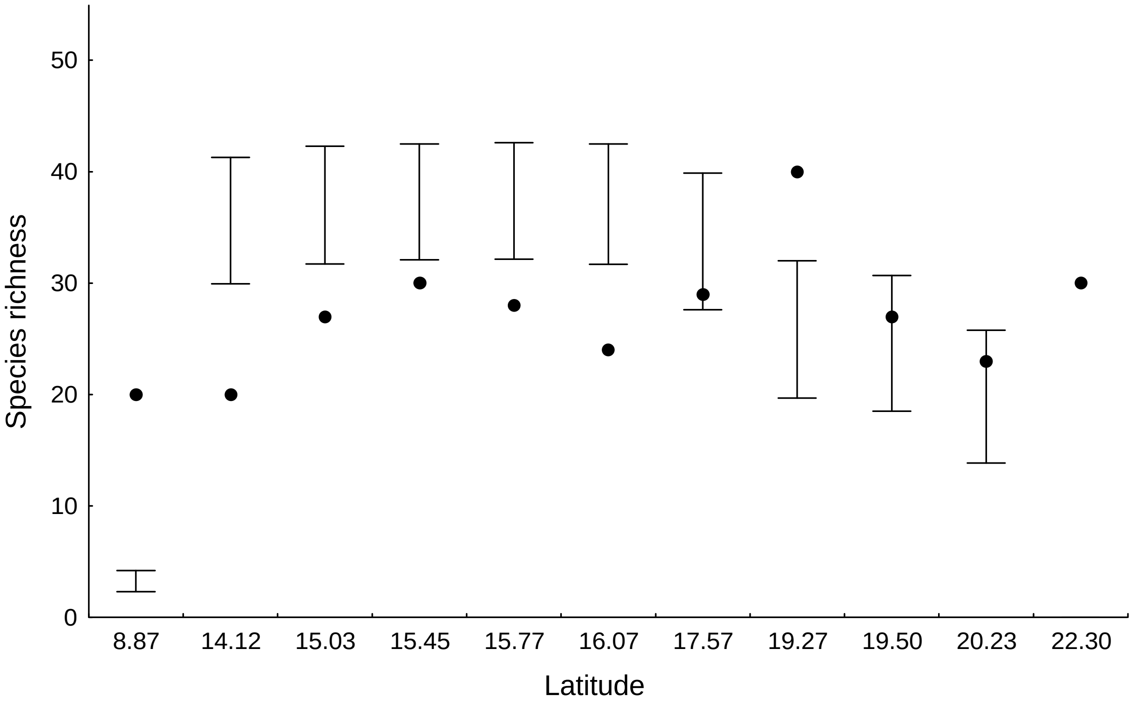
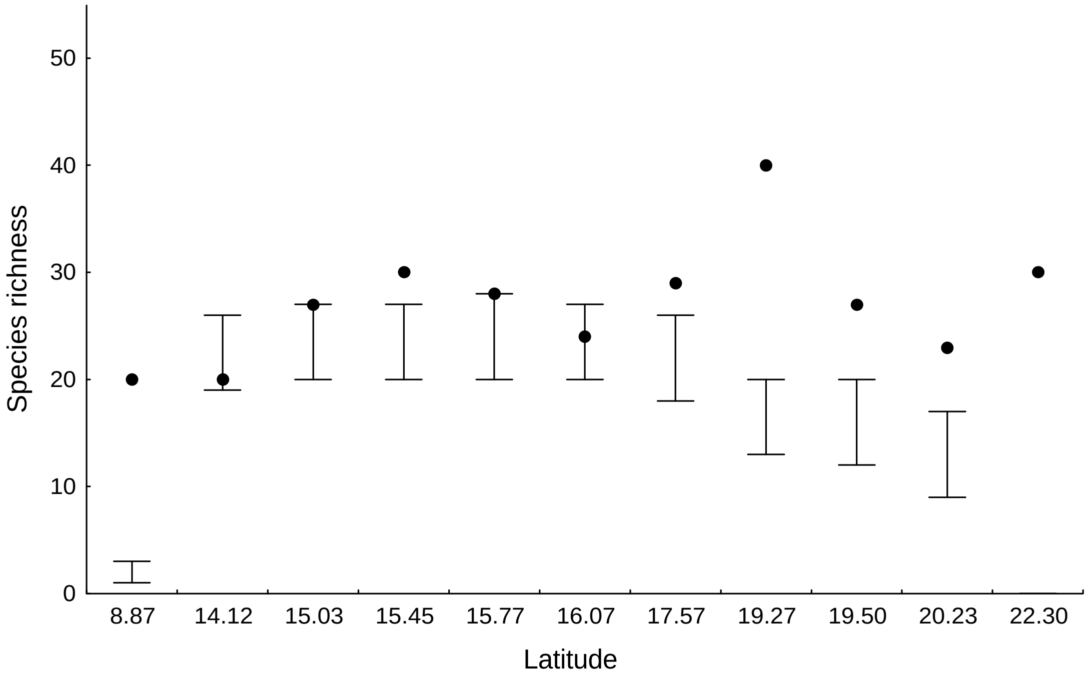

Species richness
50
40
30
20
10
0
8.87
14.12
15.03
15.45
15.77
16.07
17.57
19.27
19.50
20.23
22.30
Latitude

Figure 4


Species richness
0
10
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8.87
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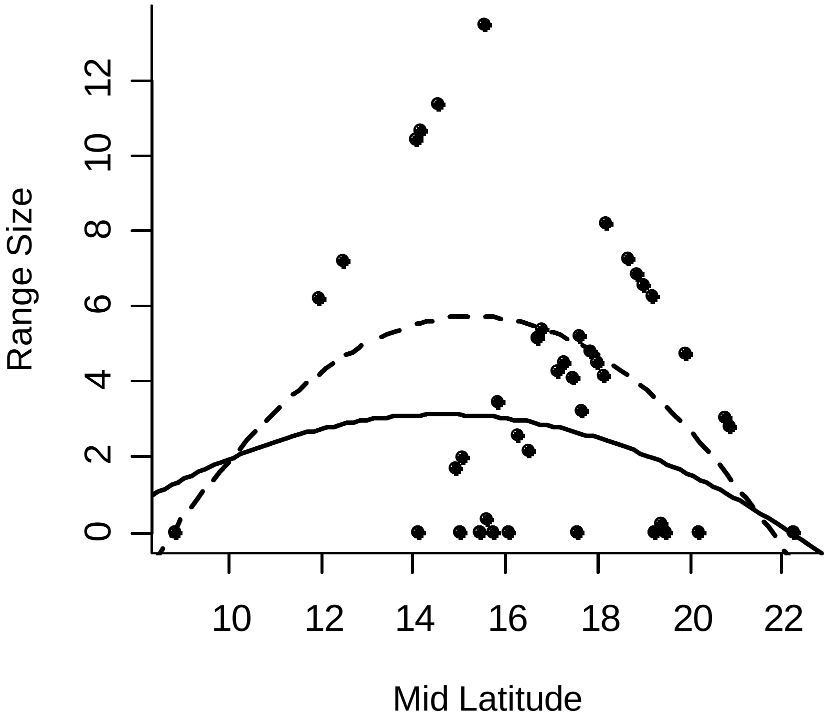
20.23
22.30
Latitude

Figure 5



CONCLUSÕES GERAIS

Apesar do gradiente latitudinal de riqueza de espécies ser um padrão bem documentado para vários grupos de organismos, para formigas arborícolas no Cerrado o padrão encontrado foi o oposto do comumente descrito, ou seja, observamos um aumento do número de espécies com a latitude. Além disso, fatores comumente descritos como correlacionados com o gradiente latitudinal, como produtividade e heterogeneidade ambiental, além do efeito Rapoport e do domínio mediano, não foram importantes para explicar o gradiente encontrado nesse estudo.

No primeiro capítulo observamos diversos padrões de correlação entre o tamanho da distribuição das espécies e seu ponto médio de distribuição e poucos desses resultados foram indicativos do efeito Rapoport. Nós concluímos que a maioria dos métodos utilizados até hoje para testar o efeito Rapoport não são capazes de distinguir entre padrões determinísticos e aqueles gerados pelo acaso. Apesar de alguns trabalhos recentes terem demonstrado o efeito Rapoport, nossos resultados sugerem que esse efeito não deve ser considerado como um padrão em macroecologia.

No segundo capítulo observamos um aumento da diversidade alfa de formigas com a latitude, nas duas menores escalas espaciais estudadas. A diversidade alfa não apresentou uma correlação com a latitude na terceira e mais ampla escala espacial analisada, assim como a diversidade beta não variou com a latitude em nenhuma escala espacial. As variáveis ambientais analisadas, produtividade e heterogeneidade, não explicaram a variação da riqueza de espécies. Esses resultados podem ser explicados: (i) pela pequena extensão latitudinal estudada, (ii) pela distribuição geográfica do Cerrado ou (iii) pela história evolutiva das espécies de formigas. Concluímos que processos que são importantes em escalas espaciais locais podem levar a variações na riqueza de espécies só em escalas menores, perdendo sua importância quando analisamos escalas globais.

No terceiro capítulo nós não encontramos o efeito do domínio mediano e nem o efeito Rapoport. A riqueza de espécies foi maior do que esperado pelo efeito do domínio mediano em locais de maior latitude. Ao invés do efeito Rapoport, nós verificamos que os tamanhos das distribuições das espécies são maiores do que o esperado pelo acaso nos limites do domínio. Nós concluímos que nem o efeito do domínio mediano e nem o efeito Rapoport são responsáveis pelo gradiente de riqueza de espécies encontrado.

Concluindo, o gradiente de riqueza de espécies de formigas encontrado é oposto ao descrito na literatura, além de ser dependente da escala espacial estudada. Nenhum dos fatores investigados nesse trabalho foi responsável pelo gradiente, entre eles a produtividade ambiental, a heterogeneidade de recursos e estrutural, o efeito do domínio mediano e o efeito Rapoport. Dessa forma, sugerimos que outras hipóteses como a distribuição geográfica do Cerrado e a história evolutiva das espécies de formigas devem ser investigadas como causadoras do gradiente latitudinal reverso de riqueza de espécies de formigas arborícolas em Cerrado.