Journal of Biogeography (J. Biogeogr.) (2004) 31, 1219–1226

ORIGINAL ARTICLE

Should we use proportional sampling for species–area studies?

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ABSTRACT

Aim In this paper we aim to show that proportional sampling can detect species–area relationships (SARs) more effectively than uniform sampling. We tested the contribution of alpha and beta diversity in ant communities as explanations for the SAR.

Location Tropical forest remnants in Viçosa, Minas Gerais, Brazil (20 °45′ S, 42 °50′ W).

Methods We sampled 17 forest remnants with proportional sampling. To disentangle sampling effects from other mechanisms, species richness was fitted in a model with remnant size, number of samples (sampling effects) and an interaction term.

Results A SAR was observed independent of the number of samples, discarding sampling effects. Alpha diversity was not influenced by remnant size, and beta diversity increased with remnant size; evidence to the fact that habitat diversity within remnants could be the dominant cause of the SAR. Such a relationship between beta diversity and remnant area may have also arisen due to the combined effects of territoriality and aggregation of ant species.

Main conclusions The proposed model, together with proportional sampling, allowed the distinction between sampling effects and other mechanisms.

Keywords

Alpha diversity, ants, area *per se*, beta diversity, fragmentation, habitat diversity, passive sampling, remnants, sampling artefact, uniform sampling.

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INTRODUCTION

Species–area relationships (SARs) have been a central subject in community ecology theory for several decades (Kilburn, 1966; Connor & McCoy, 1979; Margules *et al.*, 1982; Ney-Nifle & Mangel, 2000), but controvacy remains around the best descriptive model (De Blasio & De Blasio, 2002; He & Legendre, 2002; Triantis *et al.*, 2003), what mechanisms cause the pattern (Turner, 1996; He & Legendre, 2002), and the best sampling design to study it (Hill *et al.*, 1994; Cam *et al.*, 2002). Understanding how and why species richness increases with remnant size is fundamental for studies on habitat fragmentation, as well as for the explanation of other patterns of species richness involving area effects, such as latitude, altitude and habitat productivity (Rosenzweig, 1995). Habitat fragmentation and SARs are usually confounded because both involve area reduction and the effects on species richness. SARs, however, are empirical phenomena that do not consider processes that occur in fragmented landscapes. These processes, such as edge and shape effects (Carvalho & Vasconcelos, 1999), isolation and species invasions from the new environments created among the remnants of natural habitat (Sobrinho *et al.*, 2003) may modify the pattern because they add new variables to SARs. Preston (1962) differentiates two kinds of sampling units that generate SARs: isolates and samples. Isolates are similar to habitat patches whose boundaries are biologically determined, e.g. true islands or remnant edges. Samples are within a larger contiguous region, which Rosenzweig (1995) calls mainland curves, and their boundaries are artefactual, e.g. political or sampling quadrats.

In the early phase of theory development on SARs, descriptive studies were carried out, aiming to describe the pattern by fitting different mathematical models to empirical data. Such studies were extremely important to explain how species number varies with remnant size, and to collate large amounts of facts which helped to consolidate theoretical expectancies on SARs.

Nowadays, as we achieve a new stage in the study of SARs, researchers are more concerned on why species number increases with remnant size (Hart & Horwitz, 1991; Holt *et al.*, 1999; He & Legendre, 2002).

Several SARs-generating mechanisms are distinguishable, which ultimately could be grouped into four categories: (i) sampling artefact (Preston, 1962; Lewinsohn, 1991); (ii) passive sampling (Arrhenius, 1921; Coleman, 1981; Andrén, 1999); (iii) area *per se* effects (MacArthur & Wilson, 1967; Stevens, 1986; Ricklefs & Lovette, 1999); and (iv) habitat diversity effects (Williams, 1943; Connor & McCoy, 1979; Ricklefs & Lovette, 1999). Species richness may increase with remnant size simply because larger remnants need greater sampling effort in order for them to be characterized fully. By doing that, more individuals are collected, hence increasing the probability of collecting more species (Hill *et al.*, 1994). Skeptics would hold that SARs are produced entirely by such a sampling artefact, which implies that the actual species richness is unaffected by remnant size. If one is able to discard sampling artefacts, therefore, it would mean that any observed SARs were real, and the result of biological mechanisms.

Larger areas could effectively hold more species than smaller ones simply because the former would act as larger samples of the original environment, thereby passively 'collecting' more species from the regional pool. Passive sampling, therefore, resembles sampling artefact, but is generated by processes which result in an actual increase of species richness with remnant size. It must be stressed, therefore, that passive sampling is not an artefact (Cam *et al.*, 2002).

The discrimination among passive sampling, area *per se* and habitat diversity may be based on how alpha and beta diversities vary with remnant size (Stevens, 1986). Passive sampling assumes that local species richness (alpha diversity) and species turnover (beta diversity) do not vary with remnant size. According to the hypothesis of area *per se*, remnant size affects the biological processes of species richness regulation. For example, immigration can increase with target area (Brown & Kodric-Brown, 1977), and extinction can diminish with remnant size due to larger local population sizes (MacArthur & Wilson, 1967). The hypothesis of area *per se* predicts that sampling sites in larger remnants produces larger local species richness (alpha), but with no detectable differences in species turnover (beta). Conversely, habitat diversity is linked to the differences in species composition between each sampling site within remnants (beta), although differences in local species richness do not occur (Stevens, 1986). Larger remnants, hence, have a larger species turnover within them, which is responsible for the increase in species richness with remnant size (Quinn *et al.*, 1987; Hart & Horwitz, 1991).

In an effort to deal only with biological mechanisms, several authors (Hill *et al.*, 1994; Davies & Margules, 1998; Golden & Crist, 1999) fix sampling effort across the study area gradient, collecting the same amount of samples across different remnant sizes. Such a procedure does prevent sampling artefacts, but – especially when areas expand one or more orders of magnitude – may easily be insensitive to variations in habitat diversity, thereby missing beta diversity effects. Using uniform sampling effort, the probability of sampling a given habitat in a remnant decreases with increasing area. Only a proportional sampling scheme can guarantee that each habitat has the same probability of being sampled. Therefore, to guarantee that beta diversity effects could be spotted, one would need to design a proportional sampling scheme, with the amount of samples being increased proportionally to the increase in habitat size. However, proportional sampling runs the risk of incorporating sampling artefacts because the probability of sampling more individuals, and therefore of finding more species, increases with sampling effort (Hill *et al.*, 1994).

This paper aims to show that proportional sampling may detect SARs more effectively than uniform sampling. We propose a method to separate sampling effects from other mechanisms that cause SARs. If sampling effects are rejected as the only explanation for SARs, then we can test the relationships between alpha and beta diversity with remnant size, to evaluate the effective contribution of area *per se* and habitat diversity to the species–area effect.

METHODS

Study site

The study was carried out at Viçosa, south-eastern Brazil (20 °45′ S, 42 °50′ W), a region that was covered by tropical rain forests up to 1930s and 1940s, when an accelerated process of fragmentation began (Valverde, 1958) to implant pastures and coffee plantations (Gomes, 1975). The extant vegetation has been restricted to a few remnants, particularly on hilltops, which correspond to the isolates of Preston (1962). From the 1960s onwards, agriculture declined in the region and several forest remnants have regenerated into secondary forests (Meira Neto & Martins, 2000; Sevilha *et al.*, 2001). Today, the region comprises a mosaic of forest remnants varying from 3 ha to 300 ha, surrounded by pastures and other agricultural fields, forming an excellent system to study the effects of fragmentation and SARs.

Sampling design

At Viçosa, 17 remnants were arbitrarily chosen, with remnant size ranging from *c.* 3 ha to 93 ha (Table 1). Despite the differences between SARs and fragmentation, because the latter involves processes beyond SARs, we used these different-sized remnants to detect a SAR. The remnants were sampled during the summer rainy season of 1995. Ants (Hymenoptera: Formicidae) were sampled by pitfall traps, using human faeces, carrion and decomposing fruit as bait. Pitfall traps were plastic containers (diameter 19 cm, height 11 cm), with an

Table 1 Remnant area (ha), number of samples carried out, and number of species sampled in each remnant in Viçosa, MG, Brazil

Remnant area (ha)	No. of samples	No. of species
3.21	1	20
3.74	1	13
4.05	1	13
4.21	1	14
4.99	1	16
5.27	1	16
5.56	1	17
5.77	1	16
6.91	1	14
7.97	2	20
8.00	2	20
8.56	2	23
30.13	6	38
39.21	8	47
46.16	9	58
60.53	12	59
93.37	19	77

inner receptacle containing the bait, and were left in the field for 48 h. Ants attracted by the bait fell into a 5% detergent solution.

The pitfalls were set in groups of three, each one containing a different bait type. Within groups, pitfalls were positioned at the vertices of an equilateral triangle, each 2 m apart. Minimum distance between groups (a triangle of three pitfalls), and between a group and the nearest forest or gap edge, was 30 m. Our sampling unit was formed by 12 pitfalls, grouped in four triangles of three pitfalls.

Passive sampling and sampling artefact are not easily distinguishable and there are authors who do not recognize these two classes (e.g. Hart & Horwitz, 1991). Our sampling procedure also cannot distinguish between passive sampling and sampling artefact, and therefore we grouped them into a broader class, named sampling effects. We used two different sampling schemes on the same set of remnants. To test the SAR, sampling effects (*sensu* Hart & Horwitz, 1991) and beta diversity, the number of sampling units used was proportional to remnant size (one sampling unit per 5 ha). We considered alpha diversity as the total number of species in one sampling unit, all of them arranged in identical sets within the remnants.

The ants were sorted, mounted and identified to genera with the help of identification keys (Hölldobler & Wilson, 1990; Bolton, 1994). Whenever possible, the ants were identified to species level. When species identification was not possible, they were sorted within each genus according to their external morphology. Voucher specimens were deposited in the reference collection of the Community Ecology Lab of the Departamento de Biologia Geral of the Universidade Federal de Viçosa.

Testing the SAR and sampling artefact

To separate sampling effects from other mechanisms that cause the SAR we fitted a generalized linear model (Crawley, 2002) using the logarithm of ant species richness in each remnant as the response variable. We deliberately did not use species richness estimators (Colwell & Coddington, 1994) because our aim was not to estimate total species richness, but to filter deviance due to sampling effects from that due to other mechanisms causing the SAR. The explanatory variables were logarithm of remnant size, number of samples in each remnant and interaction between the two variables. The complete model was fitted using normal errors, with significance being assessed by stepwise omission of non-significant terms, beginning from the maximal model (Crawley, 2002).

Remnant size and sampling effort are correlated and therefore the design is non-orthogonal, as expected in observational studies. In such designs we must be careful to judge the significance of factors when they are removed from the optimal model (Crawley, 2002). Because the two variables are correlated, there is a deviance attributed to each of them and there is a deviance that is attributable to both. The first variable entered in the model removes its own deviance and the deviance attributable to both variables, leaving less deviance for the second variable. We opted to enter the number of samples first in the model, in a more conservative analysis, because it will remove more deviance and we would then be more confident of any observed area effects.

If sampling effects are the factors responsible for the SAR, then we expect that only the number of samples would be significant. If species richness responds to remnant size, regardless of the mechanisms involved, then we expect that remnant size would be significant in the model. The interaction represents how remnant size modifies the effect of sampling effort, or how sampling effects vary with remnant size. If, for instance, in larger remnants sampling effects are larger, then we expect that the interaction would be significant. Deviance in species richness due to sampling effects is removed by the variable representing number of samples and by the interaction term, with the remaining deviance (if any) being explained by other mechanisms. In order to distinguish between these mechanisms, additional tests have to be performed.

The usual procedure to remove the effect of sampling is to carry out the analysis correcting for the number of individuals, with the help of rarefaction (Gotelli & Colwell, 2001). The use of number of individuals in ant communities, however, produces another bias in the analysis, because this number is dependent on the recruiting ability of each ant species and on the distance from the nest site to the pitfall trap (Hölldobler & Wilson, 1990). We could use ant frequency (number of records of a species relative to the total number of records) as a surrogate of nest density, but this estimate is also dependent of sampling: a single record of a species among a small total of samples produces a higher frequency than the same occurrence among several samples.

Testing the SAR with null communities

To test if our model is adequate to separate sampling effects from other mechanisms in communities where we are certain that a SAR exists, we created a landscape with 20 remnants varying from 5 ha to 100 ha (Table 2). Such remnants were created simulating a constant alpha diversity (34 species per 4 ha), which is the average alpha diversity observed in the studied remnants. First, total number of species (S) in each remnant was determined using the power function of Arrhenius (1921), using a slope of 0.3, as suggested by several authors for isolated habitat patches (e.g. Triantis *et al.*, 2003). Then, within each remnant, species (rows) were assigned randomly to 5 ha (columns), providing that column sum was equal to 34 for all 5 ha, and row sum was non-zero for all S species in the remnant. We proportionally sampled the remnants with the same sampling effort used in the observed communities (one sample per 5 ha), choosing at random which column(s) would be sampled.

The same analysis described for the observed communities was carried out to test the SAR and to separate sampling effects from other mechanisms. We expected that if our model was adequate, species richness of simulated remnants would increase with remnant area and with sampling effort.

Testing the mechanisms involved in the SAR

In the event that the test for sampling effects does show evidence of other processes, such mechanisms can be distinguished based on how alpha and beta diversity vary with remnant size, as suggested by Stevens (1986). To do so, we fitted a generalized linear model to check whether remnant size affected alpha diversity, using Poisson errors corrected for overdispersion. Our test for alpha diversity is equivalent to testing SARs with uniform sampling, as the number of samples per remnant was the same. Alpha diversity was used as response variable, and the logarithm of remnant size was the explanatory variable. A similar statistical procedure was used to test beta diversity (response variable) against the logarithm of the remnant size (explanatory variable), using normal errors. There are several ways to measure beta diversity, all of them with their limitations and advantages (Koleff *et al.*, 2003); we used the Sørensen similarity index, which is one of the most commonly used. Beta diversity was estimated as the inverse of Sørensen similarity index (Krebs, 1989), calculating the average similarity between all possible pairs among all sampling units available in proportional sampling. As similarity is known to be affected by sample size (Krebs, 1989), the number of samples taken in each remnant was included in the model. Because in some small remnants only one sampling unit was allocated in the proportional sampling, we eliminated such remnants from the analysis, keeping only eight remnants. In this case, we did not fit the interaction term because there were not enough degrees of freedom.

Table 2 Null simulated communities: remnant area (ha), number of samples carried out, total number of species and number of species sampled in each remnant

Remnant area (ha)	No. of samples	Total no. of species	Sampled no. of species
5	1	55	34
10	2	68	42
15	3	77	64
20	4	84	73
25	5	89	82
30	6	94	85
35	7	99	92
40	8	103	101
45	9	107	104
50	10	110	107
55	11	113	111
60	12	116	113
65	13	119	118
70	14	122	120
75	15	124	124
80	16	127	126
85	17	129	129
90	18	131	129
95	19	133	132
100	20	135	134

All analyses were performed under R (Ihaka & Gentleman, 1996), and were followed by residual analyses to check for the error distribution and the suitability of the model.

RESULTS

Ant species richness increased with the number of samples ($F_{1,15} = 332.49$; $P << 0.0001$), and with remnant size ($F_{1,14} = 30.06$; $P = 0.0001$; Fig. 1) and the slope of this SAR was affected by sample size ($F_{1,13} = 8.63$; $P = 0.011$). That is, as we sample remnants more exhaustively, we collect more species, and this changes the general aspect of the SAR for

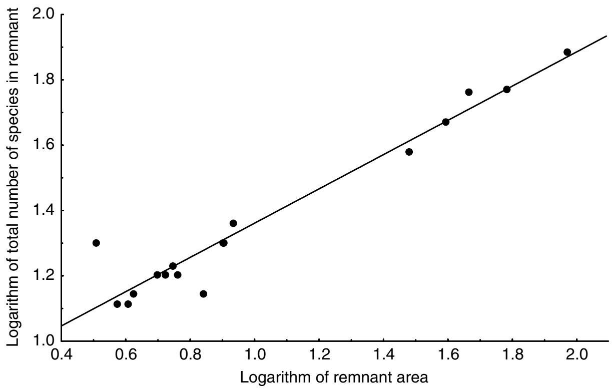

Figure 1 Relationship between the logarithm of total ant species richness and the logarithm of remnant size in Viçosa, south-eastern Brazil. The highly significant relationship was maintained when sampling effects were removed. $\log(S) = 0.837 + 0.525 \times \log(\text{area})$.

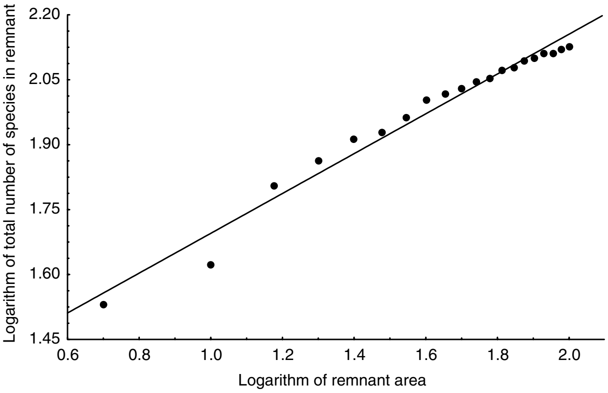

Figure 2 Relationship between the logarithm of total species richness and the logarithm of remnant size in the null communities. The highly significant relationship was maintained when sampling effects were removed. $\log(S) = 1.235 + 0.46 \times \log(\text{area})$.

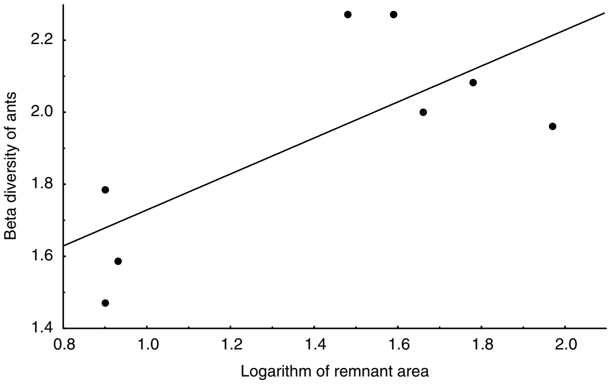

Figure 4 Relationship between ant species beta diversity and logarithm of remnant size in Viçosa, south-eastern Brazil. The significant relationship is maintained when sampling effects are removed. Beta diversity was estimated as the inverse of Sørensen index of similarity. Beta diversity = $1.229 + 0.499 \times \log(\text{area})$.

those ants. Residual analysis supported the use of the linear model and normal errors.

In the null communities, species richness increased with the number of samples ($F_{1,18} = 1189.68$; $P << 0.0001$) and with remnant size ($F_{1,17} = 349.48$; $P << 0.0001$; Fig. 2). The slope of this SAR was not affected by sample size ($F_{1,16} = 0.0001$; $P = 0.99$). Residual analysis supported the use of the linear model and normal errors. These results confirm the power of proportional sampling allied to our proposed model to separate sampling effects from other mechanisms causing the SAR.

Alpha diversity did not vary with remnant size ($F_{1,15} = 0.54$; $P = 0.46$; Fig. 3): larger remnants tend to hold the same number of species per unit of remnant size as small remnants. Residual analysis supported the use of Poisson errors.

Beta diversity did not increase with the number of samples ($F_{1,6} = 5.86$; $P = 0.06$), but increased with remnant size ($F_{1,5} = 6.73$; $P = 0.041$): in large remnants the samples were more dissimilar (Fig. 4). Figure 5 shows the residual analysis for this regression, which supports the use of the model.

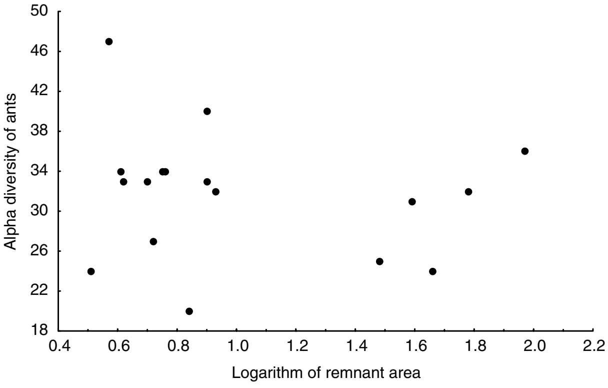

Figure 3 Relationship between ant species alpha diversity and logarithm of remnant size in Viçosa, south-eastern Brazil. Alpha diversity is the number of species in four pitfall traps that sample an area of 5 ha, and is similar to uniform sampling of remnants.

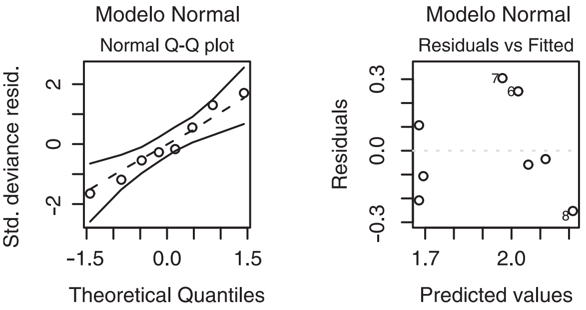

Figure 5 Residual analysis of the regression represented in Fig. 4. Normal Q-Q Plot analyses whether the error distribution used was adequate. Lines in the normal Q-Q Plot represent the 95% confidence interval limits. Residuals vs. fitted evaluates whether the model used was adequate.

DISCUSSION

Proportional sampling and SARs

The usual sampling design for species–area studies is to sample different remnant sizes with equal sampling effort (Hill *et al.*, 1994; Davies & Margules, 1998; Golden & Crist, 1999), a procedure that is commonly called 'uniform sampling'. Authors tend to use this in an effort to exclude sampling effects from SARs, while considering other processes. Uniform sampling, however, does not guarantee the detection of beta diversity, as observed in our results, unless sufficiently large samples are collected. Establishing and collecting sufficiently large samples is not always feasible. First, it is not trivial to determine the scale at which beta diversity changes, for a given taxa in a given habitat. Moreover, one cannot discard the possibility that beta diversity for a given taxa would change at different scales in different remnant sizes (Loreau, 2000), thereby overruling any attempt to fix a single sampling size for all sites being studied. Secondly, in the unlikely event that the behaviour of beta diversity is fully known and manageable, it may happen that the optimum sample size would exceed the dimensions of smaller sites. In addition to all this, 'sufficiently large' sample sizes may well exceed permissible costs.

Proportional sampling, i.e. sample sizes which are proportional to site dimensions, could be thought as a strategy to overcome such problems. Proportional sampling, however, may easily allow sampling effects to pervade SARs (Hill *et al.*, 1994), as it is based on the principle that more samples are to be taken from larger remnant sizes.

What we need is, therefore, some tool which could 'filter' sampling effects from proportional sampling, thereby allowing SARs to be conveniently separated into its several components. The procedure we proposed here seems to be such a tool. By including the number of samples, remnant size and their first-order interaction in a generalized linear model, one can partition total deviance of SARs into its sampling mechanisms as well as others, while guaranteeing the correct error distribution to be accounted for. Moreover, the interaction term safely allows different behaviours of sampling effects to be accounted for: if sampling errors modify SARs more in smaller rather than in larger remnants (see Crawley & Harral, 2001 for a comprehensive analysis), the interaction term would be significant. This should be particularly useful, for instance, for situations when SARs are strongly affected by edge effects (Fowler *et al.*, 1993; Golden & Crist, 2000; Zheng & Chen, 2000).

Our results in null communities demonstrated that our proposed model is powerful enough to separate out the effects of sampling and remnant area. Most important is that our model detected a SAR even removing the effect of proportional sampling. Success with the simulation approach bolsters the findings from empirical data.

The mechanisms of the SAR

In our data, significant portions of deviance were allocated to remnant size as well as to the number of samples. This would mean that other biological mechanisms do contribute to the SAR of ants in these forest fragments. Discarding sampling effects, the SAR may be explained by two possible mechanisms, according to Stevens (1986): area *per se* or habitat diversity. The absence of relationship between alpha diversity and remnant size implies that the area *per se* hypothesis cannot explain the SAR (Stevens, 1986). In these remnants, it appears that species richness is limited within sampling sites (approximately 5 ha), as per sampling site richness is independent of total remnant richness. Such saturated relationships between local and regional species richness in these ant communities have already been described (Soares *et al.*, 2001), and several mechanisms may account for it. Ants are considered strongly aggressive and one could expect there to be priority effects at local scales. For example, a small patch could be easily dominated by a single species and a large patch by chance could have different species that established and dominated at different places. Coexistence at the landscape scale would be facilitated by large patch area, although there might be only one or few species per locality within that large patch. Therefore there would be no difference in alpha diversity between the large and small patch, and a difference in beta diversity. The above scenario would be an effect of area *per se* that would permit the coexistence between species.

The positive significant relationship between beta diversity and remnant size suggests that habitat diversity may be the dominant explanation for the SAR of the ants in Brazil forest remnants. Coupled with the absence of relationship between alpha and remnant size, this result allows us to discard the hypothesis of passive sampling (Stevens, 1986). Habitat diversity has already been suggested as a causal mechanism for SARs by Williams (1943), Ricklefs & Lovette (1999) and by Hart & Horwitz (1991). This hypothesis could only be accepted if ant species were habitat specialists or, at least, if ant species were not uniformly distributed among habitats. At least for the environment we are studying, this could be true, as there is evidence (Soares *et al.*, 2001) that some of its ant communities are confined to a few local habitats. However, even in the absence of habitat heterogeneity, organisms may be distributed in aggregates, and therefore samples taken at random from large patches would be more dissimilar than samples taken from small patches. Thus, the observed increase in beta diversity with remnant size might reflect an increase in habitat diversity or passive sampling of species with a clumped distribution (Hart & Horwitz, 1991).

Our method offers a different approach when compared with that offered by Stevens (1986), because he used only the relationship of alpha and beta diversity with area to distinguish three sets of hypotheses. We propose here a model that first detects SARs, which filters sampling effects, and then tests for mechanisms involved in such a relationship. Such an approach is similar to that of Hart & Horwitz (1991), although we are proposing an analytical model to separate sampling effects from other SAR-generating processes.

In conclusion, ant species communities in forest fragments were found to follow a SAR that was not solely created by sampling effects, and whose main cause seems to be the existence of higher beta diversity within larger remnants. We reach such a conclusion by using a proportional sampling approach that is statistically filtered for sampling effects. Using such an approach, we believe that we have demonstrated that proportional sampling is essential for the detection of SARs.

ACKNOWLEDGMENTS

We gratefully acknowledge the comments by two anonymous referees. This paper was partially supported by FAPEMIG (Fundação de Amparo à Pesquisa do Estado de Minas Gerais). Sandra M. Soares helped us in the first ideas of the paper. J.H.S., O.D.S., T.G.S. and C.L.A. are supported by CNPq grants; C.R.R. and C.G. are supported by CAPES grants; C.F.S. was supported by PICD-CNPq grant.

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