

Diversity Patterns in Termite Communities: Species-Area Relationship, Alpha and Beta Diversity (Isoptera: Termitidae)

by

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ABSTRACT

Several processes may generate the relationship between species richness and area. The relationship between alpha and beta diversity with area may indicate which biological process was involved in a given species-area relationship. In this paper we aimed to test the response of termite species richness to remnant area, testing how alpha and beta diversity vary with remnant area, and which processes may be involved in such relationships. We sampled termites in 12 remnants with areas ranging from 3.21 to 60.63 hectares in Viçosa, Minas Gerais, Brazil. The species area relationship was not confirmed for termites in these remnants, and alpha and beta diversity did not increase with remnant area. The SARs found in termite communities by other authors was attributed to sampling effects. There was no significant relationship between local and regional species richness. Therefore, termite communities were considered saturated. Habitat specialists seem to be an explanation for the absence of a relationship between alpha and beta diversity with remnant area.

Keywords: Isoptera, local diversity, regional diversity, remnant area, termite species richness.

INTRODUCTION

Species-area relationships (SARs) are considered a central subject in community ecology, being represented by positive relationships between species richness and area (Rosenzweig 1995). Such relationships are commonly used to explain why species richness decreases after fragmentation events (Fahrig 2003), although several processes might also influence species richness in remnants. Edge and shape effects, isolation and species invasions may alter the SAR in remnants (DeSouza *et al.* 2001), making the analysis of species richness in remnants more complex.

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Several studies have been carried out to explain the processes involved in SARs (Golden & Crist 2000; Cook *et al.* 2002; Triantis *et al.* 2003). These processes may be included in three main classes of explanations: i) sampling effects, ii) area *per se*, and iii) habitat diversity (Schoereder *et al.* 2004). Sampling effects are usually split into sampling artifacts and passive sampling effects. The distinction between these two effects is that the former results from an increase of sampling effort in larger areas, while the latter results from an actual increase of species richness in larger areas (Cam *et al.* 2002). Area *per se* refers to the increase of local species richness (alpha diversity) in larger areas, because the biological processes responsible for species richness regulation change their effects with area increments (Ricklefs & Lovette 1999). Habitat diversity allows the co-occurrence of species that would not co-occur if the habitat were homogeneous, resulting in a higher species turnover (beta diversity) among sites in larger remnants (Rosenzweig 1995).

According to Stevens (1986), the relationship of alpha (a) and beta (b) diversities with area may be used to know the processes that contribute to SARs. A positive relationship between alpha diversity and area would indicate area *per se* effects, while a positive relationship between beta diversity and area would indicate habitat diversity effects. The same rationale was used by the author to explain the absence of relationships of both diversities with area, which would indicate sampling effects.

However, the determination of the relationship between alpha and beta diversities with area does not guarantee the determination of the biological processes involved in SARs (Schoereder *et al.* 2004). Accordingly, the absence of relationship between alpha diversity and area does not necessarily preclude processes related to area *per se* effects. Similarly, homogeneous habitats may produce a positive relationship between beta diversity and area, provided that species have a clumped distribution.

It is necessary, then, to test the relationship of heterogeneity with area, and how organisms respond to heterogeneity, to test habitat diversity effects. To test area *per se* effects, it is necessary to evidence, for instance, how resource abundance varies locally in different areas, how organisms respond to resource abundance variation, and what are the processes involved in local limits of species richness.

A proposed method to study the influence of local processes on species richness is the local-regional richness plot (Srivastava 1999). A positive linear relationship between local and regional species richness indicates the absence of limitations to local richness. On the other hand, an asymptotic relationship indicates that there is a limit to local

species richness, and therefore that local processes are relevant to explain this species richness (Soares *et al.* 2001).

The increase of species richness with area is the usual pattern in several taxa (Gascon *et al.* 1999; Moreno & Halffter 2000; Zanette 2000), although there are some papers describing other patterns (see Fahrig 2003). There are few studies on the response of termites to habitat area and fragmentation, and the data is controversial. DeSouza (1995) found a positive species-area relationship for termites in the Brazilian 'cerrado', but Davies (2002) found no significant relationship in the rainforest of French Guiana. Abensperg-Traun *et al.* (1996) found no relationship between termite species richness and remnant area. Abensperg-Traun and Smith (1999), collecting four arthropod species, including two termite species, found a positive correlation between species richness and remnant area.

SARs would be expected to occur in termites. Larger areas would support different environments, and in each of these environments a different termite assembly would occur. There is evidence that termite species are resource specialists (DeSouza & Brown 1994, Eggleton & Tayasu 2001, Tayasu *et al.* 2002) and consequently a positive relationship between species richness and remnant area would be produced.

This paper aims to test the response of termite species richness to remnant area, checking how alpha and beta diversity vary with remnant area, and which processes may be involved in such relationships.

Hypotheses tested

If there is a positive relationship between species richness and area, this SAR may be caused by a positive relationship between alpha diversity and area and/or a positive relationship between beta diversity and area. A SAR might occur even in the absence of a relationship of alpha and beta diversities with area, which would indicate sampling effects. A positive relationship between alpha diversity and area might indicate that termite species are more extinction-prone in smaller areas, because local processes reduced their populations. This population reduction would increase the probability of demographic constraints and stochasticity. The increase of beta diversity with area could be determined by the increase of habitat diversity or by the aggregation of individuals (Schoereder *et al.* 2004).

On the other hand, if there were no positive relationships between termite species richness and area, we would expect that both alpha and beta diversity would not vary with area. The absence of a relationship between alpha diversity and area may indicate that local processes limit species richness. This would result from a saturated community, in

which alpha diversity does not increase with regional species richness. The absence of a relationship between beta diversity and area might occur due to an absence of a relationship between habitat diversity and area, or to an absence of response of termites to habitat diversity.

METHODS

Sampling sites

We sampled 12 forest remnants in the semi-deciduous mountain forest of Viçosa (20° 45'S, 42° 50'W), Minas Gerais, Brazil, at 650 m a.s.l., from January to February 2002. Remnant areas ranged from 3.21 to 60.53 ha, and were surrounded by pasture and coffee plantations (Meira Neto & Martins 2000).

Sampling and Identification of Termites

In the center of each remnant, at 40 m minimum distance from the edge, we established a grid composed of 22 to 418 points proportional to remnant area. These points were set 5m apart. We set a toilet paper roll (Lafage *et al.* 1973; French & Robinson 1980; Dawes-Gromadzki 2003) in each point, leaving it there for 25 days. To collect samples, we initially divided the grid in quadrats containing four baits, which we called a sampling unit. We randomly selected sampling units, the number of sampling units again proportional to remnant area (one sampling unit per each 3 ha). The use of a proportional sampling is recommended by Schoederer *et al.* (2004) and allows the detection of heterogeneity effects.

We sorted and identified termites to species with the help of identification keys, comparing with the reference collection of the Laboratory of Termitology (Dept. of Animal Biology, Federal University of Viçosa), and with the help of Reginaldo Constantino (University of Brasília). Voucher specimens were deposited in the reference collection of Laboratory of Termitology.

Spatial scales and the SAR

We considered the total species richness in each remnant as regional species richness, because the probability of encounter between termite species from different remnants is lower than inside remnants. The division between local and regional species richness is usually based on the probability of interactions between individuals (Srivastava 1999). To determine spatial scales in which different processes occur, it is fundamental consider dispersal abilities of the taxon studies. Termite species have low dispersal mobility (Nutting 1969; Grassé 1982), the winged forms disperse to distances varying from 400 to 600 m (Mill 1983), and workers cover a larger area when foraging. *Nasutitermes*

corniger (Isoptera: Termitidae), for instance, presents one of the largest foraging areas so far reported (8000 m²) (Levings & Adams 1984). It is possible that workers from a given colony have been sampled in different local scales, if the sampling units were closely located. However, the use of average species richness in the local scale minimizes the problems caused by such sampling design. The same rationale was used in ant communities by Soares *et al.* (2001), who worked on similar spatial scales.

To test for the existence of a positive relationship between regional species richness and remnant size, we have used a linear regression $\log x \log$. The natural logarithm of regional species richness in each remnant was the response variable and the natural logarithm of area was the explanatory variable. We used the number of sampling units as a covariable to remove the effects of proportional sampling. According to the suggestions of Schoereder *et al.* (2004), the number of sampling units was entered before the area in the model, in a more conservative design. A third explanatory variable in this model was the interaction term between logarithm of area and the number of sampling units. We used linear generalized models and Poisson errors (Crawley 2002).

Alpha diversity

Small remnants received less sampling units than large remnants, and therefore the estimate of alpha diversity varied with remnant size. In remnants that received only one sampling unit we considered alpha diversity as the total number of species sampled by this unit. In remnants that received more than one sampling unit, alpha diversity was the average of species richness in these sampling units.

To test the relationship between alpha diversity and area, we carried out a regression using the natural logarithm of alpha diversity as response variable and the natural logarithm of area as explanatory variable. To do so we used a linear generalized model and Poisson errors corrected for over-dispersion (Crawley 2002).

Beta diversity

To estimate beta diversity similarity indices are usually employed, despite the limitations in their use (Koleff *et al.* 2003). The most used index, Sørensen, gives an exaggerated importance to species occurring in both samples. On the other hand, the Williams index gives less weight to the species occurring in both samples. We have chosen to use the Williams index, because few species occur in more than one sample, and giving more weight to species in common might introduce a bias in the estimate of beta diversity.

We calculated the similarity indices for all pairs of sampling units in the remnants with more than one sampling unit, and averaged them to produce one value per remnant.

To test the relationship between beta diversity and area, we carried out a regression using beta index as response variable and natural logarithm of area as explanatory variable. We included the number of sampling units and the interaction between the variables in the model, allowing the removal of these effects from the model. To test beta diversity we used linear generalized models and normal errors (Crawley 2002).

Local-regional plot

In our analyses alpha diversity and local species richness have the same meaning. To test the relationship between local and regional species richness, we carried out a linear regression between these variables, considering that the null model was the absence of relationship, and therefore a saturated pattern (Srivastava 1999; Soares *et al.* 2001). We used a linear generalized model and normal errors (Crawley 2002).

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

RESULTS

We sampled 15 termite species, distributed in 10 genera (Table 1).

Regional species richness did not increase with area ($F_{1,8}=0.68$, $p=0.41$), or with interaction between area and number of sampling units ($F_{1,8}=2.10$, $p=0.15$). Regional species richness, however, responded to the number of sampling units ($F_{1,8}=5.72$, $p=0.02$).

Alpha diversity did not respond to remnant area ($F_{1,10}=2.36$, $p=0.16$), neither did beta diversity (Williams index, $F_{1,6}=1.08$, $p=0.34$).

There was no significant relationship between local and regional species richness ($F_{1,10} = 0.1697$, $p = 0.6891$), evidencing a saturated plot (Fig. 1).

Residual analyses confirmed all results.

DISCUSSION

Our study did not show a positive relationship between termite species richness and area, revealing only a sampling effect on species richness. This means that larger areas do not support more termite species than smaller areas in this environment. Such result may have occurred due to a substitution of lost species with area reduction, or

Table 1. Occurrence species of termites in the sampled remnants. Viçosa, MG, Brazil.

Species	Subfamily
<i>Anoplotermessp1</i>	Apicotermittinae
<i>Anoplotermessp2</i>	Apicotermittinae
<i>Anoplotermessp3</i>	Apicotermittinae
<i>Anoplotermessp4</i>	Apicotermittinae
<i>Ruptitermessp1</i>	Apicotermittinae
<i>Araujitermes caissara</i>	Nasutitermittinae
<i>Cornitermes cumulans</i>	Nasutitermittinae
<i>Diversitermes aporeticos</i>	Nasutitermittinae
<i>Embiraetermes heterotypus</i>	Nasutitermittinae
<i>Ibitermes curupira</i>	Nasutitermittinae
<i>Nasutitermes jaraguae</i>	Nasutitermittinae
<i>Nasutitermes rotundatus</i>	Nasutitermittinae
<i>Procornitermes lespesii</i>	Nasutitermittinae
<i>Dentispicotermes conjunctus</i>	Termitinae
<i>Dihoplotermes inusitatus</i>	Termitinae

with fragmentation, thereby resulting in a change of species composition. The change in the number of species composing different feeding guilds with fragmentation event may represent this species substitution, and have already been observed in termites (DeSouza & Brown 1994; Davies 2002; Bandeira *et al.* 2003). Nevertheless, the variation of species composition with area must be tested, to evaluate how termite communities respond to fragmentation.

SARs have been found in termite communities in the Brazilian cerrado (DeSouza 1995) and *Eucalyptus* forests in Australia (Abensperg-Traun & Smith 1999). These SARs may have occurred due to sampling effects. We did observed an increase of species richness with area, although such an increase was considered spurious. The species richness increase with area has been removed when we

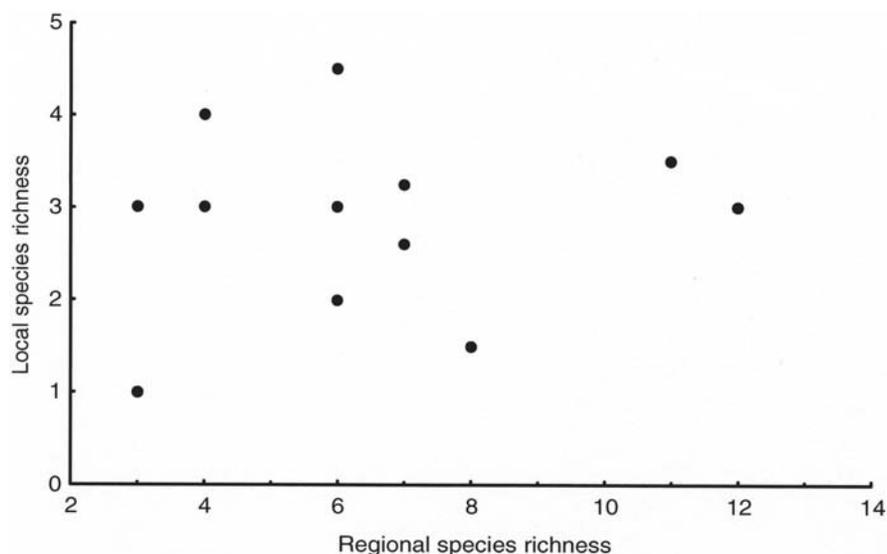


Fig. 1. Local species richness of termites in relation to regional richness, normal error distribution. Each dot corresponds to the number of termite species in remnants.

considered the number of samples (sampling effect). The variation attributed to sampling effect should be included in the models testing SARs. Several models and data sets are not orthogonal (Crawley 2002), which means that the order of variable inclusion in the model may alter their significance. In the specific case of SARs, Schoereder *et al.* (2004) suggest that it is more appropriate to include the sampling effect term in the model before the area effect term, because it a more conservative approach.

The hypothesis that sampling effect generated a false SAR in termites seems to be acceptable, because authors who did not increase sampling effort with remnant area did not observed SARs (Abensperg-Traun *et al.* 1996; Davies 2002).

Beta diversity did not increase with area possibly because there was not a habitat diversity increase with remnant area. Beta diversity may be determined by habitat diversity (Rosenzweig 1995), and therefore this would explain the absence of a relationship between beta diversity and remnant area.

Nevertheless, if habitat diversity increases with remnant area, as expected (Rosenzweig 1995; Ricklefs & Lovette 1999), there still would be a chance of finding a non-significant relationship between beta diversity and area, if termite beta diversity did not respond to habitat diversity. Habitat diversity was not estimated in the present paper, due to the difficulties to estimate it (Triantis *et al.* 2003) and to find out what are habitats to most termite species (Constantino 1999). Termite species, however, are described as habitat specialists (DeSouza & Brown 1994; Eggleton & Tayasu 2001; Tayasu *et al.* 2002) and therefore it is more acceptable that habitat diversity does not increase with remnant area, than termite species does not respond to habitat diversity.

Alpha diversity did not increase with area, which means that area *per se* effects did not limit species richness in small remnants. One area *per se* effect is the increase of species local extinction due to a decrease of population size with area, which in turn is caused by a decrease of carrying capacity. Termites have small home ranges (Abensperg-Traun 2000). *Armitermes obeuntis* (Isoptera: Termitidae), for instance, needs a minimum of 50 m², while *Drepanotermes tamminensis* (Isoptera: Termitidae) needs less than 102 m² (Abensperg-Traun & Smith 1999). *Nasutitermes* species have larger home ranges, occupying areas with vary from 5,000 to 8,000 m² (Levings & Adams 1984), which are smaller than the smallest studied remnant (32,000 m²). It is possible, therefore, that carrying capacity for termites has been maintained even in small remnants, and resource abundance did not reduce with area.

Alternatively, resource abundance might increase with area, provided that alpha diversity does not respond to resource abundance. It is necessary, therefore, to test the response of termites to resource variation.

There was no relationship between local species richness and regional species richness, which means that the studied community is saturated (Srivastava 1999). In saturated communities, local processes limit local species richness. One of these processes is competitive exclusion, which may locally limit species richness (Cornell & Lawton 1992). Because termites are detritivorous, their resources are possibly very abundant, and competitive exclusion is less probable.

The occurrence of competitive exclusion is difficult to be estimated and there is little evidence of competition in termites, other than in habitats with few nesting sites, as has been observed in *Nasutitermes* in flooded habitats (Levings & Adams 1984; Adams & Levings 1987). In forests, where there are several nesting sites, competition may not limit local species richness.

Saturated local-regional plots may also be caused by a stochastic equilibrium between local colonization and extinction rates of resident species (Soares *et al.* 2001). Termite species, however, are not expected to have high rates of local colonization and extinction. They have low dispersion ability (Nutting 1968; Mill 1983), which results in low colonization rates as the distance between sites increases. The longevity of termite colonies is considered high (20 to 25 years, Abensperg-Traun 2000), and the colonies are sessile, decreasing the chance of high extinction rates.

Another process that may cause saturated local-regional plots is habitat specialization (Soares *et al.* 2001), which corresponds to a restricted number of species in each site, determined by the degree of specialization of each species. Fragmentation may change the number of habitats occupied by termite species, which DeSouza & Brown (1994) attributed to habitat specialization. Termites present preference for food with high nitrogen content (Shellman-Reeve 1994; Eggleton & Tayasu 2001; Tayasu *et al.* 2002), which may be considered a condition for the occurrence of habitat specialist species.

Concluding, the most plausible hypothesis to explain why alpha diversity did not increase with remnant area is habitat specialization, which is the same hypothesis to explain why beta diversity did not vary. Habitat specialization may generate sites with different species composition, which may be detected by the increase of beta diversity with habitat diversity. Before testing whether beta diversity responds to habitat diversity, it is necessary to evaluate whether habitat diversity increases with area. Only after these tests it would be possible to

confirm habitat specialization as a determining factor of species richness in termite community.

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