

Processes involved in species saturation of ground-dwelling ant communities (Hymenoptera, Formicidae)

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Abstract The species saturation hypothesis in ground-dwelling ant communities was tested, the relationship between local and regional species richness was studied and the possible processes involved in this relationship were evaluated in the present paper. To describe the relationship between local and regional species richness, the ground-dwelling ant fauna of 10 forest remnants was sampled, using 10 1 m² quadrats in each remnant. The ants were extracted from the litter by using Winkler sacs. Using regression analyses, an asymptotic pattern between local and regional species richness was detected. This saturated pattern may be related to three processes: (i) high interspecific competition; (ii) habitat species specialization; or (iii) stochastic equilibrium. It is concluded that non-interactive processes, such as stochastic equilibrium and habitat specialization may act as factors regulating species richness in this community. The predominance of locally restricted species, in all sampled remnants, seems to indicate the occurrence of a high degree of habitat specialization by the ant species. This result is evidence for the hypothesis that community saturation has been generated by non-interactive processes. Although ants are frequently described as highly interactive, it is possible that interspecific competition is not important in the structuring of ground-dwelling ant communities.

Key words: habitat specialization, interactions, local diversity, regional diversity, species richness, stochastic equilibrium.

INTRODUCTION

Ant communities are usually referred to as being highly interactive and exhibiting clear intra- and interspecific relationships (Oliveira & Della Lucia 1992). Although several papers point to interspecific competition as an important structuring factor in ant communities (Levings & Franks 1982; Fellers 1987; Savolainen & Vepsäläinen 1988; Andersen & Patel 1994), there are few studies testing this role of competition. The relative role of biological interactions in the determination of species diversity thus remains largely unknown in ant communities.

An adequate method for evaluating the relative roles of local processes, such as competition, on species diversity regulation is the analysis of the relationship between local and regional species richness (Terborgh & Faaborg 1980; Cornell 1985a,b; Ricklefs 1987; Huguency & Paugy 1995; Griffiths 1997). Two different patterns may be detected in this analysis: (i) unsaturated, a linear relationship between local and regional species richness; and (ii) saturated, an asymptotic relationship between these two variables, which means that the local species richness increases proportionally with regional species richness up to a level when local species richness becomes independent from regional

species richness (Cornell & Lawton 1992; Cornell 1993; Cornell & Karlson 1997). The absence of a relationship between local and regional species richness is also interpreted as evidence of saturation (Caley & Schluter 1997; Srivastava 1999). Although some authors prefer to use the term saturation only when the pattern is due to species interactions (Cornell 1993), we use the term *sensu* Terborgh and Faaborg (1980) to describe the pattern of the general relationship between local and regional species richness, disregarding the processes involved in generating the pattern.

Saturated patterns may be generated by strong biotic interactions, such as interspecific competition (Cornell 1985a; Cornell & Lawton 1992). When the competition is intense and widespread, it may act by limiting the species number present in a given community. In this case, there is a maximum species number able to coexist and, when the community reaches such a number, the local species richness remains constant, even if the regional species richness increases.

Although species saturation is frequently associated with interspecific competition, non-interactive processes, such as species pool exhaustion and stochastic equilibrium (Cornell 1985b; Cornell & Lawton 1992; Srivastava 1999) may produce the same pattern.

Species pool exhaustion corresponds to the restriction of the number of species adapted to a given local environment and it is determined by the degree of

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Accepted for publication September 2000.

specialization of the species present in the region. The community reaches exhaustion point when there is a maximum number of species able to colonize and live in a given locality. After the colonization of the locality by all species adapted to it, local species richness becomes constant and independent of regional species richness. In this case, species saturation is determined by the existence of a limited number of species adapted to the local environment, and not by interspecific interactions.

Stochastic equilibrium refers to the balance between colonization by new species and extinction rates of resident species. It occurs when there is an uninterrupted substitution of species, some becoming extinct and some immigrating. The higher the species number in a given site, the higher the probability for some of these species to undergo random extinction. Consequently, as species richness rises, the local extinction rate also rises, and it may equal the immigration rate of new species, leading to local saturation. When a local community attains equilibrium, local species richness becomes invariable, even in the event of an increase in regional species number.

Unsaturated patterns are expected in communities with weak or no biotic interactions. Therefore, the detection of an unsaturated pattern means that, even in the presence of interspecific competition in the community, this process is not strong enough to limit the local number of species and to generate saturation (Cornell 1985a; Cornell & Lawton 1992).

The present paper investigates the pattern of the relationship between local and regional species richness in ground-dwelling ant communities, evaluating the possible processes involved in the production of such a pattern.

METHODS

The ant fauna was sampled in 10 forest remnants in Viçosa, south-east Brazil (20°45'S, 42°50'W). In the

1930s and 1940s, the region suffered from intense forest fragmentation because of activities associated with cattle farms and coffee plantations (Gomes 1975).

Collections were carried out during the day, from January to April 1998, during the rainy season. In each remnant, there were 10 1 m² quadrats 20 m apart along a 200 m transect. The transect was located at least 50 m from the forest edge, thereby minimizing edge effects. In some small remnants, which were not large enough to accommodate one 200 m-long transect, two shorter transects with a combined length of 100 m were used; these were located parallel to each other, 20 m apart. Ants present in the surface litter of each quadrat were extracted by using Winkler sacs (see Olson 1991). This method collected the ants that nest or forage inside or on litter, which are usually called ground-dwelling ants.

The ant specimens were identified to genus (Hölldobler & Wilson 1990; Bolton 1994) and, when possible, to species. Voucher specimens were deposited in the collection of the Setor de Ecologia, Departamento de Biologia Geral, Universidade Federal de Viçosa and in the personal collection of the first author.

Each forest remnant was considered one region, while the 1 m² quadrats were considered a local area. The determination of local and regional scales were carried out considering the interaction and dispersal potential of ant species, as well as the structure of forest remnants. According to Srivastava (1999), a local area must be measured on a small scale, where all the species occurring within it are able to encounter and interact in ecological time. A 1 m² scale is certainly small enough to permit all ant species living in the square to potentially interact. A region must be measured on a larger spatial scale, within which the dispersal rates, although small, are still larger than the dispersal rates between regions (Srivastava 1999). Because the studied forest remnants are isolated from each other by other vegetation types, it is plausible to assume that the dispersal rate between remnants is

Table 1. Subfamilies of ground-dwelling ants from 10 remnants in Viçosa, MG, Brazil, and the number of species belonging to each

Subfamily	No. collected species	No. soil species	No. litter species	No information
Dolichoderinae	5	1	2	3
Pseudomyrmecinae	3	2	0	1
Cerapachyinae	3	0	2	1
Ecitoninae	3	2	1	1
Formicinae	10	1	4	6
Ponerinae	31	4	5	25
Myrmicinae	83	6	42	40

The number of soil and litter species refer to the number of species already observed nesting in each habitat (Delabie & Fowler 1995; Delabie *et al.* 2000; Soares & Schoederer, pers. obs.). The last column refers to the number of species for which we have no information about nesting sites. As some species have been found nesting both in soil and litter, the sum of the rows sometimes do not agree with the number of species collected.

small compared with the dispersal rate within the remnants. Therefore, it seems acceptable to consider each remnant as a distinct region for litter ant communities.

Species richnesses on local and regional scales were determined differently. On the local scale, species richness was estimated as the average of the total number of species in each local area, as the method extracts all species present in the litter sample. However, we did not sample all species in the region, and therefore we had to estimate regional species richness, which was obtained by extrapolation, by using the Chao2 estimator (EstimateS, version 5.0.1, Colwell 1997), given by the following equation:

$$S_{\text{Chao2}} = S_{\text{obs}} + (Q_1)^2 / (Q_2)^2,$$

where S_{obs} is the observed species richness and Q_j is the number of species occurring in exactly j samples. Estimators are tools created to assess the role of beta diversity on the regional diversity. The larger the dissimilarities between local species composition, the larger will be the difference between observed and estimated species richness. The Chao2 estimator was chosen because Colwell and Coddington (1994), when comparing several estimators, considered it to be the best estimator for small samples. Furthermore, it uses frequency data, disregarding abundance data. This method is more efficient for ant communities, as it avoids overestimates due to species that recruit large numbers of workers to food sources (Leal & Lopes 1992).

Even though the areas of the sampled remnants varied from 4 to 300 ha, the sampling surface, or the distance between quadrats, was always the same, thereby minimizing area effects. Additionally, any possible influence of area effect will reflect on regional species richness, as we considered the remnant to be the region. If there is a relationship between local and regional species richness, this will also reflect on local species richness, but then this relationship will be a monotonic increase.

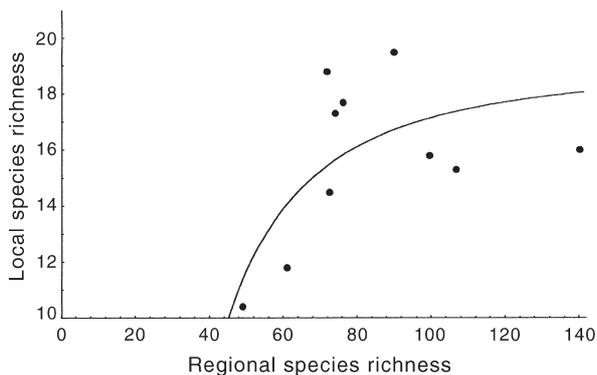


Fig. 1. Relationship between litter ant local and regional species richness.

To evaluate the relationship between local and regional species richness, we carried out linear and non-linear regression analyses, evaluating the effect of regional species richness (estimated species richness in the remnant) on local species richness (average of species richness of the 10 quadrats). Several non-linear models were fitted to the data and we selected the simplest significant model. The robustness of the selected model was checked by investigating its behaviour in the absence of outliers (e.g. datum 140, 16). The model finally chosen was the one that was not affected significantly by the outliers.

Because the above-mentioned relationship may be influenced also by the degree of habitat specialization, we plotted the number of species by the number of sites where they occurred. Species that occur in few sites were considered habitat specialists, whereas species occurring in several sites were considered habitat generalists. We expected an inverse relationship between these variables, with fewer generalist than specialist species. The relationship was appraised through generalized linear models analogous to analysis of covariance (Crawley 1993), using region (remnants) and number of sites occupied as explanatory variables and the number of species in each region as the response variable. The model was initially adjusted with all explanatory variables and their interactions. Then we removed each term, in turn, evaluating the changes in deviance. Because the removal of all terms produced a significant effect on deviance, we retained all the terms in the model. To simplify the complete model, which was composed of the variable 'number of sites occupied', by the 10 levels of the variable 'region', and by the interaction of these two variables, the data on ant species richness from these regions were assembled. This simplification was carried out by gradually grouping the levels of the variable region, evaluating the changes in deviance after each

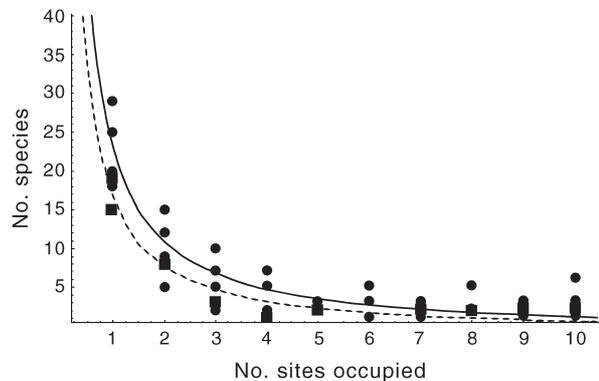


Fig. 2. Relationship between the number of ant species and the number of sites occupied. Each point represents the number of species by region. (■), Model of the group comprising two regions ($y = -1.49 + 18.42/x$); (●), model comprising eight regions ($y = -1.59 + 24.94/x$).

Table 2. Results of covariance analysis of final simplified model (with grouped regions)

Source of variation	d.f.	SST	MS	F
Number of sites occupied (x)	1	3844.00	3844.00	787.70*
Region (r)	1	52.54	52.54	10.77*
Interaction ($x.r$)	1	47.03	47.03	9.64*
Error	95	464.03	4.88	
Total	98	4407.6	44.98	

The model was initially adjusted with all explanatory variables and their interactions; then each term, in turn, was removed, evaluating the changes in deviance. The original regions were pooled into two different groups, which are represented in Fig. 2. * $P < 0.001$.

grouping. If the grouping did not produce a significant increase in deviance in relation to the original model, the grouping was maintained and the grouped levels were considered as one level. If the grouping produced a significant enhancement in deviance, the levels were kept separate.

RESULTS

We collected 138 ant species, belonging to 50 genera and seven subfamilies, from the 10 forest remnants (Table 1).

We detected no significant linear relationship between local and regional species richness ($P = 0.294$, $n = 10$). The non-linear model that best fitted the data was characteristic of a saturated pattern (local richness = $19.97 - 18300.73/(\text{regional richness})^2$; $r^2 = 0.435$, $F = 6.16$, $P < 0.05$, $n = 10$; Fig. 1).

We observed a negative relationship between the number of species and the number of sites occupied (Fig. 2). The variable region is also significant, indicating that some regions hold more species than others, as well as the interaction between region and number of sites occupied, indicating that the proportion of species restricted to few sites depends on the region they inhabit (Table 2). After the model simplification, the 10 original regions were pooled into two different groups, one with two regions ($y = -1.49 + 18.42/x$) and the other with eight regions ($y = -1.59 + 24.94/x$; Fig. 2). Nevertheless, in both groups of regions, there were more species that were restricted to few sites than those that occurred in several sites (cosmopolitan species).

DISCUSSION

The following processes may generate the observed saturated pattern:

1. Strong interspecific competition. Ground-dwelling ant communities present strong interspecific competition, which acts to limit the number of species coexisting in a given site.

2. Habitat specialization. Ground-dwelling ant species are habitat specialists, being unable to exploit all sites in a given region. Only a subsample of the total species richness of a region is able to colonize and live in a given site.
3. Stochastic equilibrium. There is a balance between local colonization and extinction rates, which is independent of interspecific relationships.

The first hypothesis is centred on interactive processes and is based on the assumption that interspecific competition is a limiting factor of species richness in ant communities. Although this hypothesis is very attractive because interspecific competition is frequently described as an important structuring factor in ant communities, it does not seem to apply to the studied communities. While studying the nest spatial pattern in litter and soil ants in one of the remnants sampled in the present work, Soares and Schoereder (1997) found no evidence that supported competition in these communities. The nests were aggregated (standardized Morisita index of dispersion = 0.52) and species were randomly placed (standardized Morisita index of dispersion = 0.26), not supporting competition as a structuring factor. Although nest overdispersion is frequently cited in ant community literature, there are other references showing that aggregated nest distributions are not rare (Doncaster 1981; Ryti & Case 1984; Herbers 1985, 1989; 1994).

The acceptance of hypothesis 2 needs the ant communities to be composed mainly of habitat specialists. Although there are no available data to evaluate the specialization degree in litter ants, Fig. 2 suggests that several species are restricted to a few locations, which is evidence of the high degree of habitat specialization of ground-dwelling ants. Although the numbers of habitat specialists vary from region to region, as shown by the existence of two different models for the regions, this variation is not relevant, as restricted species predominate in all regions. These species may be nesting or foraging in different microhabitats to which they are specialized, and therefore they are collected in few sites.

The third hypothesis is based on the assumption of an extinction rate high enough to balance the effect of

immigration of new species in the local community. Data regarding the biology of ground-dwelling ants are rare, impeding further analysis of this hypothesis. However, an evaluation of the dynamics of resource utilization by ground-dwelling ants provides evidence in favour of this hypothesis. Ground-dwelling nesting sites constitute ephemeral resources and, consequently, litter ants are constantly moving between nesting sites (Byrne 1994). Moving frequently presents great risks to the ants and can drastically reduce population sizes, because of high worker mortality (Hölldobler & Wilson 1990). Litter ant colonies are usually small (Fowler 1993) and therefore virtually any population reduction may lead to local species extinction. This situation may lead to a balance between local extinction and the arrival of new colonizers.

Local species extinction may also be generated by colony movement to neighbouring sites. If all colonies of a given species move to other sites, there is local extinction of the species within the site. If the number of immigrant species equals the number of emigrant species, local species richness will be kept constant.

Although there is evidence supporting the hypothesis of stochastic equilibrium (Hugueny & Cornell (2000) and references therein), there are few biological studies on ground dwelling ants in tropical habitats. Some species collected in the present study are not exclusive to litter, nesting also in the soil, which is not an ephemeral resource.

Because the present work evaluated only communities from litter, the results do not necessarily apply to other parts of the ant community. The ecological characteristics of ground-dwelling ants are different from those of ants that nest in soil or on trees (Byrne 1994). Therefore, other ants may produce patterns different from those obtained in the present work.

In conclusion, it seems that species saturation in ground-dwelling ant communities is produced by habitat specialization and/or by stochastic equilibrium and not by interactive processes. Although ants are frequently referred to as being highly interactive, it is possible that interspecific competition is not important for the determination of community structure in ground-dwelling ants. Complementary studies have to be carried out to detect which are the processes involved in the structure of local diversity, and in the regulation of species richness in ground-dwelling ant communities.

ACKNOWLEDGEMENTS

The authors are in great debt to Dr Jacques H. C. Delabie for the identification of the specimens. S. M. Soares is supported by a Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) grant and J. H. Schoereder is supported by

a Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) grant (300471/88–2). The work was supported by a Fundação de Amparo à Pesquisa do Estado de Minas Gerais (FAPEMIG) grant (CBS 2165/96).

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