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Species richness, abundance and distribution of myrmecophilous beetles in nests of *Formica aquilonia* ants

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Some ecological theories predict a positive relationship between species richness and resource size, resource abundance, or resource concentration. In this study, we tested these three hypotheses with myrmecophilous beetles, which use ant nests as their hosts. The resource concentration hypothesis predicts that patches with a high density of a resource support high richness of species dependent on that specific resource. The resource abundance hypothesis predicts that the hosts offering more resources support more species. The resource size hypothesis predicts that larger hosts support more species than smaller hosts. We collected beetles from nests of the nest building wood ant *Formica aquilonia*. In 49 *F. aquilonia* nests, we observed 965 individual beetles and 16 species of myrmecophilous beetle. Both the nearest neighbour distance and the volume of ant nests influenced species richness and beetle number. The beetle species utilising several hosts were more widespread and more abundant than the specialist beetle species. Thus, our findings support the resource concentration, resource size and resource abundance hypotheses.

Introduction

Understanding the factors determining species richness in communities is an important problem in ecology. Four major hypotheses have been proposed to explain the local species richness: the resource distribution hypothesis, the resource size hypothesis, the resource abundance hypothesis and the resource concentration hypothesis (*see* Marques *et al*. 2000). These hypotheses have been tested in herbivores and their host plants (Lewis and Waloff 1964, Root 1973, Lawton 1983, Ricklefs 1987, Cornell & Lawton 1992, Brändle & Brandl 2001, Goncalves-Alvim & Fernandes 2001, Sanches & Parmenter 2002), in parasites and their host animals (Ranta 1992, Guégan *et al*. 1992, Morand & Poulin 1998, Arneberg 2002, Stanko *et al*.

2002), and in host-parasitoid systems (Hawkins 1994).

The resource distribution hypothesis predicts that regionally widespread host species are able to support high local species richness of commensals (Ricklefs 1987, Cornell & Lawton 1992). The resource size and resource abundance hypotheses are very closely related in that large resources could be considered to offer abundant resources. The resource size hypothesis predicts that larger hosts can support more species than smaller ones (Lawton 1983, Ranta 1992, Guégan *et al*. 1992, Brändle & Brandl 2001, Arneberg 2002, Sanches & Parmenter 2002). The resource abundance hypothesis predicts that hosts that offer more resources are able to support more species than those offering less (Hunter & Wilmer 1989, Hunter 1992, Marques *et al*. 2000). Finally, resource concentration hypothesis predicts that hosts that occur in high density support higher species richness of herbivores (Lewis and Waloff 1964, Root 1973, Goncalves-Alvim & Fernandes 2001) and parasites (Ranta 1992, Morand and Poulin 1998, Arneberg 2002, Stanko *et al*. 2002).

We used myrmecophilous beetles, commonly known as “ant guests”, to test three of the species richness hypotheses listed above: resource size, resource abundance and resource concentration hypotheses. Myrmecophilous beetles provide an excellent opportunity to test these hypotheses because they live in naturally fragmented small patches, ant colonies, and they are dependent on ants or habitats created by ants during parts of their life cycle (Hölldobler & Wilson 1990). Myrmecophilous species can also be classified as specialists or generalists according to the number of host ant species (Päivinen *et al*. 2003). Myrmecophiles rarely have only one host ant species: only four out of 48 myrmecophilous beetle species have a single host ant species in Finland (Päivinen *et al*. 2002).

In our previous study, Päivinen *et al*. (2003) tested the resource size, resource abundance and resource distribution hypotheses with myrmecophilous beetles and their ant host species. The data in Päivinen *et al*. (2003) were extracted from the literature surveys. In addition to species richness of myrmecophilous beetles, Päivinen *et al*. (2003) tested the above hypotheses to explain the distribution of the beetles. They found that the distribution and the colony size of the host ants had a positive effect on both the species richness and the distribution of myrmecophilous beetles. They also found that the myrmecophilous beetle species that are generalists, i.e., have more than one host ant species, and thus have more abundant resources, were more widely distributed than the specialist species.

In this field study, we asked whether resource concentration or resource size explain the species richness and abundance of myrmecophilous beetles within a single host ant species *Formica aquilonia* Yarrow in relatively narrow geographical scale in central Finland. The nests of *F. aquilonia* were a suitable study object to test resource concentration and resource size hypotheses, because *F. aquilonia* is a common ant species in Finland (Collingwood 1979). Also, there is great variation both in the sizes of ant nests and in the distances between ant nests (Hölldobler & Wilson 1990). In addition, we also examined the ability of the resource abundance hypothesis to explain the distribution and abundance of myrmecophilous beetles. Because myrmecophilous beetles are dependent on ants (Hölldobler & Wilson 1990), we defined the host ant species as a resource for each myrmecophilous beetle species.

Material and methods

Site description

The study was conducted in 12 boreal forest patches in central Finland (62°N, 26°E), in Luhanka, Joutsa, Leivonmäki, Toivakka and Korpilahti regions within an area of 950 km^2. The distance between the patches was at least two kilometres (except in one case 500 m). The areas surveyed were mixed forests dominated by *Betula pendula* Roth, *B. pubescens* Ehrh., *Pinus sylvestris* L. and *Picea abies* L. *Juniperus communis* L., *Populus tremula* L., *Sorbus aucuparia* L., *Alnus incana* Moench and *Salix* species also existed in the area. The field layer consisted of typical wand vegetation of Finnish mixed forest (e.g. *Vaccinium myrtillus* L., *Calluna vulgaris* L. and *Vaccinium vitis-idaea* L.).

Sampling and measurements

We randomly selected five nests of the nest building wood ant *F. aquilonia* in each of the twelve forest patches. Thus, the total number of the nests studied was 60. Because eleven of our traps in the ant nest were destroyed by black woodpecker (*Dryocopus martius*), or probably by some mammal species such as badger (*Meles meles*), we had myrmecophilous beetle species data from 49 nests, which we used in statistical analyses. The beetles were sampled using plastic pitfall traps (diameter 66 mm, height 130 mm) covered with a metal net (mesh size was 2 × 2 mm). The metal net keeps ants and nest material out of the trap. On the other hand, the myrmecophilous beetle species are small and they drop through the metal net into pitfall traps. In the beginning of May 1996, the traps (one trap per nest) were placed inside the nests just under the moisture layer (Hölldobler & Wilson 1990) at the depth of 5 cm. The traps were removed after one month. According to our field observations, most of the myrmecophilous adult beetle species occur in the nests of *F. aquilonia* only in spring. For example, we observed only a few adult myrmecophilous beetle individuals in the nests of *F. aquilonia* in June 1999. Therefore, it is likely that we were able to collect most of the beetle species occurring in the studied nests.

To test the resource size hypothesis, we estimated the volume of ant nests in litres. For the purposes of estimation, we measured the height of the nest from the ground level to the top and the diameter of the nest at ground level. The shape of the nest above ground layer was roughly approximated to follow a circular cone. To test the resource concentration hypothesis we measured the nearest neighbour distance between the ant nests. The nearest neighbour distance is the distance (in meters) between the studied nest and the nearest other nest of *F. aquilonia*. Finally, we used published data on the number of host ants that each myrmecophilous beetle species has in Finland (Päivinen *et al*. 2002) to test the resource abundance hypothesis.

All beetle species were identified on species level and only the myrmecophilous species (Koch 1989a, 1989b, 1992) were taken into account. As an exception, we categorised one myrmecophagous species, *Zyras humeralis* Gravenhorst, as myrmecophilous, since it is clearly dependent on ants as a food resource (Hölldobler & Wilson 1990). Recall that the species richness in this study is defined as the number of myrmecophilous beetle species per ant nest.

Statistical analysis

Analysis of covariance (ANCOVA) was used to compare the mean number of myrmecophilous beetle species (ln $(x + 1)$ transformed) and the number of myrmecophilous beetle individuals (ln $(x + 1)$ transformed) using the SPSS 10.0 statistical package. In the model, the number of individuals and the number of species was used as the dependent variable, and forest patch was fitted as a random factor. We used the volume of ant nest and ant nest distance to nearest nest as covariates in the analysis of covariance. Both the volume and distance were transformed by the natural logarithm to correct for non-linear relationship between covariates and dependent variables before statistical tests. Because data on the distance to nearest nest and data on myrmecophilous beetle species were available only for 30 nests from seven forest patches, we did not use data from all 49 ant nests in our statistical analysis. Regression analysis was used to compare relationship between the number of ant host species that a beetle species has in Finland and the distribution and abundance of each beetle species in our data.

Results

We found 16 myrmecophilous beetle species in 49 nests of *F. aquilonia* ants. Hence, species richness was 29 percent of all previously observed myrmecophilous beetle species (56 species) in genus *Formica* (Päivinen *et al.* 2002). The myrmecophilous beetle species *Monotoma conicicollis* (Monotomidae), which uses only *Formica* species as its host (Päivinen *et al*. 2002), was the most common beetle species in our data (Table 1). The rove beetle (Staphylinidae) *Oxypoda formiceticola* (Table 1) occurred most frequently in the nests of *F. aquilonia* ants. All observed myrmecophilous beetle species have several host ant species in genuses *Formica* and *Lasius*, except the beetle species *Dinarda dentata* and *M. conicicollis* (Päivinen *et al*. 2002). In total, we observed 965 beetle individuals in 49 *F. aquilonia* nests. The mean number of species in an ant nest was 3.2 (SD = 2.6, $N = 49$) and mean number of individuals was 18.0 (SD = 26.6, $N = 49$).

The volume of ant nests varied from 64 to 1799 litres (mean = 367 litres, SD = 336, $N = 30$). The nearest-neighbour distance varied from 5 to 50 metres (mean = 25 metres, SD = 12, $N = 30$). Both the volume of an ant nest and the distance to the nearest neighbouring ant nest affect species richness and the total number of myrmecophilous beetle individuals occurring in the nests of *F. aquilonia* ants (Table 2). Also, the interaction between the distance and the volume affected both myrmecophilous beetle species richness and the number of myrmecophilous beetle individuals occurring in the ant nests (Table 2). However, we did not find any differences among forest patches or in interaction between forest patches and covariates (Table 2, Fig. 1a and b).

The number of occupied nests by the beetle species and the mean number of individuals per occupied ant nest of myrmecophilous beetles increased with increasing number of host ant species (data of host ant species from Päivinen *et al*. 2002), (linear regression: $F_{1,14} = 9.26$, $P = 0.009$, $r^2 = 0.40$ (Fig. 2a); and $F_{1,14} = 9.52$; $P = 0.008$, $r^2 = 0.41$ (Fig. 2b), respectively).

Discussion

We found that both the size and the isolation of an ant nest influence myrmecophilous beetle species richness and the number of myrmecophilous beetles within a single nest of *F. aquilonia* ants. The observation that species richness of myrmecophilous beetles was highest in large nests, with close neighbours, supports both the resource concentration hypothesis (Lewis & Waloff 1964, Root 1973, Ranta 1992, Morand & Poulin 1998, Goncalves-Alvim & Fernandes 2001, Arneberg 2002, Stanko *et al*. 2002) and the resource size hypothesis (Lawton 1983, Ranta 1992, Guégan *et al*. 1992, Brändle & Brandl

Table 1. List of the myrmecophilous beetle species collected in the studied nests of *Formica aquilonia*, and their observed total number of individuals, number of occupied nests and their number of host ant species in Finland (Päivinen *et al*. 2002).

Beetle species	Number of individuals	Number of occupied nests	Number of host ant species in Finland
PTILIIDAE			
Ptilium myrmecophilum Allibert	1	1	6
SCYDMAENIDAE			
Euconnus claviger Mueller & Kunze	1	1	4
STAPHYLINIDAE			
Quedius brevis Erichson	1	1	6
Leptacinus formicetorum Märkel	4	4	7
Gyrohypnus atratus Heer	3	3	4
Oxypoda formiceticola Märkel	175	11	7
Oxypoda haemorrhoa Mannerheim	42	6	10
Thiasophila angulata Erichson	104	10	9
Dinarda dentata Gravenhorst	2	2	6
Atheta talpa Heer	185	9	8
Atheta flavipes Gravenhorst	83	6	9
Lyprocorrhe anceps Erichson	71	10	7
Zyras humeralis Gravenhorst	4	2	5
HISTERIDAE			
Myrmetes paykulli Kanaar	8	2	5
Dendrophilus pygmaeus L.	35	9	7
MONOTOMIDAE			
Monotoma conicicollis Aube	246	9	6

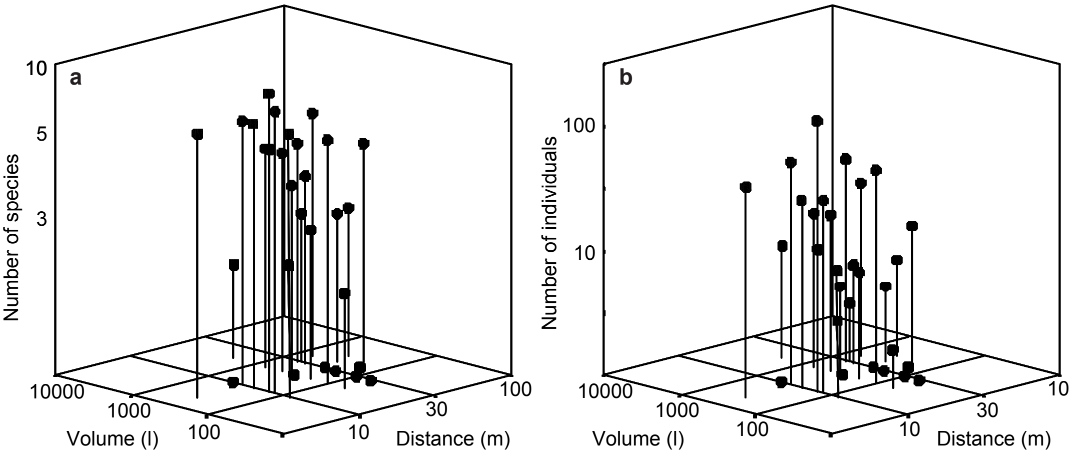

Fig. 1. — **a**: The relationship between the number of myrmecophilous beetle species, volume of ant nests (litre) and the nearest neighbour distance (metre). — **b**: The relationship between the number of myrmecophilous beetle individuals, volume of ant nests and the nearest neighbour distance. Note that all axes are in logarithmic scale.

2001, Arneberg 2002, Sanches & Parmenter 2002). However, we cannot pinpoint the most important factor explaining species richness because the interaction between nest size and nearest neighbour distance was statistically significant. Furthermore, local populations are more likely to occur in well-connected large habitat patches, suggesting that dispersal of ant guests plays an important role in local dynamics (Hanski 1994, 1999, Gonzalez *et al.* 1998, Roslin 2000). However, it is unknown how myrmecophilous beetle species discover another ant colony when they disperse. The observed pattern could arise, for example, if myrmecophilous beetles located new ant colonies randomly and the probability of finding a new nest declined with the distance from the focal nest to neighbouring nests. Moreover, species losses through local extinc-

Table 2. Results from analysis of covariance (ANCOVA) on number of myrmecophilous beetle species and number of myrmecophilous beetle individuals in the 30 nests of *F. aquilonia* in seven forest patches. The nearest neighbour distance (Distance, log transformed) and the volume of ant nest (Volume, log transformed) were used as covariates.

Source	Mean square	df	*F*	*P*
Number of species				
Forest	0.528	5	2.069	0.162
Log (Volume)	3.639	1	14.261	0.004
Log (Distance)	4.044	1	15.848	0.003
Forest × log (Volume)	0.714	5	2.799	0.085
Forest × log (Distance)	0.391	5	1.532	0.272
Log (Distance) × log (Volume)	3.793	1	14.863	0.004
Error	0.255	9		
Number of individuals				
Forest	1.758	5	0.940	0.500
Log (Volume)	12.934	1	6.917	0.027
Log (Distance)	14.372	1	7.686	0.022
Forest × log (Volume)	3.025	5	1.618	0.250
Forest × log (Distance)	1.950	5	1.043	0.449
Log (Distance) × log (Volume)	13.607	1	7.277	0.024
Error	1.870	9		

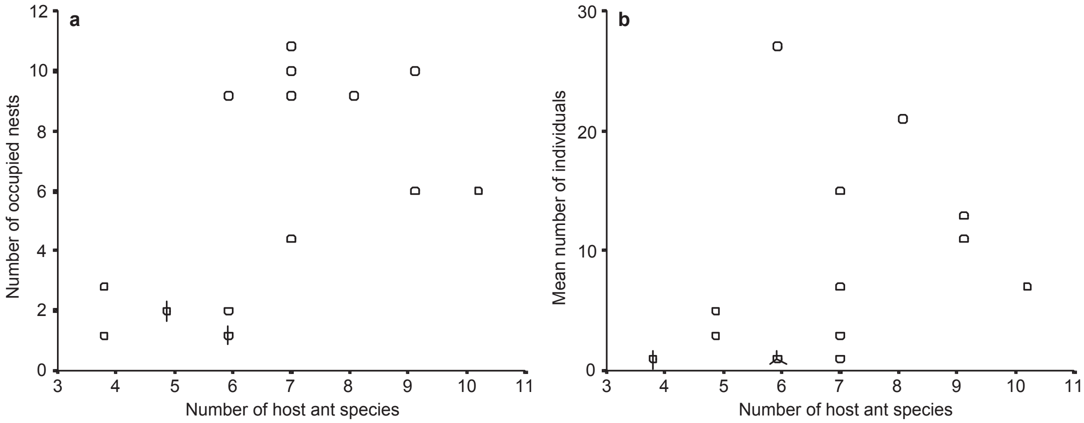

Fig. 2. — **a**: The relationship between number of Finnish host ants and the number of nests occupied by the beetle species. Number of ticks over the dot represents the number of overlapping data points. — **b**: The relationship between total number of Finnish host ants and the mean number of individuals per occupied nests. Number of ticks over the dot represents the number of overlapping data points.

tion may be reduced because large ant nests are able to support larger myrmecophilous beetle species population. Although the probability of local extinctions increases with increasing isolation for many reasons (Hanski 1999), these explanations are difficult to verify in our study because the information on the basic ecology of myrmecophilous beetles is scarce.

Many myrmecophilous beetle species occur on the trails of ants (Hölldobler & Wilson 1990). Ants carry their own eggs, larvae, pupae and adult workers between the nests along these trails (Hölldobler & Wilson 1990). It is possible that ants mistakenly carry myrmecophilous beetles at different developmental stages between nests. However, if a nest is isolated from other nests, this dispersal pattern becomes unlikely. Thus, we hypothesize that the ant trails between the nests can work as dispersal corridors for some myrmecophilous beetles. Nevertheless, nest isolation does not create a dispersal barrier for beetle species with good flying ability. Indeed, some of the myrmecophilous beetle species (*Monotoma* spp., *Oxypoda* spp.) are able to fly lengthy distances (J.P., laboratory observations).

The limited amount of available information suggests that most myrmecophilous beetle species are xerophilous, i.e., they are dependent on dryness (Koch 1989a, 1989b, 1992). It is possible that the environment is not as stable in small nests as it is in large nests. This could contribute to the observed positive relationship between ant nest size and species richness and total number of myrmecophilous beetle species individuals.

In the previous study based on literature data (Päivinen *et al.* 2003), it was found that myrmecophilous beetle species, which have more than one host ant species, and thus have more abundant resources, were more widely distributed than those species that have only one or few host species. In other words, generalist species are expected to have access to more abundant resources, as compared to specialist species, thus allowing them to be more widely distributed. Similarly, we found (cross-species comparisons) that the more host ant species a beetle species is able to use, the more widely distributed and the more abundant (mean number of individuals per occupied nests) a beetle species was in our study. Brown (1984) hypothesises that generalist species which have the ability to use a broader range of resources are assumed to be widespread and more abundant because they can tolerate broad environmental spectra. Thus, our observation could be a consequence of that a generalist myrmecophilous beetle species can more easily exploit the surrounding areas, such as different type of forests, than a specialist species, which leads in a greater abundance and distribution of ant guests in the studied areas.

To conclude, our results suggest that the resource concentration, resource size and resource abundance hypotheses, mainly verified in plant–herbivore and animal–parasite interactions, are also useful when studying host-species systems such as ants and myrmecophilous beetles. In addition to species richness, the hypotheses proposing to explain biological diversity are useful when predicting abundance of the myrmecophilous beetle species. However, the nearest neighbour distance is not the most powerful measure of resource patch density within a certain area (Moilanen & Nieminen 2002). Moilanen and Nieminen (2002) recommended measures that take into account the size of the focal patch and distances to all potential source populations. Our data support their results. We found that both nearest neighbour distance and nest size explain species richness in the focal nest. In the future, attention should be paid to studying the dispersal behaviour of myrmecophilous beetle species.

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