

Jussi Päivinen

Distribution, Abundance and Species
Richness of Butterflies and
Myrmecophilous Beetles

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UNIVERSITY OF JYVÄSKYLÄ

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Editors

Jukka Särkkä

Department of Biological and Environmental Science, University of Jyväskylä

Pekka Olsbo, Marja-Leena Tynkkynen

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ABSTRACT

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Diss.

Several mechanisms have been proposed to explain the patterns of species richness, distribution and abundance. Also several mechanisms have been put forward in explaining the generally observed positive relationship between regional distribution and local abundance of species. In this thesis factors affecting distribution, abundance and species richness were studied using butterflies and myrmecophilous beetles as study objects. The data of myrmecophilous beetles are based on the literature and a field survey and data of butterflies is based on the literature. This thesis suggests that ant colonies maintain species rich beetle fauna, and that widespread host ant species and the species with large colony size are able to maintain higher species richness of myrmecophilous beetles. Surprisingly, a strong negative relationship between local abundance and regional distribution was found for the Finnish butterflies. The study suggested that sedentary butterfly species, species at the edge of their distribution range and the most specialized species were locally abundant with restricted distribution. Mobile species, species furthest from the edge of their distribution and generalist butterfly species were locally few in number and widespread, thus, generating the negative relationship. Larval specificity, habitat breadth and resource availability were observed to be in a key role when explaining the mobility of the butterflies. Range position had strong effect both on the mobility and on the length of the flight period of the butterflies. The surprising results emphasize the importance of the study of basic ecology of species. More studies are needed to find out, whether observed negative relationship between distribution and abundance is a more general phenomenon than previously thought.

Key words: Ant-associated; ant guest; Coleoptera; distribution-abundance relationships; Lepidoptera; local abundance; regional distribution.

J. Päivinen, University of Jyväskylä, Department of Biological and Environmental Science, P.O. Box 35, FIN-40014 University of Jyväskylä, Finland

Author's address MSc Jussi Päivinen
University of Jyväskylä
Department of Biological and Environmental Science
P.O. Box 35
FIN-40014 University of Jyväskylä, Finland
E-mail: jupepa@bytl.jyu.fi

Supervisors Professor Veijo Kaitala
University of Helsinki
Department of Ecology and Systematics
P.O. Box 65
FIN-00014 University of Helsinki, Finland
E-mail: veijo.kaitala@helsinki.fi

Dr Petri Ahlroth
Ministry of Agriculture and Forestry
P.O. Box 30
FIN-00023 Government, Finland
E-mail: petri.ahlroth@mmm.fi

Reviewers Docent Marko Nieminen
University of Helsinki
Department of Ecology and Systematics
P.O. Box 65
FIN-00014 University of Helsinki, Finland
E-mail: marko.nieminen@helsinki.fi

Dr Tomas Roslin
University of Helsinki
Department of Ecology and Systematics
P.O. Box 65
FIN-00014 University of Helsinki, Finland
E-mail: tomas.roslin@helsinki.fi

Opponent Professor Jari Niemelä
University of Helsinki
Department of Ecology and Systematics
P.O. Box 65
FIN-00014 University of Helsinki, Finland
E-mail: jari.niemela@helsinki.fi

Omistettu Teijalle ja Iirikselle

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following articles, referred to in the text by their Roman numerals I-V.

- I Päivinen, J., Ahlroth, P. and Kaitala, V. 2002. Ant-associated beetles of Fennoscandia and Denmark. *Entomol. Fennica* 13: 20-40.
- II Päivinen, J., Ahlroth, P., Kaitala, V., Kotiaho, J. S., Suhonen, J. and Virola, T. 2003. Species richness and regional distribution of myrmecophilous beetles. *Oecologia* 134: 587-595.
- III Päivinen, J., Ahlroth, P., Kaitala, V. and Suhonen, J. 2003. Species richness, abundance and distribution of myrmecophilous beetles in the ant nests of *Formica aquilonia* Yarrow. Submitted manuscript.
- IV Päivinen, J., Grapputo, A., Kaitala, V., Komonen, A., Kotiaho, J. S. and Wahlberg, N. 2003. Negative interspecific distribution-abundance relationship in butterflies of Finland. Submitted manuscript.
- V Komonen, A., Grapputo, A., Kaitala, V., Kotiaho, J. S. and Päivinen, J. 2003. The role of niche breadth and resource availability on the life history of butterflies. Submitted manuscript.

THE AUTHOR'S CONTRIBUTION

Paper I

I planned the study and collected and analyzed the data in this article. I was also responsible for writing the article.

Papers II-III

The studies were planned by me and Jukka Suhonen. I collected the data and I was the main author in these articles. I analyzed the data together with Jukka Suhonen.

Papers IV-V

I planned these studies with Atte Komonen and Janne Kotiaho. I collected the data and the authors were all responsible for writing the articles. I analyzed the data with Janne Kotiaho.

Jyväskylä April 10th, 2003

Jussi Päivinen

1 INTRODUCTION

Ecology is the scientific study of the interactions that determine the distribution and abundance of organisms (Krebs 2001). Why are organisms of a particular species present in some places and absent from the others? Why organisms occur at varying densities within their areas of distribution? Researchers in many studies have tried to answer to these questions, and interest in them is growing (MacArthur & Wilson 1967, Baroni Urbani & Collingwood 1977, Brown 1984, Gutierrez & Menendez 1995, Quinn et al. 1997, 1998, Koizumi et al. 1999, Webb & Pullin 2000, Marques et al. 2000, Christman & Culver 2001, Magagula & Samways 2001, Brändl et al. 2002). In these studies, the most important biotic factors that affect diversity, distribution and abundance of species, have been shown to be dispersal, habitat selection, competition, predation, parasitism and mutualistic interactions with other species. Also many abiotic factors such as temperature, moisture and light limit diversity, distribution and abundance of species.

1.1 Species richness

At its simplest level, biological diversity can be defined as the number of species found in a community, a measure known as species richness. Gaston (1996) presented four reasons, why species richness is the most frequently and widely applied measure for biodiversity. First, species richness is thought by many to capture much of the essence of biodiversity. Second, the meaning of species richness is apparently widely understood, and there is no need to derive complex indices to express it. Third, species richness is considered in practice often to be a measurable parameter. Fourth, much data on species richness already exists.

Few generalizations have been proposed to explain the patterns of species richness. One generalization is that the number of species increases with increasing area (MacArthur & Wilson 1967). Another famous hypothesis is the

latitudinal gradient hypothesis: the number of species decline moving away from the equator, north or south (Fischer 1961). Habitat variety and resource elements are also in a key role in maintaining species richness. Four major hypotheses have been put forward to explain species richness of the species, which are dependent on a certain resource (Marques et al. 2000, Christman & Culver 2001). According to resource distribution hypothesis, regionally widespread host species are able to support richer local fauna of commensals or parasites (Ricklefs 1987, Cornell & Lawton 1992). Resource size hypothesis predicts that larger hosts may support more species than smaller hosts because large hosts are more likely to be found by the species (Lawton 1983, Brändle & Brandl 2001, Sanches & Parmenter 2002). Resource abundance hypothesis predicts that the hosts that offer more resources are able to support more species than hosts that offer limited resources (Hunter & Wilmer 1989, Hunter 1992, Marques et al. 2000). Finally, resource concentration hypothesis predicts that host species occurring in high density patches are able to support high number of species for two reasons: because such patches are most likely to be found by the species and because specialist species tend to stay longer in these patches (Lewis & Waloff 1964, Root 1973, Goncalves-Alvim & Fernandes 2001).

1.2 Distribution-abundance relationships

The distribution and abundance of species can be divided into three classes according to spatial scale: local, regional and continental (Hughes 2000). Recently, the studies of the relationship between local abundance and regional distribution have gained a lot of attention (Hanski 1982, Bock & Ricklefs 1983, Brown 1984, O'Connor 1987, Hanski 1991, Harvey & Pagel 1991, Wright 1991, Gyllenberg & Hanski 1992, Hanski et al. 1993, Gaston 1994, Gaston et al. 1997a, b, Holt et al. 1997, Hartley 1998, Johnson 1998, Gaston & Blackburn 2000, Cowley et al. 2001a, b). These studies reveal that the local abundance and regional distributions of species are rarely independent.

In most taxonomic assemblages, widespread species are locally more abundant than species with small geographic distribution ranges (e.g. Hanski 1982, Brown 1984). This positive relationship between the local abundance and regional distribution of species is almost universal pattern in ecology (Hanski et al. 1993, Gaston et al. 1997b, Gaston & Blackburn 2000). The pattern has been observed in a variety of taxa and over a spectrum of spatial scales. However, some studies reveal a negative relationship between regional distribution and local abundance (Adams & Anderson 1982, Schoener 1987; but see Schoener 1990, Arita et al. 1990, Gaston & Lawton 1990, Ford 1990, Novotny 1991, Johnson 1998).

Gaston et al. (1997b) argue that negative relationship between distribution and abundance deserves more attention. Negative relationships can largely be generated by the same mechanisms that give rise to positive correlations, but

for substantially different circumstances and parameter values (Gaston et al. 1997b). Nine mechanisms have been proposed to explain positive distribution-abundance pattern, and five of them can also generate negative relationships (e.g. Gaston et al. 1997b, Gaston & Blackburn 2000). Below the mechanisms that have been proposed to explain positive relationships have been discussed briefly, including evaluation whether they could also produce negative ones.

1. *Sampling artefact*: the positive relationship results from the systematic under-recording of the distributions of species that occur at lower density, as they are less likely to be detected on surveys (Brown 1984, Wright 1991, Hanski et al. 1993). This mechanism cannot generate negative distribution-abundance relationships (Gaston et al. 1997b).

2. *Phylogenetic non-independence*: positive or negative relationships result from species being considered independent data points in analysis, which is often not the case, as species are phylogenetically related. Thus, observed distribution-abundance relationships could represent differences between taxonomic groups, rather than any general tendency for high-density species to have wide distributions, or restricted in the case of negative correlations (Harvey & Pagel 1991, Harvey 1996). Phylogenetic non-independence has been rejected as an explanation for the distribution-abundance relationship in all previous studies that have controlled for its effects (Gaston et al. 1997a, Cowley et al. 2001b).

3. *Patterns of aggregation*: a positive relationship can be generated as a result of an underlying (theoretical) spatial distribution of individuals. For a given level of aggregation, a species with more individuals in a given patch is expected to occur in more locations and at a higher average density than a species with fewer individuals in the same patch (Wright 1991, Hartley 1998). However, whether this purely statistical mechanism is strictly a mechanism for distribution-abundance relationship, rather than essentially a restatement of the relationship in another form, is questionable (Gaston et al. 1998). This mechanism cannot generate negative relationships.

4. *Range position*: a decline in occupancy and density moving from the centre to the margins of a species' geographical range has been documented for a variety of taxa (e.g. Hengeveld & Haeck 1982, Brown 1984). Assuming that this pattern is general, a positive distribution-abundance relationship in any particular region might result because species are at different positions relative to the centre of their ranges (Bock & Ricklefs 1983). According to Gaston et al. (1997b), this mechanism cannot generate negative distribution-abundance relationships.

5. *Niche breadth*: the range of resources a species can exploit might be expected to affect local population density and regional distribution (Brown 1984). Negative distribution-abundance relationships can be generated if local abundance is measured in habitats, which are atypical of the spectrum of habitats in the geographical region of interest (Ford 1990, Gaston & Lawton 1990).

6. *Resource availability*: if the local density and regional distribution of resources determine the density and regional distribution of the species utilizing them, then a negative distribution abundance relationship for the resource will generate the same relationship in the consumer (Hanski et al. 1993, Gaston 1994). Intuitively, negative distribution-abundance relationship is likely for many plant species, which require specific environmental conditions (e.g. soil type) and thus occur patchily but with high density in such suitable sites.

7. *Density-dependent habitat selection*: if species tend to choose to inhabit more habitats when densities are high and fewer when they are low, then locally abundant species will tend to occupy more habitats and have wider distributions (O'Connor 1987). At present there is only little evidence for positive density-dependent habitat selection in butterflies (Gaston et al. 1997b see also Cowley et al. 2001b). Instead, some evidence exists for negative density – dependent habitat selection (Gilbert & Singer 1973, Brown & Ehrlich 1980, Kuussaari et al. 1996). Negative distribution – abundance relationship arises when species have wider distribution, i.e., inhabit more habitats when density of individuals is low.

8. *Mobility*: metapopulation dynamics may explain both the positive as well as negative relationships between distribution and abundance (Gyllenberg & Hanski 1992). Positive distribution-abundance relationship may be generated from metapopulation dynamics as a result of (i) species that has high abundance is less likely to go extinct on a patch of a given area than a species that has lower abundance, and (ii) immigration is likely to increase with density in other patches, promoting the colonization of empty patches and the rescue of small populations (Hanski 1991, Hanski et al. 1993). On the other hand, negative distribution-abundance relationships may be generated from metapopulation dynamics as a result of species with high dispersal rate in relation to the intrinsic growth rate being less affected by environmental stochasticity (Gyllenberg & Hanski 1992, Hanski et al. 1993).

9. *Vital rates*: if species abundance on a site is determined by the population growth rate, and species distributions is the number of sites with a positive population growth rate, any factor that increases the rate of population growth across all sites will increase both the number of occupied sites and abundance within occupied sites, thus generating a distribution-abundance correlation (Holt et al. 1997). In the special case when species differ in their spatial responses to environmental variation, have the same mortality rate but greatly differ in their birth rates, species with the greater range will have lower mean local abundance (i.e. negative relationship between distribution and abundance). This hypothesis is difficult to test, as it requires data on density-dependent birth and death rates (Gaston et al. 1997b), and that kind of data is not available for many taxa.

1.3 The species used in the study

1.3.1 Ant-associated beetles

Ant-associated insects can be divided in two groups: ant guests and other ant-associated species. "Ant guests", commonly known as myrmecophiles, are dependent on ant societies, at least during a part of their life cycles (Hölldobler & Wilson 1990). Other ant-associated insects do so occasionally, functioning as casual predators or temporary nest commensals. Both of these ant-associated insect groups include a great variety of springtails (Collembola), beetles (Coleoptera) and butterflies (Lepidoptera), as well as less abundant representatives of a wide range of other insect groups (Hölldobler & Wilson 1990).

One of the most diverse myrmecophilous insect taxa is beetles. According to Hölldobler & Wilson (1990), 35 different myrmecophilous beetle families, consisting of thousands of species, have hitherto been recorded. Although the literature on myrmecophilous beetle species is enormous, a large part of the available data consists only of incidental observations or ecological studies of individual species. Only a few detailed lists of the host ants and their myrmecophilous beetles have been previously published (e.g. Johansen 1904, Donisthorpe 1927, Larsson 1943, Collingwood 1957, Wilson 1971, Kistner 1982, Hölldobler & Wilson 1990, Wojcik 1990, Franck 1992, Kistner et al. 1997).

A generally accepted classification of myrmecophilous arthropods is based on a series of works by Wasmann (e.g. Wasmann 1910), (translated into English by Wheeler 1910). Wasmann devised 5 behavioural categories (1) synechthrans (persecuted guests), (2) synoeketes (indifferently tolerated guests), (3) symphiles (true guests), (4) ectoparasites and endoparasites and (5) trophobionts (provide secretions to the ants). According to Hölldobler and Wilson's (1990) definition, all the beetle species belonging to these behavioural categories are myrmecophilous.

1.3.2 Butterflies

Butterflies (Hesperioidea and Papilionoidea) are conspicuous insects. They are usually easily identified and their distributions for the most part are well known (Dennis 1992, Hulden et al. 2000). Butterflies have featured in a wide range of experimental, observational and evolutionary studies, involving important work of biochemistry, physiology and parasitology (Vane-Wright & Ackery 1989).

Large numbers of butterfly species in the northern Europe have been included in red data books in response to alarming reduction and fragmentation of their distribution and decreasing local abundance over the past decades (Kotiranta et al. 1998, Rassi et al. 2001). Therefore, different ecological studies concerning butterflies have nowadays become increasingly

important. Butterflies have been used as study objects especially when studying distribution, abundance and distribution-abundance relationships (e. g. Hanski et al. 1993, Quinn et al. 1998, Webb & Pullin 2000, Cowley et al. 2001a, b).

Many butterfly species are regarded as relatively sedentary (Dennis 1982, Dempster 1989, Thomas 1993, Thomas et al. 1999). This may be related to immediate reproductive gains and potential risks associated with moving from existing areas to new areas (Shreeve 1992). For a dispersing butterfly female, successful location of suitable larval host plant is vital for its reproductive success. Thus, butterfly species with large niche breadth, i.e., species the larvae of which are polyphagous foraging on several host plant species or butterfly species with high resource availability i.e. species of which larval food plant is widespread and abundant may be expected to be more mobile than the more specialized species (Shreeve 1992). In addition, there are some indications that resource availability may be a factor determining butterfly mobility (White & Levin 1981, Murphy & White 1984, Kuussaari et al. 1996).

Length of the flight period of a butterfly species can reflect at least two things: the average longevity or life span of an individual or variance in the timing of hatching. There is evidence that the length of the flight period varies between the species but also between years within a species (Warren 1992). Variance in the length of the flight period between years suggests that it is at least partially dependent on environmental factors. Indeed, there is evidence that temperature, aridity and the openness of the habitat has an effect on the length of the flight period (Pollard & Greatorex-Davies 1997, Garcia-Barros 2000). Perhaps ecologically more interesting, however, are the findings that the flight period tends to be longer among polyphagous butterfly species which are able to exploit several host plant species (Garcia-Barros 2000) and that the flight period tends to be shorter closer to the edge of the species geographical distribution range (Pollard 1991).

Body size is considered to be one of the most important life history characteristics of a species (Roff 1992, Stearns 1992, Roff 2002). In Lepidoptera in general there seems to be a positive association between the niche breadth and body size such that polyphagous species tend to be larger (Niemelä et al. 1981, Inkinen 1994, Lindström et al. 1994, Loder et al. 1998). However, according to Garcia-Barros (2000), such pattern does not hold for butterflies considered as a whole. Both Loder et al. (1998) and Garcia-Barros (2000) point out that there is no single explanation for the relationship between niche breadth and body size which would enjoy solid support from the data, and that most of the evidence for such relationships comes from a few families of Lepidoptera in cool temperate areas. Kelly & Debinski (1998) found that host plant abundance affected body size of a studied butterfly species. Also latitudinal gradient in the body size has been observed in butterflies of Europe (Nylin & Svard 1991, Nylin et al. 1996). This finding suggests that range position may have an effect on the size of the species.

1.4 Aims of the study

The aim of the study was:

- a) to collect the most comprehensive list of myrmecophilous and other ant-associated beetles in Fennoscandia (Finland, Norway and Sweden) and Denmark, and also to demonstrate that ant colonies are species rich habitats for beetles.
- b) to test whether resource distribution, resource size, resource abundance and resource concentration hypothesis explain distribution, abundance and species richness of myrmecophilous beetles.
- c) to assess which mechanisms (phylogenetic non-independence, niche breadth, mobility and range position) affect distribution-abundance relationship of Finnish butterflies at a regional scale.
- d) to test, how host plant specialization, habitat breadth, host plant distribution / abundance and range position are related to the life history of butterflies, namely mobility, length of flight period and body size.

2 MATERIALS AND METHODS

2.1 Literature survey of ant-associated beetles (I-II)

Data behind these studies are based on an extensive literature survey and some field observations of ant-associated beetles. In the study I, a list of host ants and beetle species, which have been observed with ants according to literature and some field observations, were collected. In publication II, data consist of beetle species that are classified as myrmecophilous according to Koch (1989a, 1989b, 1992) and are found to occur in Denmark, Sweden or Finland (Silfverberg 1992, Lundberg & Gustafsson 1995, Hansen 1996). The data based on literature are considered reliable because for most myrmecophilous beetle species and their host ant species there were several observations from independent sources (see I).

The number of myrmecophilous beetle species observed with each ant species was used as a measure of the species richness. The colony size of the host ant were divided into four classes according to the number of workers to analyse the effect of colony size on the species richness of myrmecophilous beetles, (class 1 = under 1 000 workers per colony, class 2 = 1 000 - 10 000 workers per colony, class 3 = 10 000 -100 000 workers per colony, class 4 = over 100 000 workers per colony) (Brian 1950, Breen 1979, Collingwood 1979, Savolainen & Vepsäläinen 1988, Czechowski 1990, Hölldobler & Wilson 1990).

The distribution of species can be divided into three classes according to spatial scale: local, regional and continental distribution (Hughes 2000). The regional distribution of host ants were described by the number of provinces that the species occupy (Collingwood 1979). The distribution of the host ants means the total distribution of all of the host ants. This was calculated as the number of provinces that were occupied by at least one of the host ant species. Correspondingly, in Sweden and Denmark the distribution of the beetles was described by the number of provinces that the species occupy (Lundberg & Gustafsson 1995, Hansen 1996). In Finland the provincial distributions of the beetle species are missing. Therefore, to describe the distribution of beetle

species in Finland, the number of occupied 10-km grid square ranges was used. There are 3900 such grid squares within the land area of Finland. Rassi (1993) has divided them into 12 categories. For example, if a beetle species belongs to category one, it has been observed in 3201-3900 grid squares in Finland. The minimum number of grid squares were used (in this example 3201) to describe the distribution of a beetle species. To analyse the distribution of beetle species, the data from Denmark and Sweden were pooled.

2.2 Field data of myrmecophilous beetles (III)

60 nests situated within 12 forest patches were studied in Central Finland (62°N, 26°E) in Luhanka, Joutsa, Leivonmäki, Toivakka and Korpilahti regions within a 950 km² area. Distance between the patches was at least two kilometres (except in one case only 500 m). Surveyed areas are mixed forests.

Beetle samples were collected in the nests of the nest building wood ant *Formica aquilonia* Yarrow. The studied nests were selected randomly. Plastic pitfall traps (Ø 66 mm) covered with a metal net (mesh = 2x2 mm) were used. The metal net keeps ants and most part of nest material out of the trap. The myrmecophilous beetle species are small and they drop through the metal net into pitfall traps. The traps (1 trap/nest, 5 nests/each forest patch) were placed inside the nests just under the moisture layer at the depth of 5 cm in the beginning of May 1996. Traps were removed after one month. According to field observations most of the myrmecophilous beetle species occur in the nests of *F. aquilonia* only in the spring. For example, only a few myrmecophilous beetle individuals were observed in the studied nests of *F. aquilonia* in June 1999. Therefore, it is likely that most of the beetle species, occurring in the studied nests, were collected.

To estimate the volume of each nest the height from the ground level to the top and the diameter of the nest at ground level were measured. Shape of the nest above ground layer was roughly approximated to a circular cone. Six forest patches were randomly selected (five nests/forest patch), in which the nearest-neighbour distance between nests of *F. aquilonia* were measured.

2.3 Literature survey of butterflies (IV-V)

The data on Finnish butterflies and larval host plants are based on literature (Marttila et al. 1990, Lahti et al. 1995, Hämet-Ahti 1998, Hulden et al. 2000, Marttila et al. 2001, Saarinen et al. 2002). 116 species of butterflies have been recorded from Finland (Kullberg et al. 2002) of which 95 butterfly species, which are classified as “resident” or “fluctuating” in Finland were taken into analysis (Hulden et al. 2000). The species, which are classified as “migratory”

(12 species), “irruptive” (5) or “extinct” (1) and *Lycaena dispar* Haworth (“fluctuating, irruptive”) and *Hyponphele lycaon* Kuhn (“extinct, irruptive”) were excluded (Hulden et al. 2000).

Regional distribution. Regional distribution of butterfly species is based on the “Atlas of Finnish Macrolepidoptera” (Hulden et al. 2000). The Atlas is one of the most extensive and the most detailed map data in the world and it covers almost all observations in Finland during the years 1747-1997 (Hulden et al. 2000). In our study, the regional distribution of butterflies were described by the new observations (10 km grid squares on the Finnish national coordinate system) from 1988-1997.

Local abundance. “The National Butterfly Scheme in Finland (NAFI)” is a monitoring study based on standard questionnaires for voluntary amateur and professional lepidopterists and provides quantitative abundance data for the butterfly fauna across Finland (Marttila et al. 2001, Saarinen et al. 2002). The information required on each questionnaire includes the 10 km grid square, the year, the estimated number of individuals of each species observed and the number of observation days (Saarinen et al. 2002). During the first ten-year period (1991-2000), a total of 432 lepidopterists have participated in the Scheme by providing data on 1,501,316 individuals representing a total of 105 butterfly species (Saarinen et al. 2002).

The data on the local abundance of butterflies are based on the total number of observed individuals between 1991-2000 (Saarinen et al. 2002). To get the mean local abundance per each 10 km grid square per year for each butterfly species, the total number of individuals of each butterfly species were divided by the number of squares occupied by the species. Some rare butterfly species with known high-density habitat patches may face proportionally higher sampling effort than the common species. To remove the effect of this disproportionate sampling effort on the mean local abundance (see Dennis et al. 1999), the average local abundance was divided by the number of the observation days of the species.

Range position. To determine butterflies’ distribution range in Finland, the distance between the northernmost distribution record and the southernmost point (Hankoniemi) in Finland were measured using maps included in Hulden et al. 2000. Note that the southern and western Finland borders the Baltic sea and the longest possible range is ca. 1155 km. All the butterfly species, which were included in the analyses, are present in southern Finland and their distribution range extends species-specifically to the north.

To test the range position hypothesis only the “southern” butterfly species were taken into account. The species, which occur only in the Northern Finland (n = 14, Marttila et al. 1990) and also the species *L. helle* D. & S, which distribution is limited in central Finland, and *Clossiana thore* ssp. *thore* Hubner, which is clearly “eastern” species, were excluded in the dataset.

Niche breadth. The niche breadth for each butterfly species was described either as a larval host-plant specificity or a butterfly species’ habitat breadth. The species which occur only in the Northern Finland (n = 14, Marttila et al.

1990) were excluded because their larval host-plants are poorly or at all known and they are difficult to categorize to the following four main habitat types.

The knowledge of larval host-plant specificity in Finland was based on Hulden et al. (2000) and Wahlberg (2000). The larval specificity was classified to three classes: 1, monophage (one species of host plant); 2, oligophage (restricted to one genus of host-plant); 3, polyphage (feeding on plants from one family to two families).

Marttila et al. (1990) have categorized the habitats of Finnish butterflies to four main habitat types: 1, uncultivable lands (e.g. edge zones beside industrial area, harbour and storage areas, loading places, many kinds of unbuilt areas, which have exposed to under human impact and uncropped fields); 2, meadows (includes many kinds of open fields under natural state); 3, edge areas of forests and fields (e.g. road sides); 4, bogs. Marttila et al. (1990) have described the typical habitats to each of the Finnish butterflies and based on that, it was counted that in how many of the main habitat types each butterfly species occur. That is, a butterfly species can get a value from one to three. Value one represents that a butterfly species is limited to one habitat type (specialist species), value two that a butterfly species occur in two main habitat types (intermediate species) and value three that a butterfly species occur in three or four main habitat types (generalist species), respectively.

Resource availability. To estimate the resource availability, only the monophagous butterfly species ($n = 23$) and the host plants of their larvae were taken into account because knowledge of host plants of oligophagous and polyphagous species is unreliable. The species which occur only in the Northern Finland ($n = 14$, Marttila et al. 1990) were excluded.

The plant distribution data is based on the national floristic database; the "Atlas of the Distribution of Vascular Plants in Finland" (Lahti et al. 1995). The Atlas shows the distribution of all plant species in Finland as 10-km grid square dot maps. The numerical data on the regional distribution of plants (the total number of the 10-km grid squares) were got from the authors.

Data on the abundance of plants is taken from "Field Flora of Finland" (Hämet-Ahti et al. 1998). In the Flora, the abundance of the plants is described as rare or common separately for each biogeographical province of Finland. For each species each province was assigned with rare occurrence number 0, and each province with common occurrence number 1. The mean abundance was calculated by using these numbers.

Mobility. To describe relative mobility of butterfly species, the method described in Cowley et al. (2001a) was modified. Questionnaires were sent to 13 experienced lepidopterists in Finland and asked to give a "mobility index" (0-10) for each butterfly species. In the questionnaire, value zero indicates that a given butterfly species rarely moves and is scarcely seen outside its own habitat patch, if such a discrete patch exists. Value ten means that a given butterfly species is extremely mobile and can be seen in almost any habitat, even in habitats not suitable for the species. Therefore, the higher the mobility index, the more mobile the butterfly species is. To get the relative mobility value for

each butterfly species, the average mobility index from all 13 questionnaires were calculated.

The measured mobility index correlated positively with earlier indexes based on mark-release-recapture studies and questionnaires (Bink 1992, Pollard & Yates 1993, Cowley et al. 2001a, Cook et al. 2001). These comparisons verify that the mobility index is a proper estimate of the true mobility of the butterflies.

Flight period length. The average flight period length for each butterfly species was taken from Marttila et al. (1990). Whether a butterfly species' flight period differs between Lapland and southern Finland, the flight period in southern Finland was used. However, whether a given butterfly species has two generations per year, the length of the flight period of the first generation was used because in many cases the second generation is facultative and smaller in size. To get the length of the flight period for overwintering species, the flight periods of autumn and spring were summed.

Body size. Only female wing span was used as a measurement of butterfly size because practically there is no size variation between male and female butterflies. Wing span measurements are based on Marttila et al. (1990), in which the mean of a sample of 20 females was used.

Phylogenetic relatedness. Lack of statistical independence among species for the traits of interest was tested using the method of Phylogenetically Independent Contrasts (Harvey & Pagel 1991) as implemented in the CAIC program (Purvis & Rambaut 1995). Statistical control of phylogenetic non-independence requires knowledge of the phylogeny (Harvey & Pagel 1991, Freckleton et al. 2002). Knowledge of the general phylogenetic relationships among butterfly species is still in a state of flux (de Jong et al. 1996), and there are no studies available that look explicitly at the relationships of species in Finland. However, the recent surge of published studies on various groups of butterflies allows us to compile a likely phylogeny for Finnish butterflies. The relationships of the butterfly families is taken from de Jong et al. (1996), the relationships within Papilionidae from Caterino et al. (2000), the relationships within Nymphalidae from various sources (Martin et al. 2000, Wahlberg & Zimmermann 2000, Wahlberg & Nylin 2003, Wahlberg et al. 2003). Relationships within Pieridae, Lycaenidae and Hesperidae are based on current taxonomy with morphologically well-defined groups shown as monophyletic. In the analysis all branch length were assumed equal because no estimate of evolutionary distance exist for the entire data set. However this option is justified under the assumption of punctuated evolution. In case of continuous variables, regression analysis was used to investigate the standardized linear contrasts calculated by CAIC (Harvey & Pagel 1991). Note that the regression lines must pass though the origin (Garland et al. 1992; Pagel 1992).

Controlling for the phylogenetic non-independence by using the method of phylogenetically independent contrasts (CAIC), verified that none of the results reported hereafter were an artefact of treating species as an independent

data point (IV-V). The results clearly support the previous studies on distribution, abundance or distribution - abundance relationships in which the phylogenetic non-independence has not been found to be a causative factor for any of the results (e.g. Gaston 1997a, b, Gaston et al. 1998, Gaston & Chown 1999, Dennis et al. 2000, Cowley et al. 2001a, b, Brändl et al. 2002).

3 RESULTS AND DISCUSSION

3.1 Ant-associated beetles

A total of 369 ant-associated beetle species and 64 host ant species were encountered in Fennoscandia and Denmark (I). The total number of beetle species in Fennoscandia and Denmark is about 5000 (Lundberg & Gustafsson 1995). Thus, more than 7 % of Fennoscandia's and Denmark's beetle fauna can be found occurring with ants and may belong to the ant-associated species. However, 162 species are only represented by one observation (reference) in the list. This may indicate that the total number of beetle species, which are able to live with ants, would be even higher if more information was available. On the other hand, this may indicate that many beetle species may occur with ants accidentally.

Both ant-associated beetle species and most of the host ant species are often difficult to identify. The largest number of listed ant-associated beetle species exists with *Formica rufa* L. Probably, at least in some older studies, most of the so-called *F. rufa*-group species (*F. rufa* L., *F. polyctena* Förster, *F. aquilonia*, *F. lugubris* Zetterstedt and *F. pratensis* Retzius) have been incorrectly identified as *F. rufa*. Moreover, the species *F. aquilonia* was not described until 1955. This may partly explain why the number of the ant-associated beetle species observed with *F. rufa* is six times higher than those observed with *F. aquilonia*, although the latter probably is the most common mound building wood ant in Fennoscandia. Indeed, Päivinen (1999) found in *Formica aquilonia* mounds 20 ant-associated beetle species that have not been previously recorded for *F. aquilonia*. In total, only 10% of ant-associated beetle species that Päivinen (1999) found in *F. aquilonia*'s mounds were earlier observed with this species.

3.2 Host ants and myrmecophilous beetles

Resource distribution. Species richness and distribution of the myrmecophilous beetles was positively related to the distribution of the host ant (II). This observation provide is in line with the resource distribution hypothesis, according to which the distribution of host should have a positive effect on the species richness and distribution of the species hosted (Claridge & Wilson 1981, 1982, Neuvonen & Niemelä 1981, 1983, Cornell 1985, Quinn et al. 1997, 1998). This pattern may be a direct consequence of a species-area relationship hypothesis (MacArthur & Wilson 1967), according to which the number of species increases with increasing area.

The distribution of the myrmecophilous beetle species was positively related to the distribution of their host ants (II). Also the distribution of myrmecophilous beetle species towards north was less than the distribution of their host ants (II). These results suggest that in addition to species richness, the resource distribution hypothesis may also be used to predict the distribution of species. In fact, it is rather general finding that the distribution of hosts has an effect also on the distribution of species that are dependent on the host (Koizumi et al. 1999, Webb & Pullin 2000, Magagula & Samways 2001).

Resource size and resource abundance. Resource size and resource abundance hypotheses are very closely related in that large resource could be considered to offer abundant resources. Resource size hypothesis predicts that large plants are more likely found and colonised by herbivores both in ecological and evolutionary timescale (Neuvonen & Niemelä 1981, Lawton 1983, Brändl & Brandl 2001, Sanches & Parmenter 2002). Moreover, loss of species richness through local extinction may be reduced because large plants are able to support larger herbivore populations (Lawton 1983). Similarly, the resource abundance hypothesis predicts that plants offering more abundant resources have an increased potential to maintain more species of herbivores (Hunter & Wilmer 1989, Hunter 1992, Marques et al. 2000).

The above reasoning may be applied to the occurrence of myrmecophilous beetle species in ant colonies of different sizes (II). There was a positive effect of the ant nest's size on the species richness of myrmecophilous beetles. In other words, resource size or resource abundance had a positive effect on species richness of myrmecophilous beetles. Even though it is not known how myrmecophilous beetle species discover new ant colonies when they disperse, larger and well-connected colonies may be found more easily and thus they are more likely to be colonised by dispersing myrmecophilous beetles. Interspecific competition over resources could also play a role in determining species richness of myrmecophilous beetles in ant colonies. Small and isolated ant colonies with limited resources can support only a few species, and even if colonisation of isolated colonies were successful, the number of myrmecophilous species in such colonies could be reduced through competitive exclusion. There is yet another plausible hypothesis for the result that large ant

colonies support more diverse myrmecophilous beetle fauna. Most myrmecophilous beetle species, on which such knowledge is available, are xerophilous i.e. they are dependent on dryness (Koch 1989a, 1989b and 1992). In host ants there exists a rather general positive correlation between colony size and nest size (Hölldobler & Wilson 1990). In small nests the environment is not very stable and rain, for example, has a strong effect on the inside humidity of the nest. However, larger nests, such as *Formica* nests, are more stable and their inner layer is dry most of the time. This could contribute to the observed positive relationship between colony size and species richness of myrmecophilous beetles.

Brown (1984) suggested that generalist species will be able to occupy larger geographic ranges because they can tolerate broad environmental spectra. In other words, generalist species have more abundant resources available for them and thus they may be more widely distributed. There was a positive relationship between the distribution of myrmecophilous beetles and the number of host ants they have (II and III). That is, generalist species of myrmecophilous beetles were more widely distributed than specialist species. One contributing factor could be differential colonisation success of generalist and specialist species. If generalist beetle species are more likely to find another suitable ant colony than specialist species, the colonisation success of specialist species may be weaker than that of generalist species leading to the wider distribution of generalist beetles.

Resource concentration hypothesis. More beetle species and individuals occurred in the ant nests of high density, which support resource concentration hypothesis (III). The resource concentration hypothesis predicts that host plant species that occur in high density patches are able to support high species richness of the herbivores because such patches are most likely to be found by the herbivores (Lewis & Waloff 1964, Root 1973, Goncalves-Alvim & Fernandes 2001). Furthermore, populations are more likely to occur in well-connected habitat patches in accordance with metapopulation theory (Hanski 1994, 1999, Gonzalez et al. 1998, Roslin 2000). However, it is not known how myrmecophilous beetle species discover another ant colony when they disperse. One explanation for the result could be that myrmecophilous beetles find another ant colony more or less randomly, and isolated nests are found rarely.

Many myrmecophilous beetles occur on the trails of ants (Hölldobler & Wilson 1990). Ants may carry their eggs, larvae, pupae and adult workers between nests along trails (Hölldobler & Wilson 1990). It is possible that they also accidentally carry myrmecophilous beetles of different developmental stages between nests. If a nest is isolated, this dispersal pattern becomes impossible. Thus, ant trails between the nests can work as dispersal corridors for some myrmecophilous beetles. However, nest isolation does not create a dispersal barrier for the beetle species with good flying ability.

3.3 Distribution-abundance relationship of butterflies

Although the positive relationship between the local abundance and regional distribution of species has been referred to as almost universal pattern in ecology (Hanski 1982, Brown 1984, Hanski et al. 1993, Gaston et al. 1997b, Gaston & Blackburn 2000), a strong negative relationship was found for the Finnish butterflies (IV). Negative correlations seem most likely when the habitat in which species' abundances are measured (the "reference habitat") differs markedly from the spectrum of habitats or the most common habitat in the geographical region of interest (Adams & Anderson 1982, Schoener 1987; but see Schoener 1990, Gaston & Lawton 1990, Ford 1990, Novotny 1991). However, in the study, the abundances of the butterflies were measured almost in all habitats, which are suitable for butterflies. Thus, the observed negative abundance-distribution pattern is likely to be a consequence of something else.

Range position. Gaston et al. (1997b) argue that the range position hypothesis cannot generate negative distribution-abundance relationship because species would need both higher levels of local abundance and higher levels of occupancy nearer to their range edge to create such relationship. The results (IV) strongly disagree with Gaston et al. (1997b) because species would need only higher levels of local abundance nearer to their range edge to create negative distribution-abundance relationship. Location of study area could explain this: Finland is edge area for the distribution of many butterfly species in Europe (see Higgins & Riley 1980). Furthermore, the abundances of butterfly species generally decrease towards north in Finland, that is, the local abundances are highest in southern Finland. Respectively, regional distribution is limited among species, which occur only in southern Finland.

Niche breadth. The niche breadth hypothesis predicts that a positive interspecific distribution - abundance relationship arises because species that are able to use a broader range of resources are widespread but also more abundant (Brown 1984). There is evidence for the positive relationship between niche breadth and distribution (Thomas & Mallorie 1985, Hanski et al. 1993, Hodgson 1993, Dennis & Shreeve 1996, 1997, Gaston et al. 1997b, Quinn et al. 1998, Dennis et al. 2000) but it is difficult to see why wider niche breadth should necessarily lead to higher local abundance (Gaston et al. 1997b). Many published studies on niche breadth have failed to document a positive interspecific relationship between niche breadth and abundance (see Gaston et al. 1997b, Cowley et al. 2001b). In fact, most studies summarized in Gaston et al. (1997b) show negative although not statistically significant slope between niche breadth and abundance (see also Cowley et al. 2001b). In the study of Finnish butterflies (IV) distribution of species was strongly positively related to adult habitat breadth and to the number of larval host plants, but more interestingly both variables were significantly negatively related to abundance. The negative distribution - abundance relationship may be caused by differences in the niche breadth: habitat specialist species and monophagous species are more abundant

but have smaller distribution than habitat generalist species and polyphagous species leading into negative distribution - abundance relationship. Based on the available empirical evidence it seems that the relationship between distribution and niche breadth is generally positive (Thomas & Mallorie 1985, Hanski et al. 1993, Hodgson 1993, Dennis & Shreeve 1996, 1997, Gaston et al. 1997b, Quinn et al. 1998, Dennis et al. 2000). If this hypothesis is accepted, and the distribution - abundance relationship is dependent on niche breadth in the first place, then the form of the relationship is determined by the relationship between abundance and niche breadth; in the study of Finnish butterflies (IV) this relationship was negative leading into negative distribution - abundance relationship.

Mobility. According to metapopulation theory, differences in mobility of species may generate negative distribution - abundance relationships (Gyllenberg & Hanski 1992, Hanski et al. 1993, Hanski 1999). If for any reason species differ in their mobility and mobility has a positive effect on distribution but a negative effect on density, a negative distribution - abundance relationship will result. The strong positive relationship between mobility and distribution and a strong negative relationship between mobility and abundance of the Finnish butterflies was observed (IV), which support earlier studies in butterflies (Cowley et al. 2001a, Brändl et al. 2002). That is, sedentary butterfly species have the highest abundance but lowest distribution while mobile species have the lowest abundance but highest distribution leading into the observed negative relationship between butterfly distribution and abundance.

3.4 Life history of butterflies

The effect of niche breadth, resource availability and range position on mobility. Niche breadth, resource availability and range position all had an effect on butterfly mobility (V). The two measures of niche breadth, larval feeding specificity and adult habitat breadth, indicate that species that are more specialised i.e. have more narrow niche breadth, are less mobile. Resource availability had a similar effect: species with low resource availability, measured as resource distribution or as resource abundance, were less mobile than species with high resource availability. Finally, range position affected the mobility of species such that species that were the closest to the edge of their geographical range were the least mobile. These results lend direct support to Shreeve's (1992) hypothesis that monophagous butterfly species should rarely move outside the habitat patch in which their larval food resources are located while species with less specialized requirements may be more mobile (but see Hanski & Kuussaari 1995).

Restricted niche breadth, low resource availability and being on the edge of geographical distribution range are all likely to increase the dispersing

individuals hazard of not finding a new suitable habitat patch. If mobility is at least partially determined by additive genetic variance, and dispersing individuals do not enjoy reproductive success due to their unsuccessful location of a new habitat patch, there will be strong selection against high mobility (Hamilton & May 1977, Ahlroth 1999). Such negative selection could be responsible of the observed pattern of low mobility among specialist and edge species.

The effect of niche breadth, resource availability and range position on length of flight period. Niche breadth and range position had an effect on the length of the flight period while resource availability did not seem to have an effect (V). From the two measures of niche breadth, larval specificity had no main effect while adult habitat breadth had a positive effect on the length of the flight period. Interestingly, however, length of the flight period was influenced by an interaction between larval specificity and adult habitat breadth: the most specialised species in terms of their larval feeding specificity which at the same time were habitat generalists as adults had the longest flight period. Range position had an effect of flight period such that species the closest to the edge of their geographical range had the shortest flight period.

Length of the flight period of a butterfly species can reflect the average longevity or life span of an individual or variance in the timing of hatching. Accurate information on adult longevities in wild populations of butterflies is extremely difficult to obtain. However, based on mark and recapture studies, the average residence time for many butterfly species has been estimated to be less than 10 days (see the review in Warren 1992). Because of dispersal, residence time based on mark and recapture studies is likely to be an underestimate of the adult life span. However, as there seems to be no relationship between residence time (data from Warren 1992) and our estimate of butterfly mobility, residence time may be used as an unbiased, albeit, underestimate of adult life span. In our data the average length of adult flight period was about four weeks. Thus, it is likely that the length of the flight period is more determined by hatching asynchrony than adult life span.

The result that species with narrow niche breadth had shorter flight period than species with wide niche breadth (see also Pollard et al. 1986, Garcia-Barros 2000) may be explained by the lower environmental variance in growth conditions resulting into lower variance in hatching synchrony. Similarly, the result that species closer to the edge of their distribution range have shorter flight period (see also Pollard 1991), may be more readily explained by hatching synchrony than the adult life span. Provided that the number of suitable habitat patches, and thus distribution of a given species, decline towards the edge of the species range (e.g. Brown 1984, Thomas et al. 1998, 1999, IV), the environmental variation on hatching synchrony is likely to be less at the edge of the distribution range than at the centre of the distribution range.

The effect of niche breadth, resource availability and range position on body size. No evidence after phylogenetic controlling was found that the body size of the butterflies would be influenced by any of the three factors studied, corroborating the results by Garcia-Barros (2000).

4 CONCLUSIONS

The study suggests that ant colonies maintain species rich beetle fauna in Fennoscandia and Denmark (I). Furthermore, the hypotheses predicting species richness of plants and herbivores turned out to be useful when studying ants and myrmecophilous beetles. The results from the study of myrmecophilous beetles provide support for the resource distribution, resource size, resource abundance and resource concentration hypotheses in defining the species richness, distribution and abundance of myrmecophilous beetles (II-III). In the future, attention should be focused on studying the dispersal of myrmecophilous beetle species. Without the knowledge of dispersal of myrmecophilous beetle species, for example, the connections to metapopulation theory are difficult to draw.

Distribution – abundance relationship of Finnish butterflies was observed to be negative (IV). The study suggests that at least the range position, the niche breadth and mobility mechanisms could explain the negative distribution-abundance relationship on Finnish butterflies. The main reason for negative relationship could be the northern location of the study area: Finland is edge area for many butterfly species. The results show that Brown's (1984) niche breadth hypothesis could generate negative rather than positive distribution-abundance pattern. The negative distribution-abundance pattern could be a more common phenomenon than previously expected, but the rarity of the negative pattern in many other studies may be a straight consequence of too small sample size. That is, in many studies, rare species are lacking, when abundance data are collected by transect counts.

Niche breadth, resource availability and range position play also an important role in determining the mobility of butterflies (V). Shorter flight period in the species with narrow niche breadth and in the species at the edge of their distribution range is likely to represent differences in hatching synchrony due to lower environmental variance in their growth conditions. The studies on the relationships between species specific ecological variables and life-history characteristics in a distribution - abundance relationship framework are needed to able us to understand the ultimate factors driving any particular

distribution - abundance relationship. In Finnish butterflies there is an unusual negative distribution - abundance relationship which is likely to be partially driven by the differences in butterfly mobility (IV). Thus, explaining the variance in butterfly mobility may aid in explaining the variance in distribution - abundance relationships.

Several butterfly and beetle species are threatened in the northern Europe (Kotiranta et al. 1998). Therefore, much more attention should be focused on the study of the basic ecology of butterflies and beetles. The significance of the knowledge of basic ecology of species will grow in the future, because the need to evaluate the threat status of species will increase.

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YHTEENVETO

Perhosten ja muurahaispesissä elävien kovakuoriaisten levinneisyys, runsaus ja lajistollinen monimuotoisuus

Eliöiden levinneisyyttä ja runsautta voidaan tarkastella paikallisella, alueellisella ja maantieteellisellä tasolla. Viime aikoina tutkimus on keskittynyt erityisesti alueellisen levinneisyyden ja paikallisen runsauden välisen vuorovaikutuksen aiheuttavien biologisten tekijöiden selvittämiseen. Tutkimuksissa on havaittu, että paikallisesti runsaslukuiset lajit ovat laajalle levinneitä, kun taas paikallisesti harvalukuisten lajien levinneisyys on rajoittunut. On kuitenkin havaittu, että joissain erikoislaatuissa tilanteissa suhde voi myös olla negatiivinen. Alueellisen levinneisyyden ja paikallisen runsauden välisen riippuvuussuhteen aiheuttajiksi on esitetty useita biologisia mekanismeja.

Biologista monimuotoisuutta voidaan kuvata lajistollisena monimuotoisuutena. Lajistolliseen monimuotoisuuteen, kuten myös levinneisyyteen ja runsauteen vaikuttavia tekijöitä on tutkittu erityisesti kasvinsyöjillä. Kasvinsyöjien joukossa on erinomaisia tutkimuskohteita, joiden esiintyminen riippuu tiettyjen kasvilajien esiintymisestä. Neljää hypoteesia on kirjallisuuden mukaan ehdotettu selittämään eliöiden levinneisyyttä. Hypoteesien mukaan resurssi, joka on laajalle levinnyt, isokokoinen, monipuolinen tai esiintyy tiheässä, voi ylläpitää monilajista eliölajistoa.

Päiväperhoset ovat kasvinsyöjähyönteisistä ehkä tunnetuimpia. Koska monet päiväperhoset on helppo tunnistaa ja niitä on helppo havainnoida, niiden levinneisyys ja runsaus tunnetaan paremmin kuin monien muiden hyönteisryhmien. Koska päiväperhoset ovat toukkana riippuvaisia tietyistä resurssista eli kasveista, ne tarjoavat erinomaisen tutkimuskohteen tutkittaessa levinneisyyteen ja runsauteen vaikuttavia tekijöitä.

Toinen selkeästi tiettyyn resurssiin erikoistunut eliöryhmä ovat muurahaispesissä elävät hyönteiset. Osa muurahaispesistä tavattavista eliöistä luokitellaan varsinaisiksi muurahaisvieraksi eli myrmekofiileiksi. Nämä muurahaisvieraat ovat riippuvaisia jossakin elämänsä vaiheessa jonkin tai joidenkin muurahaislajien läsnäolosta. Tämän vuoksi muurahaisvieraat ovat kasvinsyöjien ohella erinomainen tutkimuskohde tutkittaessa lajien levinneisyyteen, runsauteen ja monimuotoisuuteen vaikuttavia tekijöitä.

Tässä tutkimuksessa käytettiin tutkimuslajeina päiväperhosia sekä muurahaisvieraskovakuoriaisia. Osatutkimuksessa I selvitettiin kirjallisuuteen ja maastohavaintoihin perustuen, mitä kovakuoriaislajeja on havaittu muurahais-ten seurasta Pohjois-Euroopasta. Osatutkimuksissa II ja III selvitettiin kirjallisuuteen ja maastotöihin perustuen, mitkä tekijät vaikuttavat muurahaisvieraskovakuoriaisten levinneisyyteen, runsauteen sekä lajistolliseen monimuotoisuuteen. Kirjallisuustietoihin perustuen osatutkimuksessa IV puolestaan selvitettiin alueellisen levinneisyyden ja paikallisen runsauden väliseen suhteeseen vaikuttavia biologisia mekanismeja Suomesta tavattavilla päiväperhoslajeilla.

Näiden mekanismien vaikutusta päiväperhosten ekologiaan tutkittiin osatutkimuksessa V.

Osatutkimuksen I mukaan Suomessa, Ruotsissa, Norjassa ja Tanskassa elää muurahaisten seurassa melkein 400 kovakuoriaislajia. Määrä on todella huomattava, sillä se käsittää noin 7 % alueen kovakuoriaisten kokonaislajimäärästä. Luultavasti ainakin osa kovakuoriaisista on tavattu muurahaispesistä satumalta, sillä ainoastaan 73 lajia on luokiteltu muurahaisvieraiksi. Toisaalta muurahaispesistä tavattavien kovakuoriaisten ekologia on puutteellisesti tunnettu, joten on mahdollista, että muurahaisista riippuvaisia lajeja on huomattavasti luultua enemmän. Osatutkimuksessa II havaittiin, että laajalle levinneiden ja isoja pesiä rakentavien muurahaislajien pesissä elää enemmän kovakuoriaislajeja. Osatutkimuksessa III puolestaan havaittiin, että tiheässä sijaitsevissa muurahaispesissä on eniten kovakuoriaislajeja. Syynä voi olla se, että kovakuoriaiset löytävät todennäköisimmin isot, laajalle levinneet ja lähekkäin olevat pesät. Isot pesät voivat tarjota myös enemmän resursseja kovakuoriaisille.

Päiväperhoslajien, jotka ovat erikoistuneita, huonosti liikkuvia sekä elävät elinalueensa reunalla, havaittiin olevan paikallisesti runsaslukuisia, mutta suppealle alueelle levinneitä (IV). Vastaavasti päiväperhoslajien, jotka ovat generalisteja ja liikkuvat paljon, sekä lajien joiden elinalue kattaa suurimman osan Suomesta, havaittiin olevan keskimäärin paikallisesti harvalukuisia, mutta laajalle levinneitä. Tämä saattaa aiheuttaa tutkimuksessa suomalaisilla päiväperhosilla havaitun vahvan negatiivisen riippuvuussuhteen alueellisen levinneisyyden ja paikallisen runsauden välillä. Osatutkimuksessa V taas havaittiin, että päiväperhoslajin erikoistuminen ja toukan ravintokasvin levinneisyys ja runsaus vaikuttavat päiväperhoslajin liikkuvuuteen. Syynä voi olla se, että luonnonvalinta karsii liikkuvat yksilöt pitkälle erikoistuneiden päiväperhoslajien populaatioista, koska levittäytymään lähtenyt yksilö ei välttämättä löydä tiettyä yksittäistä resurssia, esim. tiettyä toukan ravintokasvilajia.

Muurahaispesissä elävien kovakuoriaisten tutkiminen tulevaisuudessa on tärkeää, koska tämän monilajisen eliöryhmän ekologia on puutteellisesti tunnettu. Havaittu negatiivinen riippuvuussuhde päiväperhosilla alueellisen levinneisyyden ja paikallisen runsauden välillä on ainutlaatuinen, ja on syytä selvittää, esiintyykö samanlaista riippuvuussuhdetta muilla eliöryhmillä vastaavissa olosuhteissa. Koska monet kovakuoriais- ja päiväperhoslajit ovat uhanalaisia, niiden levinneisyyteen, runsauteen ja lajistolliseen monimuotoisuuteen vaikuttavien tekijöiden selvittäminen on erittäin tärkeää. Tämän väitöskirjatutkimuksen tulokset voivat osaltaan olla tukemassa päätöksiä, joissa määritellään lajien uhanalaisuutta levinneisyyteen ja runsauteen perustuen, sekä määriteltäessä puutteellisesti tunnettujen eliöryhmien tutkimustarpeita.

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