Hotspots of Insect Diversity in Boreal Forests

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Abstract: *Insect diversity patterns in boreal forests are largely unknown, and many specific microhabitats have been overlooked in the past. I reviewed some of the evidence on species richness, host specificity, and rarity of insects confined to one such specific microhabitat, namely the fruiting bodies of wood-decaying macrofungi. I concluded that the insect communities occurring within the fruiting bodies are rich in species, many of which show preference for a specific fungal host. The relatively high number of rare insect species underscores the importance of fungal fruiting bodies for biodiversity maintenance in boreal forests. In the light of this importance and the fact that fruiting bodies occur as distinct, species-rich islands in the boreal forest landscape, I suggest that the fruiting bodies of wood-decaying macrofungi can be considered hotspots of insect diversity. Because many forest insects are negatively affected by forestry, practical forest management should pay more attention not only to fungal fruiting bodies but also to other similar microhabitats.*

Áreas de Importancia para la Diversidad de Insectos en Bosques Boreales

Resumen: *Los patrones de diversidad de insectos en bosques boreales son prácticamente desconocidos, y muchos microhábitats específicos no se han estudiado en el pasado. Revisé datos sobre riqueza de especies, especificidad de hospedadores y rareza de insectos confinados a un microhábitat específico, es decir los cuerpos fructíferos de macrofungi de madera podrida. Concluí que las comunidades de insectos en los cuerpos fructíferos son ricas en especies, muchas de las cuales muestran preferencia por un hospedador fungoideo específico. El número de insectos raros relativamente alto acentúa la importancia de los cuerpos fructíferos para el mantenimiento de la biodiversidad en bosques boreales. En base a lo antedicho y considerando el hecho de que los cuerpos fructíferos ocurren como islas distintas, ricas en especies, en el paisaje del bosque boreal, sugiero que los cuerpos fructíferos de macrofungi de madera podrida pueden ser considerados como áreas de importancia para la diversidad de insectos. Debido a que muchos de los insectos de bosque son afectados negativamente por la explotación forestal, el manejo forestal práctico debería prestar mayor atención no solo a los cuerpos fructíferos de los hongos sino también a otros microhábitats similares.*

Introduction

Fennoscandian boreal forests are among the best-studied regions in the world, with a history of research dating back to the days of Carl von Linné in the eighteenth century. Yet biodiversity patterns in boreal forests remain largely unknown, and even less is known about the specific ecological requirements of individual species (Haila 1994). The great diversity of species confined to decaying wood in boreal forests has been acknowledged (Hanski & Hammond 1995). Although decaying wood is undeniably a key resource for thousands of organisms (Siitonen 2001), related issues have so strongly dominated the science, as well as forest conservation and management in the boreal region, that many other components of forest biodiversity have been overlooked.

Only recently, for example, the nest mounds of ants have been identified as hotspots for litter-dwelling earthworms (Laakso & Setälä 1997), and 37 of the 369 ant-associated beetle species recorded in Fennoscandia and Denmark can be classified as myrmecophilous (species dependent on ants) (Päivinen et al. 2002). And there are other important but ignored microhabitats. I sought to further dissect the biodiversity of boreal forests and to discuss insect diversity in the fruiting bodies of wood-

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decaying macrofungi. The material for this article comes mainly from Fennoscandia, because very little research has been conducted in boreal forests elsewhere or in other forest biomes. Hence, I hope that this article further promotes research on the biodiversity of this key microhabitat. I use the term *biodiversity* to denote species richness, especially that of rare and ecological specialists.

Unknown Microhabitat

By definition, insects inhabiting wood-decaying fungi or fungal mycelia in dead wood have often been clumped together with other species associated with dead and decaying wood (e.g., Speight 1989). Although this may have been practical in many cases, I believe that such oversimplified definitions have been partly responsible for concealing insect communities in fruiting bodies from wider scientific interest. Globally, few ecological studies were conducted on insect communities in wood-decaying fungi before the 1990s (but see, for example, Paviour-Smith 1960; Pielou & Verma 1968; Fig. 1). Recent studies have predominantly focused on species composition and community structure (e.g., references in Table 1). Furthermore, the two related fungus beetles, *Bolitophagus reticulatus* in Europe and *Bolitotherus cornutus* in North America, have received a great deal of attention (Conner 1988; Whitlock 1992; Nilsson 1997; Rukke & Midtgaard 1998; Sverdrup-Thygeson & Midtgaard 1998; Kehler & Bondrup-Nielsen 1999).

It is somewhat surprising that the fungal-insect systems have not interested ecologists more, as have plant-herbivore interactions, for instance. This difference may be due to the economic importance of herbivory on the one hand and problems in identifying fungi and fungivores on the other (Hanski 1989). Wood-decaying macrofungi are by no means a marginal species group, however, as there are about 1500 species in Fennoscandia (Siitonen 2001), and they play an important role in forest ecosystems as parasites and decomposers of wood (Swift 1982). Furthermore, ecologists are often faced with problems in delineating their study units in a biologically meaningful way. Because fungal fruiting bodies harbor compact, natural units of insect populations and communities, they should be an attractive choice for studying a variety of ecological questions. Yet the insect fauna of only 1% (15 spp.) of the wood-decaying macrofungal species recorded in Fennoscandia has been studied in detail (Økland 1995; Fossli & Andersen 1998; Jonsell 1999; Komonen 2001). The best-studied wood-decaying fungi are the bracket fungi (Polyporaceae; approximately 200 spp.), and the following discussion concerns these species only, unless otherwise stated. At present, it is difficult to evaluate how well the patterns of species richness and host specificity of insects in bracket fungi, for example, apply to the other wood-decaying fungi.

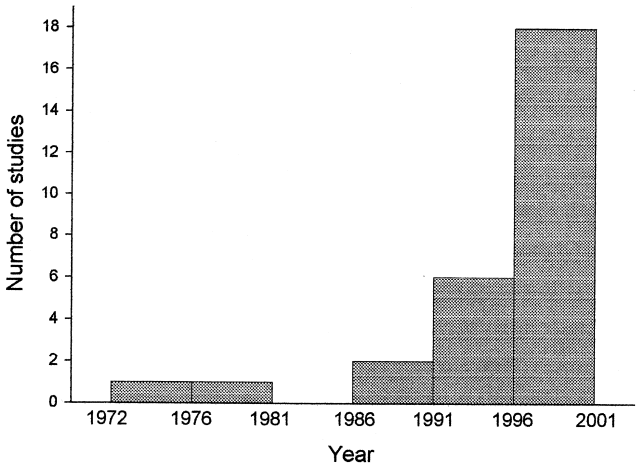

Figure 1. Number of studies (1972–2001) on insects inhabiting bracket fungi. Data from CAB Abstracts that contain key words fungivo*, polypor*, *and* bracket fung* *with English in language specification. Journal articles on systematics and notes on species are not included.*

Species Richness

Beetles and flies are the most conspicuous and species-rich invertebrates directly dependent on dead wood or wood-decaying fungi. They comprise up to 1000 species each in these microhabitats in Fennoscandia (Siitonen 2001). Nevertheless, the literature on the microhabitat preferences of dead-wood associated insects, even the well-known beetles, is patchy and based on circumstantial observations rather than on quantitative studies (Jonsell et al. 2001). In a comprehensive review of beetles associated with all kinds of fungi in the boreal region, Benick (1952) listed 1116 species, of which 202 were considered "truly" fungivorous, 767 entirely accidental, and 147 species intermediate. More specifically, Ehnström (1999) calculated that 61 of the 380 beetle species recorded from Scots pine in Sweden are dependent on fungal mycelium, and 46 are connected with the fruiting bodies of fungi, mainly the bracket fungi. However, estimates of the number of species actually confined to fungal fruiting bodies, especially taxa other than beetles, can be only very rough at best, and many species may prove to have a more than casual association, although evidence for obligate mycophagy is lacking presently (Hammond & Lawrence 1989).

A fungal fruiting body—a microhabitat that often fits neatly in the hand—can harbor surprisingly large populations of many fungivorous species (e.g., Pielou & Verma 1968; Komonen 2001): hundreds of individuals

Table 1. Some studies on insect communities occurring within bracket fungi in boreal forests.

Fungal species	*Country*	*Total species (individuals)*	*Specialist species*[a]	*Rare species*[b]	*Reference*
Fomitopsis pinicola	Norway	36 (12,373)[c]	5	6	Thunes et al. 2000
	Sweden	27 (23,700)	4	4	Jonsell et al. 2001
Fomes fomentarius	Sweden	31 (26,400)	6	5	Jonsell et al. 2001
	Norway	43 (1751)[c]	3	?	Thunes 1994
	Canada	133 (5242)	?	?	Matthewman & Pielou 1971
Piptoporus betulinus	Norway	37 (515)[c]	0	?	Thunes 1994
	Canada	172 (21,213)	?	?	Pielou & Verma 1968
Fomitopsis rosea	Finland	53 (533)	1	4	Komonen 2001
Amylocystis lapponica	Finland	60 (2273)	1	5	Komonen 2001

[a] *Species with a strong preference towards one host fungus, although they may be encountered in small numbers from other fungal species; only primary fungivores are included.*
[b] *Rare species refer to species on national red lists, new records from the given country, or to species classified as rare nationally in other written sources. Specialist and rare species are not mutually exclusive categories.*
[c] *Only beetles.*

can be regularly encountered in a single fruiting body. Although larger samples of fruiting bodies of one fungal species typically yield about 50 insect species, up to 170 have been recorded (Table 1). The record, summing up observations from a large number of independent studies, is held by *Polyporellus squamosus*, for which Benick (1952) lists 246 species of beetles. Many species-rich insect groups, such as wasps and flies, are often not identified to species level, making the total number of species considerably larger than the figures given above. The noninsect arthropods, which constituted 33% of all species and 57% of all individuals in a comprehensive study by Pielou and Verma (1968), have been ignored almost completely.

Similar to that of many other biotic communities, species richness in fungal-insect communities is promoted by the spatial aggregation of species and their specialization in resource exploitation (Toda et al. 1999; Wertheim et al. 2000). Some species prefer either living or dead fruiting bodies, some consume spores or microorganisms growing on the fruiting bodies, and some are predators or parasitoids. The core of fungal-insect communities is formed typically by two to four co-occurring primary fungivores, which are often but not always taxonomically related (Thunes 1994; Fossli & Andersen 1998; Jonsell et al. 2001; Komonen 2001). Yet there is little direct or indirect evidence of interspecific competition between the fungivorous insects (but see Thunes 1994). Whether this is a real phenomenon rather than a consequence of bias in research remains to be explored. The relationships between trophic levels are better documented, especially host-parasitoid interactions, because predators in the fungal-insect systems are not abundant (Jonsell 1999; Komonen 2001). To better understand species diversity in the fruiting bodies of wood-decaying fungi, more emphasis should be placed on research on the relationship between species interactions and community structure.

Host Specificity

Of the forest invertebrates in Fennoscandia, the distribution and general habitat requirements of beetles are well known (Saalas 1917, 1923; Palm 1951, 1959). Many species have been recorded as being associated with fungus-infected trees, fungal mycelia, or fruiting bodies (Palm 1951, 1959). These records have been largely based on indirect evidence, however, and the detailed ecology—especially the host preference of most of the species—has remained spurious (Jonsell et al. 2001). This may have given the impression that fungivorous insects are more generalist in terms of their host specificity than they actually are (see also Hanski 1989).

By collecting the fungal fruiting bodies for laboratory rearing, researchers have been able to specify and quantify many previous observations of fungal-insect relationships. Consequently, the distinction between the obligate mycetophages and the other users of fruiting bodies has become clearer, as has their host-fungus preference. Jonsell et al. (2001) designated as monophagous 31% and 35% of the primary fungivorous species reared from *F. pinicola* and *F. fomentarius*, respectively. Also, the fruiting bodies of one fungal species share very similar insect fauna over large geographical areas (i.e., among the Fennoscandian countries), whereas those of other fungal species are dissimilar. This further supports the relatively high host specificity of many fungivorous insects (Økland 1995; Jonsell 1999; Komonen 2001). Even ecologically and taxonomically related fungal species may host almost completely different fauna, even if their fruiting bodies often co-occur on fallen logs (Komonen 2001). Furthermore, most primary fungivores are associated with parasitic wasps and flies, many of which are extremely host-specific (Jonsell 1999). This host specificity of the primary fungivores and their parasitoids is important because species that are specialists in terms of their microhabitat preferences are often con-

sidered more prone to extinction than habitat generalists (e.g., Schoener 1989; Pimm 1991) and thus more likely to be negatively affected by forestry.

Rare Species

Of the threatened and nearly threatened forest-dwelling beetles in Finland, 75% are dependent on dead-wood habitat, including fungal fruiting bodies and mycelia (Rassi et al. 2001). The trend is similar in other parts of Fennoscandia (Ehnström et al. 1993; Hanssen et al. 1997). Many of the fungivorous insects that have been encountered from fruiting bodies in recent studies represent new records for the given country, classified as rare nationally or included on national red lists (Jonsell 1999; Thunes et al. 2000; Komonen 2001; Table 1). This may indicate that these species are truly rare or that they are just poorly studied. In those studies where the authors indicated the nationally rare species, these constituted 8–17% of the total number of species (Table 1). Given that the two species-rich groups, wasps and flies, have not been identified to species level, these figures suggest that up to 20% of the species in fungal-insect communities can be considered rare and that these systems therefore have a high species- and biodiversity-conservation value. In his studies, Økland (1994) found further support for the importance of dead wood and unlogged forests to fungus gnats and suggested that many species of this poorly known group are potentially rare.

Insects associated with bracket fungi also represent a high proportion of all threatened species: 13% of beetles in the proposed Norwegian Red List, for example (Thunes et al. 2000). Although this figure is low in comparison with species directly dependent on decaying wood, it is rather high for an insect group that lives in such a specific microhabitat. On the other hand, given that our knowledge of fungal-insect communities is limited, many of the species considered dependent on decaying wood may actually be confined to fungal fruiting bodies or the mycelia of a specific fungal host (Kaila et al. 1994; Jonsell 1999). The relatively high proportion of rare species in fungal-insect communities may reflect the inherent rarity of species that live in a specific, patchily distributed resource, or their extinction proneness (Jonsell 1999; Komonen et al. 2000).

Forestry and Fungivorous Insects

Decaying wood is crucial for many forest species, including wood-decaying fungi (Esseen et al. 1997). In the managed forests that so dominate the landscape in Fennoscandia, decaying wood is scarce and, consequently, about one-fourth of the bracket fungi are threatened (Rydin et al. 1997; Rassi et al. 2001). Even common species have considerably lower densities in managed than in the old-growth forests (e.g., Lindblad 1998). Thus, it is no surprise that the amount of decaying wood in a forest stand is also a good predictor of the diversity of fungus-dwelling insects (Økland 1994; Jonsell 1999; Thunes et al. 2000). There are two reasons particularly important in explaining why some rare insect species are absent from the managed forests: (1) these species require old-growth forest because of their specialization on fungal species that occur primarily in old-growth forest (e.g., the moth *Agnathosia mendicella*; Komonen 2001), or (2) these species occur in common fungal species but only when the fungi are growing in mature managed or old-growth forest (e.g., the beetle *Cis quadridens*; Jonsell & Nordlander 2002). Species in the latter group may, for example, require a high density of fruiting bodies to maintain viable populations in the long run, and densities of this size are available only in the old-growth forests at present (Jonsson et al. 2001). However, naturally high amounts of dead wood were available after stand-replacing disturbances, such as forest fires and storms. The old-growth forest beetle *Oplocephala haemorrhoidalis*, for instance, can actually survive in fruiting bodies in sun-exposed sites (Palm 1959), but it requires continuity of dead wood and fungal fruiting bodies (Jonsson et al. 2001), rather than old-growth forests as such.

Not only the loss of old-growth forest but also the fragmentation of the remaining forests have negative impacts on populations of the most specialized fungivorous insects. Species have been reported to have a lower incidence and/or abundance in small, old-growth forest islands than in larger stands (Rukke & Midtgaard 1998; Jonsell et al. 1999; Kehler & Bondrup-Nielsen 1999; Komonen et al. 2000). The results of these studies suggest that the density of the fruiting body and the area and spatiotemporal isolation of the forest fragment are all important, the underlying reason being the limited dispersal ability of the fungivorous species (Jonsell et al. 1999; Jonsson et al. 2001). On the other hand, there is one obvious pitfall, specific to fungal-insect systems, in the interpretation of the typical presence/absence snapshot data. About one-fifth of the bracket fungi are perennial, and their fruiting bodies may last for decades. Therefore, their presence in a particular forest fragment does not necessarily indicate that the fungal population is viable or that there is an adequate density of fruiting bodies to support viable populations of fungivorous species in the long term.

Recognizing microhabitats that harbor high biodiversity, such as the fungal fruiting bodies, also has practical implications for boreal forest management. For example, indicator species are often used in the evaluation of forest conservation values (e.g., Kotiranta & Niemelä 1996). When P. Martikainen and J. Kouki (in press) analyzed the existing data on beetle surveys in Finland, they found a positive, exponential relationship between the

number of species sampled and that of the threatened species. Due to practical constraints, however, in virtually none of the studies did researchers reach the threshold sample size after which the number of threatened (or indicator) species encountered increased greatly. In comparison, relatively small samples of fruiting bodies comprise a high number of species, including those considered useful as indicators. Thus, in addition to the other sampling methods (e.g., window trapping) currently used in forest insect surveys, the sampling of specific insect microhabitats, such as the fruiting bodies of bracket fungi, could give a better overall estimate of insect diversity in a given forest stand.

Conclusions

Although the boom in research on fungal-insect communities during the past decade has provided new insights into the insect diversity patterns in boreal forests, few studies have been conducted in other forest biomes (but see, for example, Paviour-Smith 1960; Klimaszewski & Peck 1987), and much still remains to be discovered, especially concerning the tropical species. As is the case for other patchily distributed resources, such as dung pats or carcasses, fungal fruiting bodies offer excellent opportunities to answer many interesting questions concerning ecologically and taxonomically related species (e.g., Jonsson et al. 2001). The direct dependence of fruiting bodies on decaying wood makes them, and their associated insects, of great importance in maintaining biodiversity in boreal forests and thus relevant to practical forest management. In addition, fruiting bodies not only provide food and shelter for the insects, but the odors from the fruiting bodies can function as cues in mate finding (Jonsson et al. 1997). The fruiting body is only the "tip of the ice-berg," however, because the mycelia of the fungus regulates the decomposition of wood and thus makes it suitable for a variety of invertebrates. In fact, many insect species living in dead wood may actually depend on wood-decaying fungi as specifically as the species that live in the fruiting bodies, even though they use the fungal mycelia and rot specific to a particular fungal species (Kaila et al. 1994; Jonsell 1999).

Biodiversity hotspot is a relative concept dependent on the scale and taxa in question. It has often been used to denote a biogeographical region that hosts many endemics and a higher species diversity than other adjacent regions (World Conservation Monitoring Centre 1992). Within each biogeographical region, ecosystem, or habitat there are certainly smaller areas or (micro) habitats that have a higher species diversity than the surrounding matrix. Following this logic, Laakso and Setälä (1997) used the term simply as a synonym for the higher abundance and diversity of earthworms in ant mounds than in the surrounding forest soil. Ant mounds certainly appear as distinct spots in the relatively homogeneous boreal forest landscape. Similarly, given the evidence I have discussed in this paper, the fruiting bodies of wood-decaying fungi can be considered hotspots of insect diversity. In boreal forests, as well as in other forests around the world, there are almost certainly similar high-diversity microhabitats that have been overlooked in the past. To understand forest biodiversity patterns, we must conduct more baseline studies of its components, especially in high-diversity hotspots.

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