Distribution and abundance of insect fungivores in the fruiting bodies of *Fomitopsis pinicola*

Atte Komonen

Faculty of Forest Sciences, University of Joensuu, P.O. Box 111, FIN-80101 Joensuu, Finland (e-mail: atte.komonen@joensuu.fi)

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This paper describes patterns of distribution and abundance of insect fungivores inhabiting the polypore *Fomitopsis pinicola*. I sampled fruiting bodies of the polypore from nine old-growth forest sites in southern Finland. Most species encountered in the present study were rare and only a few species were abundant and widely distributed among the fruiting bodies and study sites. Feeding guild and host-fungus specificity were the best predictors of species abundance and distribution in the fruiting bodies in that obligate fungivores, and *F. pinicola* specialists were more common than generalists, facultative fungivores and parasitoids. Two specialist beetles on *F. pinicola*, *Cis glabratus* and *C. quadridens* (Cisidae), constituted over 78% of all individuals in the pooled sample. *Cis quadridens*, an old-growth forest species, had lower abundance and frequency of occurrence in the fruiting bodies than *C. glabratus*, which is a common species also in managed forests.

Introduction

Insect species assemblages, or communities, occurring within patchily distributed resources have gained popularity in analyses of spatial population structures (Hanski & Gilpin 1997). The studies have largely focused on ephemeral resources, such as dung pats (Roslin & Koivunen 2001), carrions (Kouki & Hanski 1995), fruits (Atkinson 1985) and mushrooms (Hackman & Meinander 1979, Shorrocks & Charlesworth 1980). These insect-resource systems typically comprise many coexisting, ecologically and taxonomically related species. Despite their relatedness, however, these species can demonstrate variety of distribution and abundance patterns, resulting from differences in resource breadth

or dispersal, for example (Roslin & Koivunen 2001, Jonsson 2003).

Insects occurring within the fruiting bodies of perennial polypores offer a similar kind of insect-resource system. As these insect populations and communities can persist for years in a given fruiting body, the spatial distribution and abundance patterns are potentially different from the short-lived insect populations and communities in ephemeral resources (e.g. mushrooms). It is known that in polypore-dwelling insect assemblages even the taxonomically closelyrelated species within one feeding guild can have different responses to landscape structure. Documented differences exist in species' colonization ability of isolated forest stands and in the frequency of occurrence in areas with different forest management measures (Jonsell *et al.* 1999, Jonsson *et al.* 2001).

Studies on long-lasting communities of polypore-inhabiting insects have focused on species composition, diversity and community structure (Økland & Hågvar 1994, Thunes 1994, Økland 1995, Thunes & Willassen 1997, Thunes et al. 2000, Komonen 2001, Komonen et al. 2001), substrate associations (Nilsson 1997, Fossli & Andersen 1998, Jonsell et al. 2001), extinction and colonization (Whitlock 1992, Jonsson et al. 1997, Jonsell et al. 1999), and spatial variation, especially on the effects of forest fragmentation (Kehler & Bondrup-Nielsen 1999, Sverdrup-Thygeson & Midtgaard 1998, Rukke & Midtgaard 1998, Jonsson et al. 2001, Komonen et al. 2000, Jonsell & Nordlander 2002). Most of these studies have been rather applied an outlook focusing on the impacts of forest management, and general patterns of species distribution and abundance are scarce, although such studies provide the benchmark upon which more applied research can be built.

In this paper, I present results on the distribution and abundance patterns shown by fungivorous insects inhabiting the fruiting bodies of the perennial bracket fungus *Fomitopsis pinicola* (Swartz : Fr.) Karst. (Aphyllophorales: Polyporaceae). I also compare the distribution and abundance of two *F. pinicola* specialist beetles, *C. glabratus* and *C. quadridens*, of which the former is a common species in all kinds of forests, whilst the latter species prefers old-growth forests. Polypore-feeding insects have several advantages for studies of this kind. Most importantly, the community contains an adequate, but not overwhelming, number of species and it is easily delineated and sampled. Also, given the abundance of *F. pinicola* in many kinds of forests, this species is ideal to studies on distribution and abundance patterns of fungivorous insects and could serve as a model system to which insect communities occurring within other patchily distributed resources can be compared.

Material and methods

The fungus

Fomitopsis pinicola is a conspicuous and often the most abundant wood-decaying macrofungus in boreal forests (Ryvarden & Gilbertson 1993). Although the species is common in managed forests, its population density is considerably higher in areas with large amounts of suitable Coarse Woody Debris (CWD), particularly in the oldgrowth forests (Lindblad 1998, and pers. obs.). The fungal fruiting bodies grow predominantly on stumps, snags and downed logs of dead and dying Norway spruce (Picea abies), although it can be found in numerous other tree species. The fruiting bodies of F. pinicola are perennial and there is remarkable variation in their size. the smallest fitting neatly in the hand while the largest can reach a size of about 40 cm in cap diameter (Ryvarden & Gilbertson 1993).

Statistic	Area (ha)	Area sampled ¹	Age ²	Decaying wood ³		<i>F. pinicola</i> /ha⁴
				Spruce	Other	
Mean	114.3	7.8	153.9	67.9	44.1	16.5
Median	50.0	9.0	154.0	49.0	37.0	16.0
SD	179.7	2.5	21.2	46.5	18.6	12.8
Range	3–580	1.3–9.0	125–185	25–174	25–85	5–48

Table 1. Stand characteristics of the nine old-growth forest sites from which fruiting bodies were sampled (data from J. Siitonen *et al.* unpubl. data and Forest and Park Service).

¹ Refers to area from which forest stand characteristics were measured.

²Mean age of ten spruces belonging to the dominant canopy storey.

³ Number of snags and logs per hectare with a diameter ≥ 10 cm at breast height; "Other" includes pine, birch and aspen.

⁴ Number of snags, stumps and logs with living fruiting bodies.

Study area

This study was conducted in southern Finland (61°-62°N, 23°-25°E) in the southern and middle boreal zones (see Ahti et al. 1968). Forests in the region are dominated by Norway spruce on mesic and moist sites, and Scots pine (Pinus sylvestris) on drier sites and pine bogs, with birches (Betula spp.) and aspen (Populus tremula) as the most common admixed deciduous trees (Anon. 1996). The study was conducted in old-growth forests as some of the specialist fungivores on F. pinicola are absent from managed forests. The area of old-growth forests in the study region is about 0.1% of forest land (Anon. 1996), and the remaining fragments are isolated and predominantly less than one hundred hectares in area.

I collected fungal samples from nine oldgrowth forest sites (Table 1). Jonsell and Nordlander (2002) and M. Jonsell (pers. comm.) have shown that the so-called old-growth forest fungivores (species that are associated with *F. pinicola* predominantly in the old-growth forests) are indifferent in terms of stand size and management history, as long as there is plenty of dead wood (*see* also Thunes *et al.* 2000). Thus, differences in the forest stands in the present study possibly add some unexplained variation in the data but this is unlikely to have a great effect on the general conclusions of the present study.

Sampling

I sampled 180 fruiting bodies of *F. pinicola*, 20 from each site, between 15 and 27 May 1999 (Table 1). The fruiting bodies appear visibly on trees and as the forest stands were relatively small in area I was able to cover the entire stand area in sampling; in the largest stand (580 ha, of which large areas are pine dominated), the sample was collected from about 20 ha area. I collected samples haphazardly from spruce stumps and trunks, no more than one fruiting body per trunk. Insects were reared from the fruiting bodies in cloth-covered plastic boxes, which were kept outdoors but were protected from sunshine and rain. I checked the rearings for insects in late September and all the emerged

individuals were preserved; Collembola were not recorded.

Fungal host is the most important variable explaining occurrences of insect species in fruiting bodies (Thunes & Willassen 1997, Fossli & Andersen 1998, Jonsell et al. 2001). Jonsell et al. (2001) further demonstrated that the tree species, stem diameter, sun exposure, stem type and height above ground, size and age of fruiting bodies and their successional stage (dead/living) affect the occurrence of insects associated with F. pinicola. Most fungivores, particularly Cisidae, Tineidae and many dipteran species, occur almost exclusively in dead fruiting bodies. In the present study, all sampled fruiting bodies were growing on Norway spruce, less than 1 m above ground, inside a closed forest, and only dead fruiting bodies with visible marks of insect damage were included. The size distribution and the quality of the fruiting bodies sampled reflected natural variation, although not controlled for statistically.

Nestedness analysis

The magnitude of nestedness between the sample sites is important in offering an estimate of the coherence of the species assemblage. Using the information on species' presenceabsence in the samples, the nestedness analysis provides a measure (T) of order and disorder, or in other words, whether the species compositions of the species-poor samples are proper subsets of the more speciose samples. The metric T ranges between zero for a perfectly nested matrix and 100 for complete disorder (Atmar & Patterson 1993). The metric and its significance based on Monte Carlo-derived probability that matrix was randomly generated was calculated with the Nestedness Calculator (http://aics-research.com/ nestedness/tempcalc.html).

Results

Sampling of 180 fruiting bodies from nine sites yielded 3736 insect individuals of 54 species; 16 individuals of non-fungivorous Diptera and 153 individuals of Cecidomyiidae (Diptera) were not

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Fig. 1. Rarefaction curves for all species (above) and fungivores only (below).



Fig. 3. The frequency distribution of the number of fruiting bodies occupied by the 53 species encountered from *F. pinicola* fruiting bodies (Cecidomyiidae excluded).

identified and these are excluded from analyses. The numerically-dominant guild was the obligate fungivores with 3447 individuals (92.3% of all individuals) and 17 species. Of these, 88.6% (n = 3054) were obligate fungivorous beetles belonging to Cisidae (8 spp.) and Anobiidae (1 sp.).

Due to one numerically-dominant species in all the nine samples (*Cis glabratus* Mellié; Coleoptera: Cisidae) and the high proportion of singletons and doubletons in the samples, the rarefaction curve for all species did not reach asymptote (Fig. 1). When only the 17 obligate fungivorous species were included, the rarefaction curve converged so that a sample of a hundred fruiting bodies harbored 91% of the species. This indicates the overall sample size



Fig. 2. The incidence matrix for the obligate fungivores associated with *F. pinicola*. Sites are numbered from the smallest (1) to the largest (9). Specialist beetles on *F. pinicola* are typed in bold.

was adequate to detect most fungivorous species and more detailed analyses of distribution and abundance of fungivores are justified.

Distribution patterns

Species presence-absence patterns among the nine sites for the obligate fungivores exhibited pronounced nestedness (matrix fill = 45%, T = 27.91, P < 0.01; Fig. 2), but not for the entire species assemblage (matrix fill = 27.6%, T = 57.2, P = ns). Most species encountered were rare: 41 species occurred in no more than three sites, eight species in four to six sites, and only five species were common occurring in at least seven sites. There was also a great deal of variation in species distribution patterns among the fruiting bodies, however, most species were present in fewer than eight fruiting bodies (Fig. 3).

Abundance patterns

Variation in the abundance of species in the pooled data was great: most species were rep-



Fig. 4. The relative abundance of the five most abundant species in each site. Sites are numbered from the smallest (1) to the largest (9).

resented by few individuals only, while just one species, *C. glabratus*, accounted for 66.8% of all individuals (Fig. 4). Similarly, the large differences in the number of individuals reared between the samples were mainly due to the disproportionate abundance of this species. The beetle was also the most common species in all the samples and accounted for 43% to 86% of the total number of individuals, whereas a pool of 15 species shared the four subsequent ranks. Altogether, the five most abundant species comprised 87% to 97% of the total number of individuals in the samples.

Sometimes the frequency of occurrence, instead of the total number of individuals, has been used as a measure of abundance in fungalinsect systems (Jonsell *et al.* 2001, Jonsell & Nordlander 2002, but *see* Thunes *et al.* 2000, Komonen 2001). In the present study, there was a positive correlation between the frequency of occurrence and total number of individuals for the *F. pinicola* associated species (log-transformed variables, $r_p = 0.95$, n = 53, P < 0.01). This indicates that both abundance measures give similar results with regards to fungal-insect systems.

Distribution-abundance patterns

Overall, there was a positive relationship between the frequency of occurrence in the fruiting bodies and mean abundance per fruiting body



Fig. 5. Regional distribution and local abundance of the fungivores (n = 17) and the rest of the species (n = 36) encountered in this study. Abbreviations refer to the *F. pinicola* specialists (*see* Fig. 2).

occupied (log-transformed variables, $r_{\rm p} = 0.60$, n = 53, P < 0.01). Of the fungivores, those species that were widely-distributed among the sites were also more common in individual sites on average, as measured by the fraction of fruiting bodies occupied (fruiting bodies occupied were log-transformed, $r_{p} = 0.62, P < 0.01, n = 17$). The relationship between the distribution and abundance among the sites was positive for all species and fungivores only ($r_p = 0.77, P < 0.001$, n = 53; $r_{\rm p} = 0.76$, P < 0.001, n = 17, respectively, Fig. 5). Figure 5 also illustrates that the secondary species and parasitoids all had a restricted distribution and low abundance among the sites, whereas the fungivores were more "scattered" in terms of their distribution and abundance, possibly reflecting differences in resource specificity.

Cis glabratus vs. C. quadridens

Cis glabratus (66.8% and 82.7% of all individuals and fruiting bodies) and *C. quadridens* Mellié (12.0% and 25.5%) were the most abundant species in the sample, yet there were considerable differences in the distribution and abundance patterns between the two species. *Cis glabratus* was present in all the sites studied, while *C. quadridens* was absent from three sites. Overall, the proportion of *C. glabratus* occupied fruiting bodies was significantly higher than that of *C. quadridens* ($\chi^2 = 119$, P < 0.001, n = 180; 149



Fig. 6. Distribution and mean abundance of *Cis glabratus* and *C. quadridens* in the fruiting bodies. Each value for abundance had one added to allow plotting of zero values on the logarithmic scale.

and 46 occupied fruiting bodies, respectively). There was a significant difference between the abundance of *C. glabratus* and *C. quadridenss* per sample site (mean \pm SD = 277.3 \pm 186.5, median = 269 individuals and 49.7 \pm 88.0, median = 17, respectively; Mann-Whitney *U*-test; *U* = 5, *P* < 0.001, *n* = 9). The average abundance of *C. glabratus* per fruiting body occupied by the species was higher than that of *C. quadridens* (mean \pm SD = 16.75 \pm 22.93, median = 7 individuals and 9.72 \pm 14.92, median = 4, respectively; $U_{149.46} = 2615.5$, *P* < 0.05).

The magnitude of intraspecific aggregation in the fruiting bodies was similar between C. glabratus and C. quadridens (CV = 1.37 and 1.54, $s_{cv} = 0.17$ and 0.39, respectively, t = 0.41, df = 193, P = ns). Although the species cooccurred in 46 fruiting bodies, C. quadridens was more abundant in one fruiting body only and it was never present without C. glabratus. Also, interspecific aggregation in the fruiting bodies in which both species were present was high: $C_{\rm gla,qua} = 1.11$, which is the covariance between the abundances of the species divided by the product of the means. The measure reflects the increase in the average number of interspecific interactions an individual faces due to aggregation, in comparison with a random distribution of individuals. The mean abundance of C. glabratus and C. quadridens per fruiting body correlated positively with the proportion of occupied fruiting bodies (abundance log-transformed, $r_{\rm p} = 0.93, P < 0.001$ and $\log(x + 1)$ -transformed, $r_{\rm p} = 0.87, P < 0.01$, respectively, n = 9; Fig. 6).

Discussion

Patterns of nestedness

Species' distribution patterns among the sample sites exhibited patterns of pronounced nestedness. This is typical for species distribution patterns within fragmented habitat (Atmar & Patterson 1993). Four presumptions govern the theory behind the metric: (i) the islands of fragmented habitat were originally populated by a single common source biota, (ii) the islands were initially uniform in their habitat heterogeneity and type mix, and have remained so throughout their post-fragmentation history, (iii) no significant clinal (latitudinal) gradation exists across the "archipelago" so as to promote species turnover across the archipelago, and (iv) all species of interest are equally isolated on all islands (Atmar & Patterson 1993). The data of the present study fit well presumptions i-iii, whereas presumption iv is unrealistic for most biological assemblages. Different randomization procedures (null models) generate matrices with different degrees of nestedness, and thus statistical significance is difficult to evaluate (Cook & Quinn 1998, Jonsson 2001). To allow comparison with a wide range of studies, I applied the procedure used by the Nestedness Calculator and also applied by most of the previous studies (Patterson & Atmar 1986, Atmar & Patterson 1993).

In the present study, the value T for the insect community in F. pinicola is very close to the one reported for the insect community in the polypore *Fomes fomentarius* (Jonsson *et al.* 2001). The nestedness analysis and the relative abundance of species among the sites show that the insect assemblage associated with the fruiting bodies of F. pinicola is consistent in taxonomic composition in general. This indicates "structured", as opposed to fortuitous, nature of this ecological assemblage at the spatial scale in question. High taxonomic similarity of the F. pinicola associated insect assemblage has also been demonstrated between Finland and NE China (Komonen *et al.* 2003).

Patterns of distribution and abundance

The insect community associated with the bracket fungus F. pinicola comprised species in different feeding guilds, most importantly fungivorous beetles, facultative fungivores and parasitoids. The species that were locally most abundant belonged to obligate fungivores and these were also widely distributed among the sites. There was also a positive relationship between the distribution and abundance of insects inhabiting F. pinicola. Although this applied also to the fungivorous species separately, a large proportion of the variation was due to the difference between the obligate fungivores vs. facultative fungivores and parasitoids. In general, positive interspecific relationships between the local abundance and regional distribution of the species in a taxonomic assembly are very general (Hanski et al. 1993, Gaston et al. 1997).

One exception to the observed distributionabundance pattern in this study was the fungivorous dipteran *Gaurax maculipennis* (Zett.; Chloropidae), which had a very low frequency of occurrence but produced a relatively high number of individuals when present. This possibly indicates that only a small proportion of fruiting bodies are suitable for the species but the species has a high reproductive capacity in such suitable fruiting bodies (*see* also Komonen *et al.* 2001). Only in one fragment was a non-obligate fungivore (i.e. the hymenopteran parasitoid *Kleidotoma* sp. (Eucoilidae)) among the five most abundant species.

Four fungivorous beetle species encountered in this study are F. pinicola specialists (cf. Thunes et al. 2000, Jonsell et al. 2001). However, the fungal-host specificity of many dipteran are poorly known, yet they are often considered less host-specific than beetles (Hanski 1989). Differences in the host-fungus preference cannot, naturally, explain the variation in the abundance and distribution of F. pinicola specialists. However, preference towards fruiting bodies of different quality (e.g. moisture, decay stage; Thunes et al. 2000, Jonsell et al. 2001) together with differences in species macrohabitat preferences (e.g. old-growth vs. managed forests; Jonsell & Nordlander 2002) can account for the observed differences between the monophagous beetles. For example, *C. glabratus* occurs frequently in managed forests and in living fruiting bodies, *C. quadridens* is more common in less managed forests, and *E. laricinum* occurs frequently in most decayed fruiting bodies (Jonsell *et al.* 2001, Jonsell & Nordlander 2002). In general, species that have broad environmental tolerances and are able to use a wide range of resources will in so doing achieve high local densities and will be able to survive in more places and hence over a larger area (resource breadth hypothesis; Brown 1984, Gaston *et al.* 1997). However, why greater niche breadth should lead to higher local abundance is not clear at all (Kouki & Häyrinen 1991, Gaston 1994).

For the four F. pinicola specialist species, the higher the average population size in the fruiting bodies, the higher is the frequency of occurrence in the fruiting bodies. In the case of patchily distributed resources, such as fungal fruiting bodies, this pattern could be explained by metapopulation dynamics (Hanski et al. 1993). The species that are more abundant on average in the fruiting bodies have longer population persistence time in a given fruiting body and higher colonization rate due to high numbers of potentially migrating individuals; thus they have also wider distribution among the fruiting bodies at a given time. Even though very little is known about life-history and dispersal of fungivorous insects, metapopulation dynamics could contribute to the positive distribution-abundance relationship for the fungivorous insects. This applies particularly at a small spatial scale, that is, among fruiting bodies within a forest stand. It is known that the frequency of occurrence of cisid beetles on fruiting bodies and fungus-infested trees depends on spatial isolation of these habitat patches, even at a relatively small scale of some tens of meters (Jonsell et al. 1999, Rukke 2000).

Cis glabratus vs. C. quadridens

Of the specialist beetles on *F. pinicola*, only the common *C. glabratus* and the old-growth forest congeneric *C. quadridens*, were abundant enough to allow detailed analysis of the intraspecific distribution and abundance patterns among the sites and fruiting bodies. Both *C. glabratus* and

C. quadridens showed marked spatial variation in abundance among the fruiting bodies, often co-occurring. This interspecific aggregation most likely results from the preference towards fruiting bodies of similar quality (Thunes *et al.* 2000, Jonsell *et al.* 2001). Intraspecific aggregation, which was similar between the species, is largely a consequence of the life history of the two species: the population size of the beetles in a given fruiting body increases after colonization until the resource is almost fully consumed.

There was a positive intraspecific distribution-abundance relationship for both species in the fruiting bodies. Cis quadridens had significantly smaller average population size and frequency of occurrence in the fruiting bodies. Being slightly smaller in body size (Freude et al. 1967), C. quadridens could be a poorer disperser. Jonsell et al. (1999) found out that the species was absent from fruiting bodies placed out in small and isolated (350-2000 m) forest fragments, suggesting poor dispersal ability, whereas C. glabratus had higher frequency of occurrence. It seems obvious that C. quadridens is an ecological specialist, which has a very discrete distribution in the landscape but which can be very abundant in the suitable resource patches, that is, in the fruiting bodies in old-growth forests. Put together the specialization on old-growth forests and possible poor dispersal ability these could very well explain the observed differences between C. glabratus and C. quadridens.

Conclusions

I studied the distribution and abundance of insect species occurring in the fruiting bodies of a polypore *F. pinicola*. Previous research on distribution and abundance patterns of insects living in patchily distributed resources come largely from non-arboreal habitats (e.g. dung in pasture), which are inherently rather dissimilar systems in comparison with forest landscapes. Thus, this study expands our knowledge on distribution and abundance patterns of insects dependent on specific resources to forest ecosystem, and to polypore-insect systems in particular. There are also other patchily distributed microhabitats in forests that host speciose insect communities, such as

decaying logs and ant mounds, but whether these systems confirm the general patterns established in this study, and in the earlier studies in other ecosystems, deserves further study.

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References

- Ahti, T., Hämet-Ahti, L. & Jalas, J. 1968: Vegetation zones and their sections in northwestern Europe. — Ann. Bot. Fennici 5: 169–211.
- Anon. 1996: Statistical yearbook of forestry. Finnish Forest Research Institute, Helsinki.
- Atkinson, W. D. 1985: Coexistence of Australian rainforest Diptera breeding in fallen fruit. — J. Anim. Ecol. 54: 507–518.
- Atmar, W. & Patterson, B. D. 1993: The measure of order and disorder in the distribution of species in fragmented habitat. — *Oecologia* 96: 373–382.
- Brown, J. H. 1984: On the relationship between abundance and distribution of species. — Am. Nat. 124: 255–279.
- Cook, R. R. & Quinn, J. F. 1998: An evaluation of randomization models for nested species subset analysis. — Oecologia 113: 584–592.
- Fossli, T.-E. & Andersen, J. 1998: Host preference of Cisidae (Coleoptera) on tree-inhabiting fungi in northern Norway. – *Entomol. Fennica* 9: 65–78.
- Freude, H., Harde, K. W. & Lohse, G. A. 1967: Die Käfer Mitteleuropas. Band 7. Goecke & Evers Verlag.
- Gaston, K. J. 1994: Rarity. Chapman & Hall.
- Gaston, K. J., Blackburn, T. M. & Lawton, J. H. 1997: Interspecific abundance-range size relationships: an appraisal of mechanisms. – J. Anim. Ecol. 66: 579–601.
- Hackman, W. & Meinander, M. 1979: Diptera feeding as larvae on macrofungi in Finland. — Ann. Zool. Fennici 16: 50–83.
- Hanski, I. 1989: Fungivory: fungi, insects and ecology. In: Wilding, N., Collins, N. M., Hammond, P. M. & Webber, J. F. (eds.), *Insect-fungus Interactions*: 25–68. Academic Press, London.
- Hanski, I. A. & Gilpin, M. E. 1997: Metapopulation biology: Ecology, genetics, and evolution. — Academic Press, London.
- Hanski, I., Kouki, J. & Halkka, A. 1993: Three explanations of the positive relationship between distribution and

abundance of species. — In: Ricklefs, R. E. & Schluter, D. (eds.), *Community diversity: historical and geographical perspectives*: 108–116. Chicago University Press, Chicago.

- Jonsell, M. & Nordlander, G. 2002: Insects in polypore fungi as indicator species: a comparison between forest sites differing in amounts and continuity of dead wood. *— For. Ecol. Manage.* 157: 101–118.
- Jonsell, M., Nordlander, G. & Jonsson, M. 1999: Colonization patterns of insects breeding in wood-decaying fungi. - J. Insect Conserv. 3: 145–161.
- Jonsell, M., Nordlander, G. & Ehnström, B. 2001: Substrate associations of insects breeding in fruiting bodies of wood-decaying fungi. – *Ecol. Bull.* 49: 173–194.
- Jonsson, B. G. 2001: A null model for randomization tests of nestedness in species assemblages. — *Oecologia* 127: 309–313.
- Jonsson, M. 2003: Colonisation ability of the threatened tenebrionid beetle *Oplocephala haemorrhoidalis* and its common relative *Bolitophagus reticulatus*. – *Ecol. Entomol.* 28: 159–167.
- Jonsson, M., Jonsell, M. & Nordlander G. 2001: Priorities in conservation biology: a comparison between two polypore-inhabiting beetles. – *Ecol. Bull.* 49: 195–204.
- Jonsson, M., Nordlander, G. & Jonsell, M. 1997: Pheromones affecting flying beetles colonizing the polypores *Fomes* fomentarius and *Fomitopsis pinicola*. — *Entomol. Fen*nica 8: 161–165.
- Kehler, D. & Bondrup-Nielsen, S. 1999: Effects of isolation on the occurrence of a fungivorous forest beetle, *Bolitotherus cornutus*, at different spatial scales in fragmented and continuous forests. — *Oikos* 84: 35–43.
- Komonen, A. 2001: Structure of insect communities inhabiting two old-growth forest specialist bracket fungi. — Ecol. Entomol. 26: 63–75.
- Komonen, A., Ikävalko, J. & Wang, W. 2003: Diversity patterns of fungivorous insects: comparison between glaciated vs. refugial boreal forests. — J. Biogeogr. 30. [In press].
- Komonen, A., Penttilä, R., Lindgren, M. & Hanski, I. 2000: Forest fragmentation truncates a food chain based on an old-growth forest bracket fungus. — *Oikos* 90: 119–126.
- Komonen, A., Siitonen, J. & Mutanen, M. 2001: Insects inhabiting two old-growth forest polypore species. — *Entomol. Fennica* 12: 3–14.
- Kouki, J. & Hanski, I. 1995: Population aggregation facilitates coexistence of many competing carrion fly species. — Oikos 72: 223–227.
- Kouki, J. & Häyrinen, U. 1991: On the relationship between distribution and abundance in birds breeding on Finnish mires: the effect of habitat specialization. — Ornis Fennica 68: 170–177.
- Lindblad, I. 1998: Wood-inhabiting fungi on fallen logs of

Norway spruce: relations to forest management and substrate quality. — *Nordic Journal of Botany* 18: 243–255.

- Nilsson, T. 1997: Survival and habitat preferences of adult Bolitophagus reticulatus. – Ecol. Entomol. 22: 82–89.
- Økland, B. 1995: Insect fauna compared between six polypore species in a southern Norwegian spruce forest. — Fauna Norvegica Series B 42: 21–26.
- Økland, B. & Hågvar, S. 1994: The insect fauna associated with carpophores of the fungus *Fomitopsis pinicola* (Fr.) Karst. in a southern Norwegian spruce forest. — *Fauna Norvegica Series B* 41: 29–42.
- Patterson, B. D. & Atmar, W. 1986: Nested subsets and the structure of insular mammalian faunas and archipelagos. — *Biol. J. Linn. Soc.* 28: 65–82.
- Roslin, T. & Koivunen, A. 2001: Distribution and abundance of dung beetles in fragmented landscapes. — *Oecologia* 127: 69–77.
- Rukke, B. A. 2000: Effects of habitat fragmentation: increased isolation and reduced habitat size reduces the incidence of dead wood fungi beetles in a fragmented forest landscape. — *Ecography* 23: 492–502.
- Rukke, B. & Midtgaard, F. 1998: The importance of scale and spatial variables for the fungivorous beetle *Bolitophagus reticulatus* (L.) (Coleoptera, Tenebrionidae) in a fragmented forest landscape. — *Ecography* 21: 561–572.
- Ryvarden, L. & Gilbertson, R. L. 1993: European Polypores 1. Abortiporus–Lindtneria. – Synopsis Fungorum 6, Oslo.
- Shorrocks, B. & Charlesworth, P. 1980: The distribution and abundance of the British fungal-breeding *Drosophila*. — *Ecol. Entomol.* 5: 61–78.
- Sverdrup-Thygeson, A. & Midtgaard, F. 1998: Fungusinfected trees as islands in boreal forest: spatial distribution of the fungivorous beetle *Bolitophagus reticulatus* (Coleoptera, Tenebrionidae). – *Ecoscience* 5: 486–493.
- Thunes, K. H. 1994: The coleopteran fauna of *Piptoporus* betulinus and *Fomes fomentarius* (Aphyllophorales: Polyporaceae) in western Norway. — *Entomol. Fennica* 5: 157–168.
- Thunes, K. H., Midtgaard, F. & Gjerde, I. 2000: Diversity of coleoptera of the bracket fungus *Fomitopsis pinicola* in a Norwegian spruce forest. — *Biodivers. Conserv.* 9: 833–852.
- Thunes, K. H. & Willassen, E. 1997: Species composition of beetles (Coleoptera) in the bracket fungi *Piptoporus betulinus* and *Fomes fomentarius* (Aphyllophorales: Polyporaceae): an explorative approach with canonical correspondence analysis. – J. Nat. Hist, 31: 471–486.
- Whitlock, M. C. 1992: Nonequilibrium population structure in forked fungus beetles: extinction, colonization, and the genetic variance among populations. — Am. Nat. 139: 385–397.

Species	Ecology	Occurrence	Individuals
Cis glabratus (Col.)	Fungivore	149	2496
Cis quadridens (Col.)	Fungivore	46	447
<i>Lycoriella solani</i> (Dip.)	Fungivore	27	100
Ula bolitophila (Dip.)	Fungivore	22	105
Cecidomyiidae (Dip.)	Facultative	19	153
Ennearthron laricinum (Col.)	Fungivore	12	54
Cis jacquemartii (Col.)	Fungivore	12	23
Gaurax maculipennis (Dip.)	Fungivore	9	143
<i>Megaselia armata</i> (Dip.)	Fungivore	7	20
Pteryngium crenatum (Col.)	Facultative	6	10
Dorcatoma punctulata (Col.)	Fungivore	5	23
<i>Leptusa pulchella</i> (Col.)	Facultative	5	7
Malthodes guttifer (Col.)	Facultative	4	4
Kleidotoma sp. (Hym.)	Parasitoid	4	30
Archinemapogon yildizae (Lep.)	Fungivore	4	8
Cis bidentatus (Col.)	Fungivore	3	7
Ostoma ferruginea (Col.)	Facultative	3	3
Rhizophagus dispar (Col.)	Facultative	3	3
Anaspis marginicollis (Col.)	Facultative	3	3
Sepedophilus testaceus (Col.)	Facultative	3	3
Diospilus dispar (Hym.)	Parasitoid	3	4
Stenomacrus sp. (Hym.)	Parasitoid	3	3
Discobola annulata (Dip.)	Fungivore	3	4
Psychodidae (Dip.)	Facultative	3	10
Cis alter (Col.)	Fungivore	2	2
Rhyncolus ater (Col.)	Facultative	2	2
Orthoperus punctatus (Col.)	Facultative	2	2
	Facultative	2	2
	Facultative	2	2
<i>Lissonota</i> sp. (Hym.)	Parasitoid	2	3
Dissebula assesses (Dip.)	Facultative	2	3
Lanahasidas (Din.)	Fungivore	2	10
Cia dantatua (Col.)	Facultative	2	2
Cis lipostocribratus (Col.)	Fungivoro	1	1
	Facultativo	1	1
Denticollic linearic (Col.)	Facultative	1	1
Euclidos equescions (Col.)	Facultative	1	1
Corticaria Iongicallis (Col.)	Facultative	1	1
Ptinus rantor (Col.)	Facultative	1	1
Funlectus sp. (Col.)	Facultative	1	1
Agathidium rotundatum (Col.)	Facultative	1	1
Agathidium pisanum (Col.)	Facultative	1	1
Aleochara villosa (Col.)	Facultative	1	1
Dinaraea aeguata (Col.)	Facultative	1	1
Atheta crassicornis (Col.)*	Facultative	1	1
Atheta nirgicornis (Col.)	Facultative	1	1
Ontsira sp. (Hym.)	Parasitoid	1	1
Lasius niger group (Hym.)	Facultative	1	3
Aniseres sp. (Hym.)	Parasitoid	1	1
Aradidae (Het.)	Facultative	1	1
Scatopsciara sp. (Din.)	Facultative	1	5
Tachypeza fennica (Dip.)	Facultative	1	1
Leucophenga sp. (Dip.)	Fungivore	1	3
Indet Diptera	Facultative	3	16

Appendix. Insects encountered from the fruiting bodies of *F. pinicola*. Occurrence refers to the number of fruiting bodies (n = 180) in which the taxon was present.

* The species could also be A. paracrassicornis, but females are impossible to distinguish.