

Insect assemblage associated with the polypore *Fomitopsis pinicola*: a comparison across Fennoscandia

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Komonen, A., Jonsell, M., Økland, B., Sverdrup-Thygeson, A. & Thunes, K. 2004: Insect assemblage associated with the polypore *Fomitopsis pinicola*: a comparison across Fennoscandia. — Entomol. Fennica 15: 102–112.

We compiled the data on the insect assemblage occurring within the polypore *Fomitopsis pinicola* from six regions in Finland, Sweden and Norway. The species composition and diversity of the primary fungivorous beetles (Cisidae and Anobiidae) were similar across Fennoscandia. The beetles *Cis glabratus* Mellié (Cisidae) and *C. quadridens* Mellié were the most frequent species occurring in 70% and 23% of the fruiting bodies on average. *Sulcaxis fronticornis* (Panzer) and *Ennearthron cornutum* (Gyllenhal) were relatively common in southern Sweden, while absent from the study regions in Norway and Finland. Similarly, *Cis bidentatus* (Olivier) and *Cis dentatus* Mellié were rather common in Norway, but almost absent from the Finnish samples. Species relative abundances in the six study regions exhibit more variation, which to some extent corresponds the biogeographical zones. Our results on the high similarity in species composition indicate deterministic nature of the *F. pinicola*-associated insect assemblage over large spatial scales. On the other hand, climatic factors probably have an impact on the relative abundance of species.

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Received 9 April 2003, accepted 12 December 2003

1. Introduction

The magnitude of spatial variation in species distribution and abundance is one of the basic questions in ecology. In addition, the scale of variation is important for many applied questions, such as in assessing the effects of habitat loss and fragmentation on natural biota (Edwards *et al.* 1994). For example, if a given ecological community is relatively constant in species composition and ecological structure over large areas, then management practices (e.g. timber felling) could operate at coarser basis than if there is plenty of small-scale variation. However, most ecological studies operate at small spatial scales (Edwards *et al.* 1994, Gaston & Blackburn 2000) and information on large-scale spatial variation is urgently needed, not only because it provides the basis for understanding the spatial variation in smaller scale studies, but also to fully evaluate the consequences of habitat loss and fragmentation (Harrison & Bruna 1999).

Many insect communities occur inside relatively small and discrete resource patches, such as decaying trees, ant mounds, dung patches or fungal fruiting bodies (Hammond & Lawrence 1989, Hanski & Cambefort 1991, Siitonen 2001, Päivinen *et al.* 2002). These insect assemblages are relatively species-rich considering the small habitat size, comprise many specialized species which are unable to reproduce outside their focal resource patch, and play an important role in the decomposition of organic matter and thus promote nutrient cycling (e.g. Hanski & Cambefort 1991, Samuelsson *et al.* 1994, Siitonen 2001). Thus, these kinds of insect assemblages are likely to contribute greatly to the local biodiversity and ecosystem functioning. Partly due to the concealed life style, however, very little is known about the distribution, abundance and ecology of species in these systems, especially at large spatial scales.

In forests, polypores (Aphyllphorales: Polyporaceae) constitute an important component of ecosystem as symbionts, parasites and decomposers of wood (Swift 1982). The fruiting bodies of polypores also host speciose insect communities, including many species that are monophagous on a particular host fungus or utilize a few fungal species (Hanski 1989, Jonsell *et al.* 2001).

Research on polypore-dwelling insects, predominantly in boreal forests in Fennoscandia, has 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 (Rukke & Midtgaard 1998, Sverdrup-Thygeson & Midtgaard 1998, Kehler & Bondrup-Nielsen 1999, Jonsson *et al.* 2001, Komonen *et al.* 2000, Jonsell & Nordlander 2002). Most of these studies have operated at relatively small spatial scales, and the largest distances between study regions have been ca. 500 km (Komonen 2001). Thus, comparisons over large spatial scales are crucial to fully understand patterns of variation in these fungal-insect systems in boreal forests.

In this paper, we analyse the large-scale spatial variation in species composition, diversity and community structure of the insect fauna occurring within the polypore *Fomitopsis pinicola* (Swartz: Fr.) Karst. (Aphyllphorales: Polyporaceae) in Fennoscandian boreal forests. We compiled the data on this insect assemblage collected by the authors of the present paper from Finland, Sweden and Norway (e.g. Økland & Hågvar 1994, Thunes *et al.* 2000, Jonsell *et al.* 2001, Komonen 2003), and examined the spatial variation across six regions. Firstly, we provide an overview of the full insect assemblages encountered in the different regions. Secondly, we focus on the obligate fungivorous species, particularly Cisidae (Coleoptera).

2. Material and methods

2.1. The fungus

Fomitopsis pinicola is a conspicuous and often the most abundant polypore in Fennoscandian 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

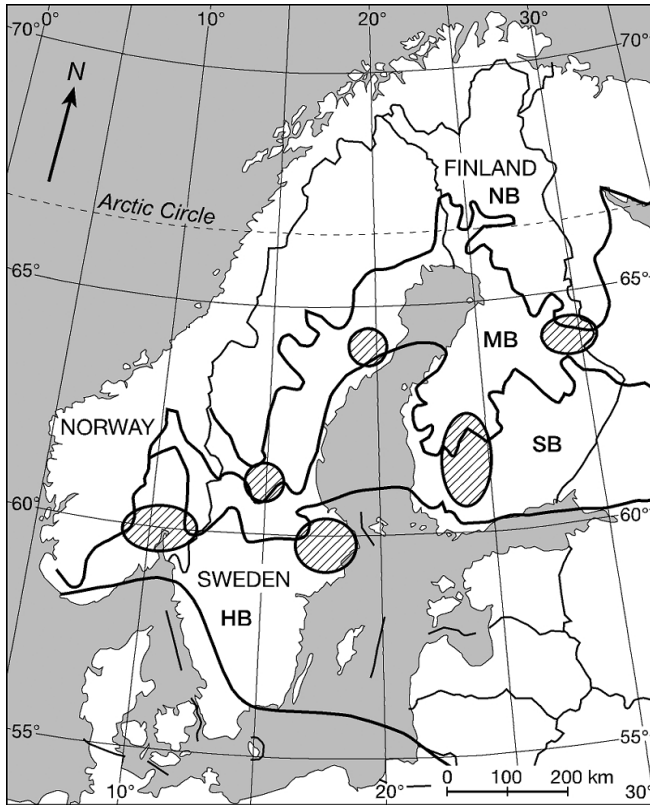


Fig. 1. Map of the study regions and boreal vegetation zones. HB = hemiboreal, SB = southern boreal, MB = middle boreal, NB = northern boreal.

woody debris (CWD), particularly in the old-growth forests (Lindblad 1998, pers. obs.). The fungal fruiting bodies grow predominantly on stumps, snags and downed logs of dead and dying Norway spruce (*Picea abies* (L.) Karst.), although they can be found on numerous other tree species (Ryvarden & Gilbertson 1993). The fruiting bodies of *F. pinicola* are perennial and the oldest can reach a size of about 40 cm in cap diameter (Ryvarden & Gilbertson 1993). The insect material in this study was obtained from within fungal fruiting bodies that were collected from the field and taken into laboratory in order to rear the insects living inside; Collembola was not recorded. The nomenclature of Coleoptera follows Silfverberg (1992).

2.2. Study areas

We sampled polypore fruiting bodies from six Fennoscandian regions, representing different climatic and biogeographical zones (Fig. 1). The

climate ranges from oceanic in the west (Norway) to more continental in the east (Finland) (Anon. 1992). There is also a south–north gradient in climate ranging from the hemiboreal vegetation zone to the middle boreal zone in the northernmost sites (Ahti *et al.* 1968).

The Häme region in Finland (61–62°N, 23–25°E) is situated in the transition zone between the southern and middle boreal zone. The Kuhmo region (\approx 64°N, 29–30°E) is the easternmost study region belonging to the middle boreal zone. The mean annual precipitation in Häme and Kuhmo is 550–600 mm, and the mean annual temperature +2–4°C and +1°C, respectively (data from the Finnish Meteorological Institute).

The province of Uppland in Sweden (59°30'–60°30'N, 17°–18°E) was the southernmost study region, belonging to the hemiboreal zone. Dalarna (60°30'N, 14–15°E) and Västerbotten (64°N, 19–20°E) are situated in the middle boreal zone. The mean annual precipitation and temperature is 544 mm and 5.6°C in Uppland, 730 mm and 2.6°C in Dalarna, and 591 mm and 1.5°C in

Västerbotten (data from the Swedish Meteorological Institute).

The westernmost region belongs to Akershus and Buskerud counties in Norway (59°51'N–60°30'N, 10°40'E–11°05'E) and is situated in the southern boreal zone. The mean annual precipitation is 760–1200 mm, and the mean annual temperature +2.9°C (data from the Norwegian Meteorological Institute).

The studied forest areas are dominated by Norway spruce on mesic and moist sites, while Scots pine (*Pinus sylvestris* Linnaeus) is the predominant tree species on dry ridges, hill tops and pine bogs. Birch (*Betula* Linnaeus spp.) and aspen (*Populus tremula* Linnaeus) are less frequent in the study areas. All forest areas studied, except some sites in Uppland, were old-growth forests.

2.3. Sampling procedure

Fruiting bodies were collected haphazardly from tree trunks and brought to the laboratory to rear the insects living inside. The size distribution of the collected fruiting bodies reflected natural size variation. The Swedish material included both living and dead fruiting bodies, whereas the Norwegian and Finnish material consisted only of dead ones. In Norway, fruiting bodies were collected in May 1991 and 1992, and June and early July 1997. In Sweden, fruiting bodies were collected during the years 1992–1996, mainly in the winter/spring but also in the autumn. In Finland, collections were made between mid-May and late June 1999. Table 1 summarizes the data on study regions and sampling.

The rearing procedure was somewhat differ-

ent in the different countries. In Norway and Finland insects were reared in cloth-covered plastic funnels (Norway) or boxes (Finland), which were kept in outdoor temperature; 122 fruiting bodies in Norway were kept in plastic boxes indoors. The rearings were checked for insects continuously until the end of September. The fruiting bodies sampled in 1997 in Norway were dissected afterwards. In Sweden, polypores were placed indoors in 1-litre containers of waxed paper (milk containers). A glass vial was inserted into the container so that emerging photopositive insects could be easily collected; the non-photopositive insects were collected by hand. Rearings were checked for insects over a half a year, after which the fruiting bodies were dissected to find the remaining insects.

2.4. Analyses

To measure species diversity in the *F. pinicola*-associated insect assemblage, we used different diversity measures (Magurran 1988). We used reciprocal of Simpson's diversity index ($1/D$), as it is not very sensitive to the number of species. In addition, we used Fisher's alpha, because it is practically independent of sample size when $n > 1000$, as was the case in this study. The index is also less sensitive to single species dominance. We also included the widely-used Shannon diversity index, as it is rather sensitive to a few abundant species and thus indicates differences in dominance patterns. To allow comparisons of similarity in species composition, we used Sørensen's qualitative (C_s) and quantitative (C_n) indices. All indices were calculated using EstimateS (Colwell 2000).

Table 1. The number of sites and *F. pinicola* fruiting bodies sampled, and the number of insect individuals and species encountered from the six regions in Finland, Sweden and Norway. The figure for the number of insect species encountered is an underestimate, as not all taxa were identified to a species level.

	Finland		Sweden			Norway
	Häme	Kuhmo	Uppland	Dalarna	Västerbotten	Akershus
Sites	9	4	11	3	2	3
Fruiting bodies	226	110	781	180	106	461
Insect species	56	30	76	35	19	57
Individuals	4,864	652	20,640	3,520	1,709	14,273

3. Results

We provide an overview of the species composition in Finland, Sweden and Norway (Table 2), followed by more detailed analyses of primary fungivorous species, particularly beetles, between regions. The total material includes 45,658 insect individuals of at least 139 species (Table 1). Not all specimens were identified to species level; thus, the total number of insect species is likely to be higher than the figure above. Hereinafter we use the term taxa, if the figures or analyses include taxa other than species. Because many fungivorous beetle species form long lasting populations in a given fruiting body (implying that population size increases as a function of time), we measured the abundance as the frequency of fruiting bodies with occurrences.

The relative abundance patterns of taxa were similar among the regions (Fig. 2) in that most taxa encountered were rare and the insect assemblages were dominated by a few very abundant primary fungivores. Overall, the beetles *Cis glabratus* Mellé (Cisidae) and *C. quadridens* Mellé were the most frequent species occurring on average in 70% and 23% of the fruiting bodies, respectively.

These species were among the three most common species in each region, except in Västerbotten and Dalarna (Table 3). Primary fungivores accounted on average for 83% of all occurrences, including all Sciaridae and Cecidomyiidae, secondary fungivores and potential predators accounted for 13%, and parasitoids 3%. Classification was based on literature as well as notes from the taxonomists who identified the material. Although the percentages for occurrences are only indicative due to differences in taxa identified, yet they demonstrate that primary fungivores are clearly most frequent in the *F. pinicola* associated insect assemblage.

Of the 139 taxa encountered, we classified 31 as primary fungivores (Table 2). Taxa with the highest frequency of occurrence belonged to Cisidae and Anobiidae (Coleoptera), and Sciaridae and Cecidomyiidae (Diptera) (Table 3). As the ecology of the presumably fungivorous Diptera is poorly known, and diversity and similarity indices require data at the same level of biological hierarchy, we focus only on the fungi-

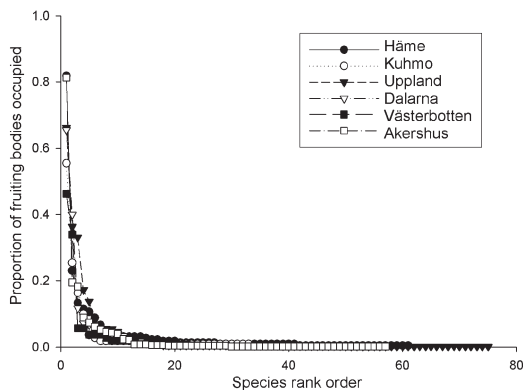


Fig. 2. Relative abundances of insect species in the six study regions associated with the fruiting bodies of *Fomitopsis pinicola*.

vorous Coleoptera ($n = 12$) in the diversity and similarity analyses (Table 4). Species diversity of the insect assemblage was similar in each of the study region (Table 5). The most similar regions in species composition were Västerbotten, Dalarna (both in Sweden) and Häme (Finland; Sörensen's qualitative index 94–100%; Table 6). In terms of species relative abundances, there was a trend in similarity, closely corresponding the biogeographical zonation. The most similar regions were Akershus and Uppland, Kuhmo and Västerbotten, and Häme and Dalarna (Table 6). Despite the overall similarity in species composition and diversity, the frequency of occurrence of the four *F. pinicola* specialist beetles [*C. glabratus*, *C. quadridens*, *Ennearthron laricinum* (Mellé) (Cisidae), *Dorcatoma punctulata* Mulsant & Rey (Anobiidae)] differed between the regions (Table 4).

In polypore-insect systems, parasitoids are typically much more abundant than predators (Komonen 2001). In this study, the number of hymenopteran parasitoids encountered was relatively high in Swedish material only (6% of total number of occurrences). The most abundant taxa in Sweden were *Lissonota* sp. (Ichneumonidae), *Kleidotoma ciliaris* (Zetterstedt) (Eucoilidae), *Diospilus dispar* (Nees) (Braconidae) and species in Mymaridae and Eulophidae. *Kleidotoma* and *D. dispar* were also the most abundant taxa in Finland. In Norway, only a few parasitoid specimens were identified.

Table 2. Species classified as primary fungivores and the country-specific percentage of fruiting bodies with occurrences. (–) refers to taxa not counted or identified in the material in question.

Species	Finland	Sweden	Norway
Coleoptera			
Cisidae			
<i>Cis glabratus</i> Mellié	73	64	81
<i>Cis quadridens</i> Mellié	21	25	18
<i>Cis bidentatus</i> (Olivier)	1	5	20
<i>Ennearthron laricinum</i> (Mellié)	9	3	5
<i>Cis alter</i> Silfverberg	1	5	4
<i>Cis jacquemartii</i> Mellié	5	3	0
<i>Cis dentatus</i> Mellié	0.3	0.6	7
<i>Sulcaxis fronticornis</i> (Panzer)	0	2	0
<i>Cis lineatocribratus</i> Mellié	0.3	0.6	2
<i>Ennearthron cornutum</i> (Gyllenhal)	0	1	0
<i>Cis comptus</i> Gyllenhal	0.3	0	0.2
Anobiidae			
<i>Dorcatoma punctulata</i> Mulsant & Rey	3	11	0.4
Diptera			
Sciaridae			
<i>Lycoriella solani</i> (Winnertz)	17	–	–
<i>Scaptosciara</i> Edwards sp.	0.3	–	–
<i>Corynoptera</i> Winnertz sp.	0.6	–	–
Indet Sciaridae	0	37	–
Dolichopodidae			
<i>Medetera impigra</i> Collin	0	6	–
<i>Medetera abstrusa</i> Thuneberg	0	0.5	–
Cecidomyiidae			
<i>Camptomyia</i> Kieffer sp.	–	–	0.7
<i>Lestodiplosis polypori</i> (Loew)	–	–	0.4
<i>Winnertzia nigripennis</i> Kieffer	–	–	0.4
<i>Winnertzia</i> Rondani sp.	–	–	0.2
Indet Cecidomyiidae	8	15	–
Phoridae			
<i>Megaselia armata</i> (Wood)	3	–	–
<i>Megaselia rufipes</i> (Meigen)	0.3	–	–
Indet Phoridae	0	3	–
Tipulidae			
<i>Ula bolitophila</i> Loew	9	–	–
<i>Discobola annulata</i> (Linnaeus)	2	–	–
<i>Discobola caesarea</i> (Osten Sacken)	1	–	–
Indet Tipulidae	0	0.8	–
Chloropidae			
<i>Gaurax maculipennis</i> (Zetterstedt)	4	0	0
<i>Gaurax dubius</i> (Macquart)	0	0	0.2
Drosophilidae			
<i>Leucophenga quinquemaculata</i> Strobl	0	0.7	–
<i>Leucophenga</i> Mik sp.	0.3	0	–
Indet Mycetophilidae	0	5	–
Lepidoptera			
Tineidae			
<i>Archinemapogon yildizae</i> Kocak	1	4	–
<i>Montescardia tessulatella</i> (Zeller)	0.3	0	–
<i>Nemapogon</i> Schrank sp.	0	0.1	–

Table 3. Five most common taxa and their frequency of occurrence (%) in the fruiting bodies of *F. pinicola*. Abbreviations: Cisgla = *Cis glabratus*, Cisqua = *C. quadridens*, Cisbid = *C. bidentatus*, Cisalt = *C. alter*, Cisden = *C. dentatus*, Lycsol = *Lycoriella solani*, Ulabol = *Ula bolitophila*, Cecido = Cecidomyiidae, Ennlar = *Ennearthron laricinum*, Dorpun = *Dorcatoma punctulata*, Leppul = *Leptusa pulchella*. Sciaridae and Cecidomyiidae are likely to host more than one species; *Lycoriella solani* reared from Finland belongs to Sciaridae, and thus could be one of the sciarid species from Sweden.

Finland			Sweden			Norway	
Häme	Kuhmo	Uppland	Dalarna	Västerbotten		Akershus	
Cisgla 82	Cisgla 55	Cisgla 66	Cisgla 66	Cisgla 46		Cisgla 81	
Cisqua 23	Lycsol 25	Sciari 36	Sciari 40	Sciari 34		Cisbid 20	
Lycsol 13	Cisqua 16	Cisqua 33	Cecido 12	Ennlar 6		Cisqua 18	
Ulabol 12	Ennlar 10	Cecido 17	Ennlar 7	Cecido 6		Leppul 9	
Cecido 11	Ulabol 4	Dorpun 14	Cisqua 7	Cisbid & Cisalt 4		Cisden 7	

Table 4. Percentage of fruiting bodies occupied for the twelve fungivorous beetles in the six study regions.

	Finland		Sweden			Norway
	Häme	Kuhmo	Dalarna	Uppland	Västerbotten	Akershus
<i>Cis glabratus</i>	82	55	66	66	46	81
<i>Cis quadridens</i>	23	16	7	33	2	18
<i>Ennearthron laricinum</i>	9	10	7	2	6	5
<i>Cis jacquemartii</i>	7	1	6	2	2	0
<i>Dorcatoma punctulata</i>	4	2	6	14	3	0
<i>Cis bidentatus</i>	2	0	5	5	4	20
<i>Cis alter</i>	1	0	2	6	4	4
<i>Cis dentatus</i>	0	0	0	1	0	7
<i>Cis lineatocribratus</i>	0	0	1	0	2	2
<i>Cis comptus</i>	0	1	0	0	0	0
<i>Ennearthron cornutum</i>	0	0	0	2	0	0
<i>Sulcacis fronticornis</i>	0	0	0	2	0	0

Table 5. Diversity indices for the fungivorous beetle species ($n = 12$).

	Finland		Sweden			Norway
	Häme	Kuhmo	Dalarna	Uppland	Västerbotten	Akershus
Fisher's alfa	1.72	1.69	1.68	1.67	1.66	1.76
Shannon	1.37	1.42	1.46	1.46	1.47	1.29
Simpson	2.62	2.71	2.79	2.76	2.76	2.51

* The reciprocal of Simpson's index.

Table 6. Similarity of fungivorous beetle assemblages ($n=12$) across Fennoscandia based on Sørensen's incidence (above) and abundance (below) based similarity indices.

	Norway	Finland		Sweden		
	Akershus	Häme	Kuhmo	Dalarna	Uppland	Västerbotten
Akershus		0.89	0.67	0.82	0.80	0.82
		0.58	0.25	0.39	0.65	0.19
Häme			0.67	0.94	0.90	0.94
			0.48	0.73	0.43	0.38
Kuhmo				0.71	0.59	0.71
				0.64	0.16	0.72
Dalarna					0.84	1.00
					0.29	0.57
Uppland						0.84
						0.13

4. Discussion

This paper is a post-hoc comparison of several studies of the insect assemblages associated with the fruiting bodies of *F. pinicola* in Fennoscandia. Our study examines similarity in species composition, diversity and community structure in six regions representing different environmental conditions, such as biogeographical zones and climate. However, we are not in a position to make explicit conclusions about the relative importance of these large-scale environmental variables on the community attributes, particularly because biogeographical zonation and climate are highly interrelated. It is also unlikely that the biogeographical zones would have a striking effect on the *F. pinicola*-associated insect assemblage, as the polypore occurs abundantly across the boreal biogeographical zones. In the following we thereby discuss differences between the six regions, which may relate to various biogeographical differences, including present climate, but also post-glacial colonization history.

4.1. Species composition

Species composition of the primary fungivorous beetles was similar across Fennoscandia. Cisitidae and Anobiidae included most individuals, *Cis glabratus* was the most common species and *C. quadridens* was among the three most common species in each of the study regions, except in

Västerbotten and Dalarna. This may result from including also living fruiting bodies in the Swedish samples. On the other hand, *C. bidentatus* (Olivier) was second to the most common in Akershus but much less frequent in the study regions of Finland and Sweden. In addition to Cisitidae, Cecidomyiidae and Sciaridae were numerically dominant groups, but as the species in these families were rarely identified, they were not included in detailed analyses. The absence of *Sulcaxis fronticornis* (Panzer) (Cisitidae) and *Ennearthron cornutum* (Gyllenhal) from the Finnish and Norwegian samples, while being relatively abundant in Sweden (particularly in the southernmost region), largely contributes to the differences in abundance-based similarity between Sweden and the other two countries.

Despite the similarities in species composition between the countries, clear differences in species relative abundance were also observed. There are at least two obvious reasons why the frequency of occurrence of the four *F. pinicola* specialist beetles was different between the countries, and that *C. bidentatus* and *C. dentatus* Mellié were rather common in Norway, whilst almost absent from the Finnish samples. Firstly, the forest insect fauna in Finland generally has more "eastern" species in comparison with Sweden and Norway (Siitonen 2001). Secondly, the climate in Norway is more oceanic than in Sweden or Finland (Anon. 1992). Thus, there may be a general turnover of species across countries from west to east, resulting from differences in climate. On the

other hand, the observed difference could also relate to latitudinal differences between the eastern and western study regions (see below). In south-western Germany, for example, where the dominating temperate climate is more similar to southern Norway and Sweden than Finland or boreal Sweden, the insect assemblage associated with *F. pinicola* frequently includes *C. bidentatus* and *C. dentatus* (Reibnitz 1999). *Cis glabratus* and *C. quadridens* are among the most abundant species in south-western Germany, but the insect assemblage also includes species such as *C. fagi* Waltl and *C. castaneus* Mellié that were absent from our Fennoscandian material. Also in hemiboreal NE China, *C. glabratus* was the most frequent species (60% of fruiting bodies occupied), and *D. punctulata* and *E. cornutum* occurred in low numbers (Komonen et al. 2003). Although a difference of just a few species may seem irrelevant ecologically, we emphasize that for an insect assemblage occurring within such a specific microhabitat, this difference is entomologically interesting.

Similarity comparisons based on relative abundances (C_n) of fungivorous beetle species between study regions reveal some interesting patterns. The regions were grouped in two's, closely corresponding the biogeographical zones. The northernmost regions (Västerbotten and Kuhmo) were more similar to each other than to the other regions, as were the southernmost regions (Akershus and Uppland). Also, Häme and Dalarna in the transition zone between southern and middle boreal zones were more similar to each other than to the other regions. These results suggest that there is a south–north trend in species abundances, working in concert with the west–east gradient, possibly resulting from differences in temperature and precipitation, although these are interrelated and difficult to distinguish. These two gradients corroborate with what is known about forest insect assemblages (Stokland 1994, Siitonen 2001).

The south–north difference in species-abundance patterns was also demonstrated for the insect assemblage associated with the polypore *Amylocystis lapponica* (Romell) Singer and *Fomitopsis rosea* (Alb. & Schwein.: Fr) P. Karsten between Häme and Kuhmo in Finland (Komonen 2001).

4.2. Diversity patterns and community structure

The diversity of primary fungivorous beetle assemblages occurring within *F. pinicola* fruiting bodies was very similar in distinct biogeographical regions, as measured by different diversity indices. More specifically, this indicates similar patterns of dominance and evenness in the fungivorous beetle assemblage, and the dominance of *C. glabratus* gives the diversity indices relatively low values. The diversity in the different regions was similar to that between countries, and there was no south–north or west–east pattern, as was observed for species composition and abundances.

The pattern of species' relative abundance was very similar between the countries, characterized by a very long tail of rare species. Similar long tail is commonly detected in many kinds of insect samples (Hanski et al. 1993), including fungal-insect communities (Komonen 2001, but see Pielou & Verma 1968). In this study, just over 20% of all species were primary fungivores, yet they were numerically dominant as measured by their frequency of occurrence in the fruiting bodies. At the same time, however, there was more variation in the frequency of occurrence of secondary species and parasitoids. Secondary species such as *Leptusa pulchella* (Mannerheim) (Coleoptera: Staphylinidae), *L. fumida* (Erichson), *Acruvia inflata* (Gyllenhal) (Staphylinidae) and *Rhizophagus dispar* (Paykull) (Coleoptera: Rhizophagidae) were very frequent in the Norwegian material and thus contributed considerably to the observed difference, particularly as the fungivorous Diptera were not identified in Norway. Most of these secondary species are primarily associated with decaying wood but often encountered as a few individuals from the fruiting bodies of wood-decaying fungi (Koch 1989–1992). Although the above pattern agrees well with observations on species frequency distribution among the feeding guilds in fungal-insect systems (Komonen 2001), we point out that the taxa counted and identified in this study were somewhat different in each country. Thus, the dissimilarities in the proportions of occurrences in different feeding guilds should be considered as indicative only.

4.3. Methodological remarks

Post-hoc comparisons of ecological assemblages sampled at different time periods is a common outlook in biogeographical research tradition, because one can rarely sample large, geographically distant areas at the same time. In our study, it is unlikely that the difference in the time of sampling in different regions (1991–1999) would have a great effect on our conclusions. The rationale is that the availability of decaying wood in old-growth and other forest habitats is rather constant from year to year, and *F. pinicola* fruiting bodies have a long duration stability (tens of years). Cisid beetles also form long-lasting populations in a given fruiting body, thus being unlikely to show great stochastic variation in local population abundances and distributions. Within each study region, samples were collected from several sites, thus representing wider range of environmental conditions than just a single forest stand.

4.4. Conclusions

Our study demonstrates that insect communities in *F. pinicola* fruiting bodies are very similar in species composition over large geographical areas in the boreal forests in Fennoscandia. Yet, species relative abundances indicate south–north and west–east trends corresponding the biogeographical zones. Similar large-scale comparisons of other ecological assemblages would greatly increase our understanding of biodiversity patterns in Fennoscandian boreal forests.

Acknowledgements. This study was initiated in SNS-meeting 2002 in Uppsala. Financial support was provided by the Academy of Finland for AK (projects 49025, 64308), WWF Sweden and SLU Faculty of Forestry for MJ, Norwegian Forest Research Institute for BØ, and Norwegian Research Council and Norwegian Forestry Association (NORSKOG) for AS-T. Petri Martikainen gave useful comments on the manuscript.

References

Ahti, T., Hämet-Ahti, L. & Jalas, J. 1968: Vegetation zones and their sections in northwestern Europe. — *Ann. Bot. Fennici* 5: 169–211.

- Anon. 1992: The times atlas of the world, 6th edition. — Times Books, London.
- Colwell, R. K. 2000: EstimateS: Statistical Estimation of Species Richness and Shared Species from Samples (Software, Version 6). <http://viceroy.eeb.uconn.edu/estimates>.
- Edwards, P. J., May, R. M. & Webb, N. R. 1994: Large-scale ecology and conservation biology. — The 35th Symposium of the British Ecological Society, Blackwell Science, Oxford. 375 pp.
- Fossli, T.-E. & Andersen, J. 1998: Host preference of Cisidae (Coleoptera) on tree-inhabiting fungi in northern Norway. — *Entomol. Fennica* 9: 65–78.
- Gaston, K. J. & Blackburn, T. M. 2000: Pattern and process in Macroecology. — Blackwell Science, Oxford. 377 pp.
- Hammond, P. M. & Lawrence, J. F. 1989: Mycophagy in insects: a summary. — In: Wilding, N., Collins, N. M., Hammond, P. M. & Webber, J. F. (eds.), *Insect–fungus Interactions*: 275–324. Academic Press, London. 344 pp.
- 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. 344 pp.
- Hanski, I. & Cambefort, Y. 1991: Spatial processes. — In: Hanski, I. & Cambefort, Y. (eds.), *Dung beetle ecology*: 283–304. Princeton University Press, Princeton. 481 pp.
- 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. 414 pp.
- Harrison, S. & Bruna, E. 1999: Habitat fragmentation and large-scale conservation: what do we know for sure? — *Ecography* 22: 225–232.
- 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. & Ehnström, B. 2001: Substrate associations of insects breeding in fruiting bodies of wood-decaying fungi. — *Ecol. Bull.* 49: 173–194.
- Jonsell, M., Nordlander, G. & Jonsson, M. 1999: Colonization patterns of insects breeding in wood-decaying fungi. — *J. Insect Cons.* 3: 145–161.
- 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. Fennica* 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.
- Koch, K. 1989–1992: Die Käfer Mitteleuropas. Ökologie Bds. 1–3. — Goecke & Evers Verlag, Krefeld.
- Komonen, A. 2001: Structure of insect communities inhabiting two old-growth forest specialist bracket fungi. — *Ecol. Entomol.* 26: 63–75.
- Komonen, A. 2003: Distribution and abundance of fungivorous insects in the fruiting bodies of *Fomitopsis pinicola*. — *Ann. Zool. Fennici*, 40: 495–504.
- Komonen, A., Ikävalko, J. & Wang W. 2003: Diversity patterns of fungivorous insects: comparison between glaciated vs refugial boreal forests. — *J. Biogeogr.* 30: 1873–1881.
- 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.
- Lindblad, I. 1998: Wood-inhabiting fungi on fallen logs of Norway spruce: relations to forest management and substrate quality. — *Nord. J. Bot.* 18: 243–255.
- Magurran, A. 1988: Ecological diversity and its measurement. — Princeton University Press, Princeton. 192 pp.
- 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 Norv. Ser. 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 Norv. Ser. B* 41: 29–42.
- Päivinen, J., Ahlroth, P. & Kaitala, V. 2002: Ant-associated beetles of Fennoscandia and Denmark. — *Entomol. Fennica* 13: 20–40.
- Pielou, D. P. & Verma, A. N. 1968: The arthropod fauna associated with the birch bracket fungus, *Polyporus betulinus*, in eastern Canada. — *Can. Entomol.* 100: 1179–1199.
- Reibnitz, J. 1999: Verbreitung und Lebensräume der Baumschwammfresser Südwestdeutschlands (Coleoptera: Cisidae). — *Mitteilungen Entomologischer Verein Stuttgart* 1869. Jahrgang 34, Seite 1–76.
- 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. 387 pp.
- Samuelsson, J., Gustafsson, L. & Ingelög, T. 1994: Dying and dead trees — a review of their importance for biodiversity. — Threatened Species Unit, Uppsala.
- Siitonen, J. 2001: Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. — *Ecol. Bull.* 49: 11–41.
- Silfverberg, H. 1992: Enumeratio coleopterorum Fennoscandiae, Daniae et Baltiae. — Helsingin Hyönteisvaihtoyhdistys, Helsinki. 94 pp.
- Stokland, J. 1994: Biological diversity and conservation strategies in Scandinavian boreal forests. — PhD thesis, Department of Biology, University of Oslo.
- Sverdrup-Thygeson, A. & Midtgaard, F. 1998: Fungus-infected trees as islands in boreal forest: spatial distribution of the fungivorous beetle *Bolitophagus reticulatus* (Coleoptera, Tenebrionidae). — *Ecoscience* 5: 486–493.
- Swift, M. J. 1982: Basidiomycetes as components of forest ecosystems. — In: Frankland, J. C., Hedger, J. N. & Swift, M. J. (eds.), *Decomposer Basidiomycetes: their biology and ecology*: 307–337. Cambridge University Press, Cambridge. 355 pp.
- 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.