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Regional diversity of mycetophilids (Diptera: Sciaroidea) in Scandinavian oak-dominated forests

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Abstract

Mycetophilids is a species-rich insect group for which the ecological requirements in temperate forests are poorly understood. This study of mycetophilids was based on trap samples from 15 oak-dominated sites in the boreonemoral zone of southern Sweden. Species richness and composition were analysed in relation to environmental variables at a local and at larger scales (multiple regression), and compared to results from similar studies in spruce-dominated sites in the boreal zone of Norway (PCA and two-sample *t* tests). Regressions showing a dominance of regional factors over local in-site variables agree with species-richness models assuming that local communities most often are unsaturated. Precipitation (inter-correlated with elevation) was the strongest factor for explaining the variation in species-richness, which is consistent with previous results indicating that mycetophilids are disfavoured by drought. In addition to precipitation, the area of mixed forest with high biodiversity values (woodland key habitats and protected areas) was a positive factor for species-richness, probably because such habitats combine elements of both coniferous and deciduous forests. PCA ordination revealed a clear separation of the species composition between boreal and boreonemoral forests. Species-richness in boreal forest was significantly higher than in boreonemoral forest, indicating a preference for boreal habitats in many of the species. For mycetophilids and other drought-sensitive insects, it is suggested that (partial) cutting in some dense successional oak stands should be avoided, and that some invading spruces should be tolerated.

Keywords: Biodiversity; Pasture woodland; Boreonemoral forest; Temperate forest; Fungus gnats

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1. Introduction

Region-wide changes in the use of broadleaf temperate forests are supposed to have significant impacts on biodiversity (Hannah et al., 1995; Vera, 2000; Nilsson et al., 2001; Svenning, 2002). Many broadleaf forests with high conservation values in southern Scandinavia contain old remnant trees, especially oaks from earlier grazing regimes. Most woodland pastures were abandoned 40–80 years ago, and have since been invaded by other deciduous and coniferous trees during secondary succession. The woodlands have become denser, and it has been alterations in tree species composition and the assortment of dead wood substrates (Nordén et al., 2004; Nordén et al., accepted). A more recent land use, thinning and harvesting of tops and branches for biofuel production, may possibly lead to a new region-wide transformation of qualities in overgrown oak-pasture lands in southern Scandinavia (Nordén et al., 2004).

The relatively fast changes of the temperate forest landscapes present a challenge to biodiversity management. Many studies have contributed with important information about habitat requirements for organism groups in Scandinavian temperate forests, such as birds, vascular plants, bryophytes, lichens, fungi and

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saproxylic beetles (Hansson, 1997, 2000, 2001; Jonsell et al., 1998; Gustafsson et al., 1999; Ranius and Jansson, 2000; Nilsson et al., 2001; Gustafsson, 2002; Lindbladh et al., 2003; Nordén et al., 2004). In conservation research, there is a taxonomic bias against insects, and especially less charismatic insect groups (percentage of research papers is much lower than percentage of species numbers; see Clark and May, 2002). Insects constitute the great majority of all species associated with forests (Nilsson et al., 2001). For many species-rich insect groups in temperate forests, we still know very little about what factors are most important for species-richness, and the relative importance of local and large-scaled factors.

No previous studies have analysed how the mycetophilid insect fauna (fungus gnats) relates to habitat qualities of the temperate forest landscape. The mycetophilids are small to medium-sized Diptera, including an estimated number of at least 550 species in Sweden (Hedmark, 2000). Most of the species with known habitat requirements develop in fungal substrates in forests (Yakovlev, 1994; Zaitzev, 1994; Økland, 1999). The habitat requirements of mycetophilids have previously been studied in boreal forests of southern Norway (Økland, 1994, 1996). Clear-cutting of semi-natural forests seems to have a long-lasting effect on the mycetophilid fauna, since a marked reduction in species richness was found in forests that had been clear-cut in the past (70–120 years ago; Økland, 1994). The proportion of oldgrowth forest in the surrounding landscapes (100 km^2) was the variable explaining most of the variation in species richness and the number of individuals of single species (Økland, 1996).

With this background for boreal forests, we conducted a study of mycetophilids in lowland temperate broadleaf forest (boreonemoral region, see below) using similar sampling methods. Forest structure and management history at the landscape level differ considerably between these two vegetation zones within Scandinavia (see below). Therefore, other environmental factors than those in the boreal zone may be important in the boreonemoral zone. Our study was based on equal trapping effort of mycetophilids in 15 sites covering a relatively large part of the Swedish boreonemoral zone. Thus, we studied insect diversity in a region composed of several landscapes (sensu Forman, 1995). Various ecological variables were recorded at study sites and in the surrounding landscapes. We focused on two major questions:

1. What factors determine (a) the general species-richness of mycetophilids in oak-dominated forests within the temperate (boreonemoral) region and (b) the richness of mycetophilids associated with wood fungi and soil fungi?
2. How big is the difference in species-richness and species composition of mycetophilids between oak-dominated forest in the temperate region and spruce-dominated forests in the boreal region?

2. Methods

2.1. Study area

We sampled mycetophilids at 15 sites in the boreonemoral zone of southern Sweden (lower rectangle of Fig. 1(a) and (b), Table 4). This zone, which is also called the hemiboreal zone, is a transition zone between the boreal and southern continental forest and includes a larger proportion of broad-leaved deciduous tree species compared to the boreal zone (Ahti et al., 1968; Nilsson, 1997; Nilsson et al., 2001). The elevation of the sites varied between 5 and 230 m. The forests of the sites were mostly regrown stands on abandoned pasture woodlands, with oaks (*Quercus robur* and *Q. petraea*) about 80–200 years old. The forest stands were closed or almost closed with a mean percentage sky visible from the ground of 15% (SD = 3.5%, range 11–23%, $n = 15$ sites). The mean basal area per hectare was 30 m^2 (SD = 4.3 m^2, range 23–38 m^2, $n = 15$), and the mean percentage of oak basal area was 42% (SD = 14%, range 23–65%, $n = 15$). Other common trees at the sites were spruce (*Picea abies*, mean basal area 12%), aspen (*Populus tremula*, 9.0%), lime (*Tilia cordata*, 8.7%), birches (*Betula verrucosa* and *B. pubescens*, 7.5%), ash (*Fraxinus excelsior*, 4.5%), hazel (*Corylus avellana*, 4.5%) and maple (*Acer platanoides*, 3.5%). The ground was mesic, and usually a bit stony. The 15 stands contained on average 10.5 m^3 of coarse dead wood per hectare, compared to an average of about 3–4 m^3 in Swedish production forest (Fridman and Walheim, 2000). The stands contained about as much fine (thin) dead wood as coarse dead wood (for details, see Nordén et al., 2004).

The mycetophilid material from a previous study based on similar methods (15 boreal sites and two boreonemoral sites in Norway; Økland, 1996) was included in the comparison between vegetation zones. The study area of this material is presented as the upper rectangle in Fig. 1(a). All sites within this area were dominated by Norway spruce *P. abies*, generally 90–95%, and the vegetation of the field layer was dominated by *Vaccinium myrtillus* and a generally poor herb flora (Økland, 1996). The study area of the previous study (33,750 km^2) was about 20% smaller than the area of the present study (42,000 km^2).

2.2. Sampling methods and insect material

Mycetophilids were sampled at each site using two Malaise traps (delivered from Marris House Nets, Dorset, England), which in previous studies effectively captured these insects (Økland, 1996). The traps were

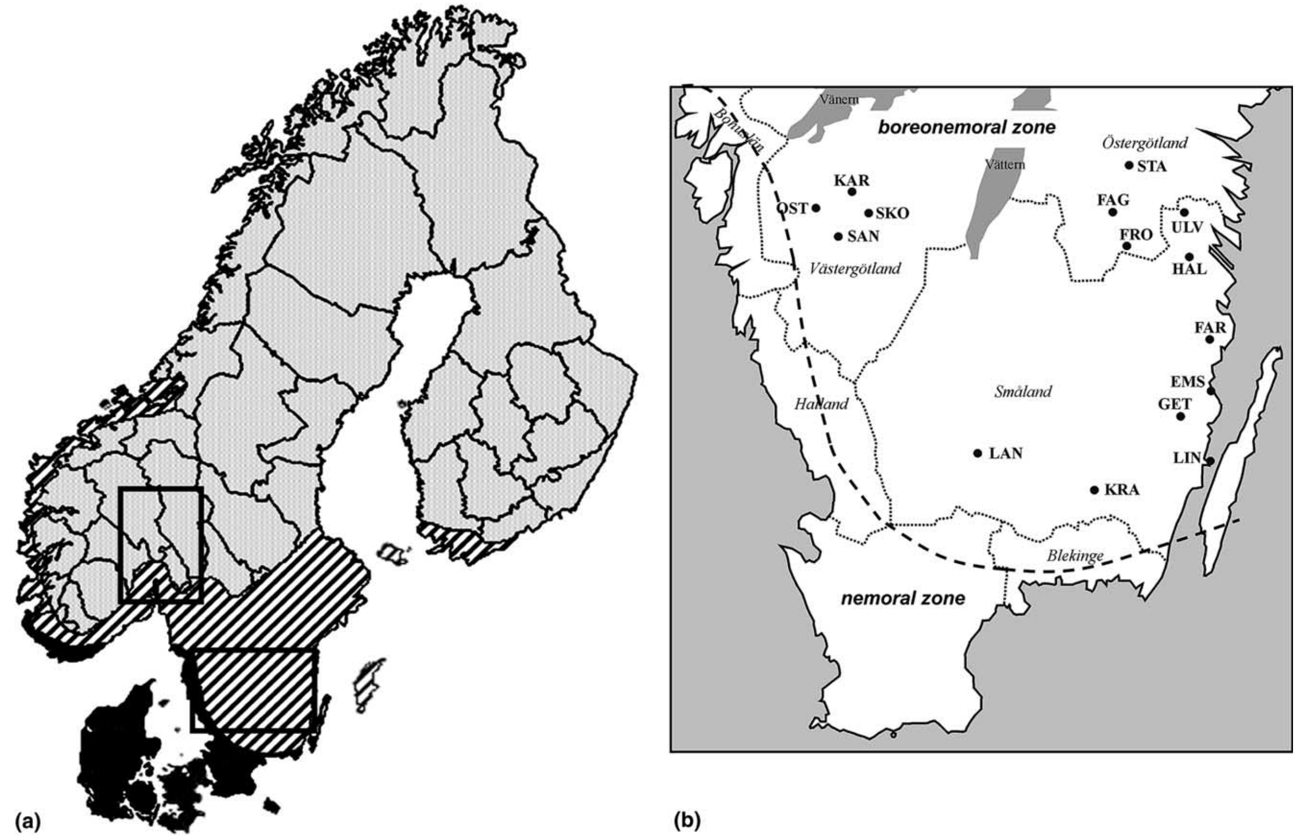


Fig. 1. (a) Map of Scandinavia marked with vegetation zones (light grey – boreal zone, diagonal stripes – boreonemoral zone, and black – nemoral zone) and study areas of the present study in boreonemoral forests (lower rectangle) and the previous study in boreal forests (upper rectangle). (b) Magnified map of study area in southern Sweden corresponding to the lower rectangle in (a), marked with sampling sites (full site names with coordinates are presented in Table 4).

operated in two periods: (1) from 14–18 May to 11–14 June and (2) from 11–14 June to 3–6 September 2002. The collecting bottle at the top of each Malaise tent was filled with 0.75 l of alcohol (70%) and then about 5% ethylene glycol was added. At each site, the two traps were placed about 150 m apart. The traps were placed in closed forest, and the tents were placed over or close to a dead oak log or branch on the ground (diameter about 8–20 cm). The highest part of the tent with the collecting bottle faced southward. Because very high numbers of individuals were caught, we divided the animals in each trap bottle into two parts of approximately equal numbers and composition. This was done by distributing the animals over a surface area of about 6.5 dm^2 and then dividing this area into two equal parts. One part was kept as a reference for the future, whereas the other was used to identify specimens. A commented species list is presented in Kurina et al. (in print).

The mycetophilid material from the previous study (15 boreal sites and two boreonemoral sites in Norway; Økland, 1996; upper rectangle in Fig. 1(a)) was sampled with a similar method, although the sampling period was shorter in Norway (mid June–end of August 1993). The previous study was based on one complete malaise trap sample from each site instead of half samples from two traps, as in the current study. For method description and species list from the boreal material, see Økland (1996). In both studies, all species included were fully identified by taxonomical experts without using morpho-species. The previous material was identified by Alexander Zaitzev (Økland, 1996), while Alexei Polevoi and Olavi Kurina identified the present material (see Kurina et al., in print).

2.3. Environmental variables

Environmental variables were recorded within 2 ha surrounding each of the 15 boreonemoral sampling sites (Table 1). *ASCOMYC* was based on inventory of fruiting bodies of wood-decaying ascomycetes in 2001, and *BASIDIO* was based on inventories of fruiting bodies of wood-decaying basidiomycetes in 2000 and 2001. Fungal variables are supposed to be important determinants of mycetophilids in the same season, but also for mycetophilids in the following season because most

Table 1
Environmental variables used in analyses of species richness and abundance

Variable	Explanation
Geography and climate	
LONGITUDE	Longitude (m) based on Swedish National Grid
LATITUDE	Latitude (m) based on Swedish National Grid
ELEVAT	Elevation (m) above sea level
PREC	Precipitation (total mm) of July, mean of 1961–1990
TEMP	Mean temperature (°C) of July
HUMID	Martonnes humidity index
Stand and soil characters	
CANOPY	Percentage of sky visible from ground within the sites (2 ha)
PH	pH from soil samples within the sites (2 ha)
Fungi and saproxylic substrates	
ASCOMYC	No of wood-decaying ascomycete species within the sites (2 ha)
BASIDIO	No of wood-decaying basidiomycete species within the sites (2 ha)
WOOD	Dead wood (m^3 per ha) within the sites (2 ha)
WOODATT	Dead wood (m^3 per ha) attached to live trees within the sites (2 ha)
WOODFINE	Fine dead wood (m^3 per ha; diameter 1–10 cm) within the sites (2 ha)
WOODCOURS	Course dead wood (m^3 per ha; diameter >10 cm) within the sites (2 ha)
WOODCONIF	Dead coniferous wood (m^3 per ha) total within the sites (2 ha)
WOODOAK	Dead oak wood (m^3 per ha) within the sites (2 ha)
WOODDECID	Dead wood of other deciduous tree species (m^3 per ha) within the sites (2 ha)
WOODSTUMP	Dead stump wood (m^3 per ha) within the sites (2 ha)
LOG	Lying dead wood (m^3 per ha) within the sites (2 ha)
SNAG	Standing dead wood (m^3 per ha) within the sites (2 ha)
WOOD20	Dead wood (m^3 per ha) within a radius of 20 km
WOODCON20	Dead coniferous wood (m^3 per ha) within a radius of 20 km
WOODDEC20	Dead wood (m^3 per ha) within a radius of 20 km
WOODOAK20	Dead oak wood (m^3 per ha) within a radius of 20 km
DECAYING20	Decaying wood (m^3 per ha) within a radius of 20 km
DECAYED20	Deeply deacyed wood (m^3 per ha) within a radius of 20 km
SNAG20	Standing dead wood (m^3 per ha) within a radius of 20 km
LOG20	Lying dead wood (m^3 per ha) within a radius of 20 km
Landscape characters	
FIELD	Percentage area of fields within a radius of 10 km
IMPCONIF	Percentage area of coniferous impediment within a radius of 10 km
MIXED	Percentage area of mixed coniferous forest within a radius of 10 km
CLEARING	Percentage area of clear-cut forest within a radius of 10 km
DECID	Percentage area of deciduous forest within a radius of 10 km
KEYHAB	Percentage area of forest key biotopes within a radius of 1 km
KEYHABCON	Percentage area of woodland key habitats and protected areas of coniferous forest within a radius of 1 km
KEYHABMIX	Percentage area of woodland key habitats and protected areas of mixed coniferous forest within a radius of 1 km
KEYHABDEC	Percentage area of woodland key habitats and protected areas of broadleaf forest within a radius of 1 km
KEYHABOAK	Percentage area of woodland key habitats and protected areas of oak forest within a radius of 1 km
KEYHAB10	Percentage area of forest woodland key habitats and protected areas within a radius of 10 km
KEYHABCON10	Percentage area of woodland key habitats and protected areas of coniferous forest within a radius of 10 km
KEYHABMIX10	Percentage area of woodland key habitats and protected areas of mixed coniferous forest within a radius of 10 km
KEYHABDEC10	Percentage area of woodland key habitats and protected areas of broadleaf forest within a radius of 10 km
KEYHABOAK10	Percentage area of woodland key habitats and protected areas of oak forest within a radius of 10 km

hibernating specimens have been found as adults under loose bark (Plassman, 1975; Ostroverchova and Isotov, 1986; Yakovlev, 1988). For sampling details, see Nordén et al. (2004).

Variables for dead wood densities within a 20 km radius are based on data from the Swedish National Forest Inventory (“Riksskogtaxeringen”) for the period 1998–2000 (Table 1). Classification into decay stage is based on the proportion of the wood volume consisting of decomposed wood: 0–9%, hard wood; 10–25%, slightly decayed wood; 26–75%, decayed wood; and 76–100%, well-decayed wood (for more details see Fridman and Walheim, 2000, or http://www-riksskogstaxeringen.slu.se).

Many of the variables applied in the study from the boreal zone (Økland, 1996) were not available in the boreonemoral study area, such as the percentage area of oldgrowth forest per 100 km^2. This variable was a strong gradient and predictor in the boreal zone (Økland, 1996). Instead we collected data on woodland key habitats and protected areas (Table 1). In southern Sweden, semi-natural forest stands with high biodiversity values occur as very small fragments in the dominating production forest; they are currently mapped as woodland key habitats (or woodland key habitats, see Gustafsson, 2002; Götmark and Thorell, 2003). In south Sweden, almost 80% of the forest is privately owned and the majority of the woodland key habitats have been identified on private land (NBF, 1999). We estimate that there are between 5000 and 10,000 woodland key habitats with an oak component exceeding 20% by volume and a mean size of about 1–2 ha (see Götmark and Thorell, 2003). However, there are even more woodland key habitats containing coniferous or mixed forest in southern Sweden (e.g., NBF, 1999). The woodland key habitats are identified on the basis of forest structure and indicators species, and are defined as 'natural' stands likely to contain red-listed species (NBF, 1999; Gustafsson, 2000). We obtained data on woodland key habitats from the regional forestry boards. In addition, we included areas of protected forests described as old, natural, with high richness of dead wood or with high numbers of red-listed species. Areas of woodland key habitats and protected forests were calculated using the GIS program ArcView.

2.4. Statistical methods

Inter-relationships among the environmental variables were analysed with Spearman rank correlation (Freund, 1992). Using probability plots, all species number variables were found to be approximately normally distributed, allowing us to use parametric statistics. The relationships between species-richness of mycetophilids and environmental variables were analysed by stepwise multiple regression (Weisberg, 1985), using a maximum number of three explanatory variables per regression (as in Økland, 1996).

In the comparisons of species numbers between boreal and boreonemoral sites we used two-sample t test (Freund, 1992). Before using the t test, we checked all variables of species numbers and found them to be very close to a normal distribution (probability plot), and without significant differences ($P < 0.05$) in variance between the groups to be tested (F test; Freund, 1992). The size of the boreal and boreonemoral study areas did not differ markedly, and comparisons were performed per site to reduce possible influence of difference in geographical sampling area. All of the above-mentioned analyses were performed in SYSTAT 8.2. In addition, we used principal component analysis (PCA) to analyse the differences in species composition between boreal and boreonemoral sites. This analysis was performed in CANOCO version 4.5A (ter Braak and Smilenauer, 2002). All species data were transformed to binary occurrences, and no species or samples were excluded. Scaling was focused on inter-sample distances (see ter Braak and Smilenauer, 2002). Box-whiskers plots were made using the program R (http://www.r-project.org).

3. Results

3.1. Analysis of boreonemoral sites

The trap captures in the boreonemoral sites contained altogether 227 species and 6614 specimens of mycetophilids (= Sciaroidea excluding the families Sciaridae and Cecidomyiidae). The number of species per family was 208 in Mycetophilidae, 13 in Keroplatidae, three in Bolitophilidae, two in Diadocidiidae and one in Ditomyiidae (Kurina et al., in print). In the present material, 66 species are known from habitats in decaying wood and 40 species are known from soil-inhabiting fungi. The largest group of species is associated with basidiomycetes (76), while smaller groups breed in ascomycetes (15) or myxomycetes (2).

The material from the 15 sites revealed a geographical gradient in species richness. Despite equal sampling effort, the most species-rich site in the north-western corner of the study area (109 species) had about four times as many species as the most species-poor site in the south-eastern corner (27 species) (Fig. 2(a)). Similar gradients were found for species within the subgroups of mycetophilids (Fig. 2(b) and (c)).

A strong correlation ($R = 0.78$) between species-richness and abundance of specimens indicated a connection between species-richness and the productivity of mycetophilids in the sites and surrounding areas (Table 4). Rarefaction showed relatively small variation between sites, and this measure was only weakly correlated with the number of species in the sites (Table 4).

In total, 43 environmental variables were considered to explain the marked variation in species richness among the sites (Table 1). Many variables with significant inter-correlations were excluded in the final round of multiple regressions (Table 2). Some of the geographical and climatical variables were strongly inter-correlated, i.e., *PREC*, *TEMP* and *ELEVATION*. The variable *PREC* was chosen as representative of this complex gradient of inter-correlated variables due to its biological role for mycetophilids (see Section 4).

In the stepwise multiple regression, the variation in species richness among sites was best explained by the above-mentioned complex gradient represented by *PREC*, accounting for 47% of the variation in species richness (Table 3). In the second step, LONGITUDE was the strongest variable in combination with *PREC*

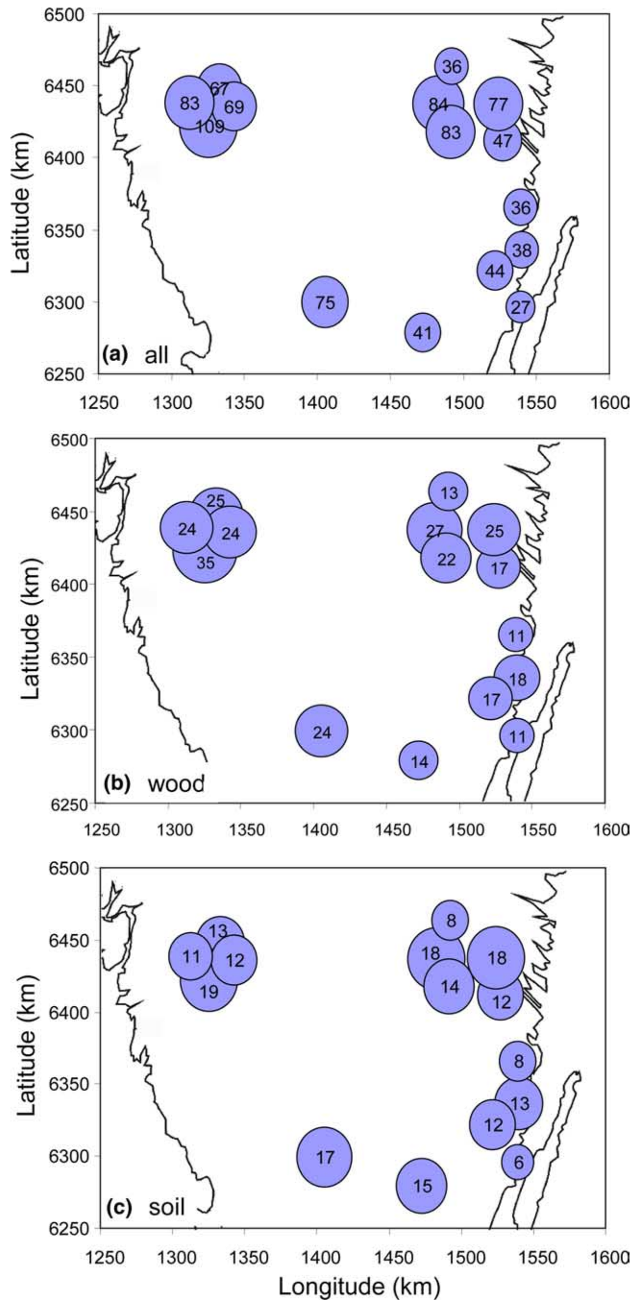


Fig. 2. Species richness of all mycetophilid species (a), mycetophilid species associated with wood-inhabiting fungi (b), and mycetophilid species associated soil-inhabiting fungi (c). Species numbers per site is given within circles and is proportional with circle area. Coordinates are according to the Swedish National Grid.

(Table 3). *LONGITUDE* was negatively correlated with total species richness of mycetophilids (decreasing number of species towards east). Furthermore, it was negatively correlated with *HUMID* ($R = -0.81$) and positively correlated with *TEMP* ($R = 0.87$). The percentage coverage of woodland key habitats and protected areas of mixed forests within a surrounding circle of 1 km radius (*KEYHABMIX*) was selected as the third factor. A multiple regression combining the three selected variables (*PREC*, *LONGITUDE* and *KEYHABMIX*) explained 79% of the variation in species richness (Table 3).

Including only species associated with wood-inhabiting fungi, the percentage coverage of woodland key habitats and protected areas of mixed forests (*KEYHABMIX*) was selected as the first factor, explaining 47% of the variation. The same variable as for all species, *LONGITUDE*, was selected as second variable. The third variable selected was a negative influence of the percentage coverage of fields within a circle of 10 km radius (*FIELD*). These three variables accounted for 79% of the variation in species richness of species associated with wood-inhabiting fungi (Table 3).

Testing the species associated with soil-inhabiting fungi, the same first predictor as for species associated with wood-inhabiting fungi, *KEYHABMIX*, was selected in the first step. *PREC* was added in the second step, and a negative influence of the percentage coverage of coniferous impediment (forest producing less than 1 m^3 per ha and year) within a circle of 10 km radius, *IMPCONIF*, was added in the third step. These three variables explained 70% of the variation in species richness (Table 3).

3.2. Comparison with boreal sites

The mean number of mycetophilid species per site was significantly higher in boreal forest (76.2) than in boreonemoral forest (58.5) (two-sample t test: $t = 2.22$, $P = 0.034$). However, there was considerable variation among sites in each vegetation zone (Fig. 3). Considering mycetophilids associated with wood- and soil-inhabiting fungi separately, boreal and boreonemoral forests had similar numbers of species per site (mean 22.3 in boreal and 20.1 in boreonemoral for mycetophilids associated with wood-inhabiting fungi, and 13.1 in boreal and 12.4 in boreonemoral for mycetophilids associated with soil-inhabiting fungi). The variation between sites was large (Fig. 3(b) and (c)), and the two-sample t tests between boreal and boreonemoral forest were non-significant for these sub groups ($t = 1.32$ and $P = 0.20$ for mycetophilids associated with wood-inhabiting fungi, and $t = 0.96$ and $P = 0.34$ for mycetophilids associated with soil-inhabiting fungi).

The analysis of species composition showed a marked difference between boreal and boreonemoral sites. Principal component analysis of the binary species values (365 species) of all boreal (15) and boreonemoral (17) sites, gave eigenvalues 0.244 for the first axis, 0.104 for the second axis, 0.061 for the third axis, and 0.046 for the fourth axis. A plot based on the first and second PCA axes revealed a clear separation of boreal and boreonemoral sites along the first axis (Fig. 4). Con-

Table 2
Spearman rank correlation (×100) between environmental variables

	LONGITUDE	*LATITUDE*	*ELEVAT*	*PREC*	*TEMP*	*HUMID*	*WOODCOURS*	*WOOD*	*WOODOAK*	*LOG*	*PH*	*MIXED*	*CLEARING*	*WOOD20*	*WOODCON20*	*WOODDEC20*	*WOODOAK20*	*DECAYING20*	*DECAYED20*	*SNAG20*	*LOG20*	*KEYHAB*	*KEYHABMIX*	*KEYHABDEC*	*KEYHABOAK*	*KEYHAB10*	*KEYHABCON10*	*KEYHABMIX10*	*KEYHABDEC10*
LATITUDE	-40	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
ELEVAT	-78	20	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
PREC	-61	17	81	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
TEMP	87	-15	-87	-64	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
HUMID	-81	22	68	60	-66	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
WOODCOURS	54	-28	-53	-76	56	-43	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
WOOD	51	-6	-48	-39	53	-54	52	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
WOODOAK	45	-20	-55	-62	49	-20	71	38	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
LOG	52	-1	-40	-38	56	-49	56	90	29	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
PH	36	3	-21	12	40	-17	-21	19	-36	29	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
MIXED	-43	8	57	36	-46	17	-40	-18	-46	-8	-10	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
CLEARING	-36	-14	54	20	-46	25	-16	-22	-13	-8	-35	83	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
WOOD20	-58	-1	36	28	-45	58	-12	-4	18	-20	-31	32	29	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
WOODCON20	-44	-7	52	62	-44	36	-35	0	-40	-13	26	34	10	61	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
WOODDEC20	-39	12	-8	-17	-16	42	14	-5	54	-17	-65	-10	11	62	-14	.	.	.	.	.	.	.	.	.	.	.	.	.	.
WOODOAK20	49	-51	-63	-72	52	-34	70	47	75	44	-23	-22	6	14	-34	42	.	.	.	.	.	.	.	.	.	.	.	.	.
DECAYING20	-25	-21	1	-2	-11	28	25	30	37	9	-31	1	6	74	47	58	29	.	.	.	.	.	.	.	.	.	.	.	.
DECAYED20	-51	22	9	-20	-32	22	9	-22	16	-39	-75	12	12	44	-7	66	12	36	.	.	.	.	.	.	.	.	.	.	.
SNAG20	-65	-8	60	61	-67	63	-33	-20	-10	-36	-27	26	18	85	75	35	-22	63	25	.	.	.	.	.	.	.	.	.	.
LOG20	-49	22	17	4	-23	50	4	8	31	-6	-28	22	20	90	42	71	25	66	53	59	.	.	.	.	.	.	.	.	.
KEYHAB	29	-45	-1	29	19	0	-13	37	-2	38	41	2	6	-1	17	-21	21	-1	-63	5	-12	.	.	.	.	.	.	.	.
KEYHABMIX	10	2	6	36	14	13	-18	37	-3	46	39	6	-3	9	11	-7	7	-8	-53	11	6	82	.	.	.	.	.	.	.
KEYHABDEC	36	-71	-27	-20	23	-25	-1	-17	2	-28	8	-2	14	-20	-7	-16	27	-1	-9	-24	-27	24	-30	.	.	.	.	.	.
KEYHABOAK	36	-67	-15	-3	19	-34	15	55	8	48	15	22	20	14	24	-16	51	21	-34	11	-1	76	52	30	.	.	.	.	.
KEYHAB10	65	-6	-29	-2	53	-51	8	40	-20	46	74	-26	-45	-65	-5	-79	-20	-41	-78	-47	-63	42	36	6	22	.	.	.	.
KEYHABCON10	35	2	17	40	15	-21	-24	19	-24	24	58	0	-5	-41	18	-72	-36	-44	-78	-20	-45	51	41	5	19	71	.	.	.
KEYHABMIX10	27	7	9	34	25	-8	-11	36	5	45	37	22	11	-1	10	-25	0	-19	-59	0	-1	69	84	-23	44	46	65	.	.
KEYHABDEC10	56	-28	-59	-40	62	-41	38	24	10	15	47	-47	-58	-31	-2	-28	14	10	-24	-33	-22	5	-16	41	6	57	3	-14	.
KEYHABOAK10	81	-21	-64	-41	77	-76	40	42	9	45	49	-29	-44	-60	-24	-51	15	-23	-48	-57	-52	17	8	25	24	79	29	24	79

The shading denotes strong correlations (abs(R_s) > 0.70).

Table 3
Multiple regressions between the three best explaining predictors and the dependent variables (a) total number of species, (b) number of species associated with wood-inhabiting fungi, and (c) number of species associated soil-inhabiting fungi

Dependent	Predictors	Coefficient	SE	*T*	*P*	Multiple R^2 adj
(a) Species total	CONSTANT	137.857	78.998	1.745	0.112	
	(1) *PREC*	1.387	0.600	2.312	0.043	0.468
	(2) *LONGITUDE*	−0.115	0.041	−2.806	0.019	0.595
	(3) *KEYHABMIX*	17.589	7.208	2.440	0.035	0.785
(b) Species in wood fungi	CONSTANT	71.038	12.904	5.505	0.001	
	(1) *KEYHABMIX*	5.37	1.608	3.341	0.007	0.472
	(2) *LONGITUDE*	−0.035	0.009	−3.995	0.003	0.718
	(3) *FIELD*	−0.168	0.077	−2.172	0.055	0.789
(c) Species in soil fungi	CONSTANT	0.891	6.197	0.144	0.889	
	(1) *KEYHABMIX*	4.967	1.369	3.629	0.005	0.424
	(2) *PREC*	0.154	0.100	1.544	0.154	0.473
	(3) *IMPCONIF*	−0.723	0.355	−2.040	0.069	0.698

Multiple R^2adj = cumulative R^2-values, adjusted for degrees of freedom.

sidering the sum across all sites within each vegetation zone, 252 species were captured in the15 boreal sites and 241 in the 17 boreonemoral sites. A total of 124 species occurred only in boreal sites, 113 species only in boreonemoral sites, and 128 were found in both regions.

4. Discussion

The regional scale is important for understanding biodiversity patterns (Ricklefs, 1987; Cornell, 1999). However, the biogeographic diversity patterns that are

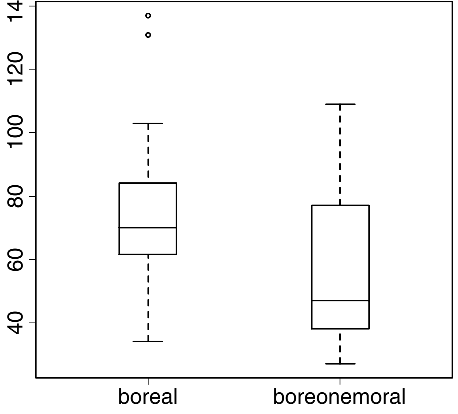
Table 4
Number of mycetophilid species (Spp.), number of individuals (Ind.) and rarefaction (Rarefact.) in each site; and Spearman rank correlation between these measurements

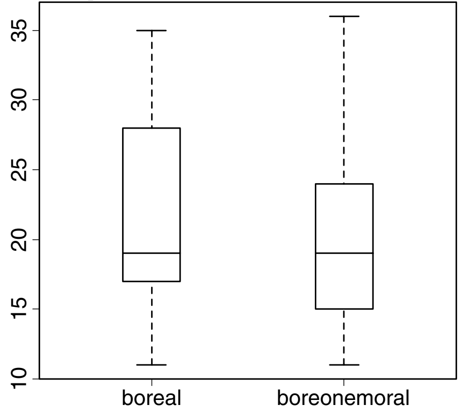
Site codes	Site name	Longitude	Latitude	Elevation.	All species			Species in wood			Species in soil		
					Spp.	Ind.	Rarefact.	Spp.	Ind.	Rarefact.	Spp.	Ind.	Rarefact.
EMS	Emsfors NB	1539723	6336257	10	38	146	33.9	18	103	14.1	13	30	12.1
FAG	Fagerhults NB	1483099	6437257	170	84	579	33.2	27	425	10.8	18	219	5.9
FRÖ	Fröåsa NB	1491305	6418101	190	83	667	34.5	22	396	11.0	14	183	5.4
FÅR	Fårbo NB	1538890	6365604	35	36	164	31.1	11	68	11.0	8	27	8.0
GET	Getebro NR	1521890	6321599	67	44	285	31.5	17	205	11.7	12	44	10.5
HAL	Hallingeberg NB	1526971	6412083	85	47	157	40.6	17	102	14.6	12	57	8.6
KAR	Karla NB	1333240	6448228	110	67	619	30.3	25	392	10.5	13	346	3.6
KRÅ	Kråksjöby NB	1472274	6279102	155	41	344	23.9	14	262	8.7	15	92	8.0
LIN	LindöNR	1539339	6296250	5	27	308	18.0	11	197	7.4	6	48	4.9
LÅN	Långhults NB	1405344	6299701	180	75	667	29.9	24	502	9.4	17	333	5.3
SAN	Sandviksås NB	1325557	6422456	200	109	692	47.1	35	308	18.3	19	196	9.0
SKÖ	Skölvene NB	1342710	6435900	140	69	569	32.3	24	392	11.7	12	232	4.5
STA	Stafsäter NR	1492277	6463954	100	36	119	36.0	13	70	12.8	8	50	6.3
ULV	Ulvsdal NB	1524191	6437347	90	77	763	32.5	25	394	11.4	18	345	5.4
ÖST	Östadkulle NB	1312401	6438527	115	83	535	40.2	24	240	14.7	11	114	6.4
Minimum value				5	27	119	18.0	11	68	7.4	6	27	3.6
Maximum value				200	109	763	47.1	35	502	18.3	19	346	12.1
Spearman correlation (R_s):													
Spp. X Ind.						0.78			0.74			0.62	
Spp. X Rarefact.						0.47			0.20			0.06	

Coordinates are given in Swedish National Grid (m).

presented for many insect groups often reflect the distribution of entomologists (Dennis and Hardy, 1999). Ecologists rarely have the opportunity to sample a taxon in many sites at a regional level, and to quantify relevant environmental variables for these sites, as has been done in the present study. Studies of environmental prediction for biodiversity patterns at a regional scale are therefore rare, at least for insect groups (but see Økland, 1996; Lobo and Martin-Piera, 2002).

The most important factors in the current study were large-scaled, such as the climatic and geographical variables *PREC* and *LONGITUDE*, and the landscape variables *KEYHABMIX* and *FIELD*. Other variables recorded locally within sites, which could be expected to be important, did not turn out to be statistically significant. It should not be excluded that local variables could be significant by choosing a different temporal resolution, such as yearly precipitation instead of a long-term mean (1960–90), or including both 2001 and 2002 of the fungal variables. However, several empirical and theoretical studies conclude that population dynamics most often are determined by ecosystem processes operating at regional or relatively large scales, and many authors point out climatical factors as particularly important (Bjørnstad, 2000; Koenig, 2002). Large-scaled variables were also the major explanatory factors in studies of mycetophilids (Økland, 1996) and saproxylic beetles (Siitonen, 1994; Siitonen and Martikainen, 1994; Økland et al., 1996) in the boreal zone. Very localised variables, including breeding substrate used by insects (e.g., *FUNGI*, *ASCOMYC*, *BASIDIO*), appear to be relatively unimportant, possibly due to their mismatch with ecosystem processes dominating over a large region (Wiens, 1989; Kotliar and Wiens, 1990; Forman, 1995), or because large-scaled variables often dominate when local communities are unsaturated. Examination of the relationship between local and regional species richness by modeling and empirical


(a) all species


(b) species in wood

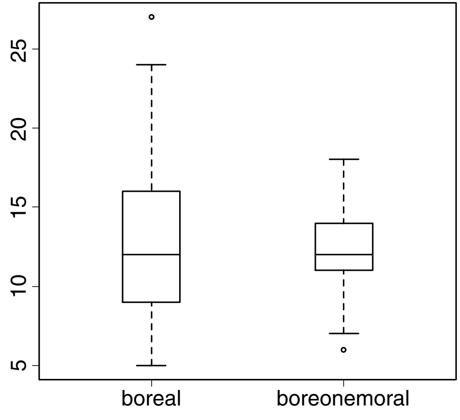

(c) species in soil

Fig. 3. Box-whiskers plots of species number per site within boreal and boreonemoral forests for all mycetophilid species (a), for species associated with wood-inhabiting fungi (b), and for species associated with soil-inhabiting fungi (c). The central line shows the median, the box indicates first and third quartiles, and the whiskers show the largest and smallest observations that fall within a distance of 1.5 times the box size from the nearest quartile. Additional points are extreme values beyond this distance.

studies shows that most local communities are unsaturated and therefore often are dominated by regional factors (Cornell, 1999).

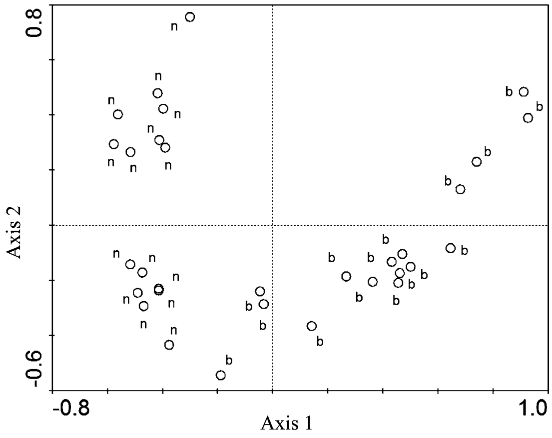


Fig. 4. PCA sample plot of mycetophilid species trapped by malaise traps in 15 boreal and 17 boreonemoral forest sites (binary data). b, boreal sites; n, boreonemoral sites.

Many organism groups decrease in species richness towards north in Fennoscandia, probably as a result of colder climate and decreasing productivity (Wright et al., 1993). For example, saproxylic beetles (Stokland, 1994) and vascular plants (Hultén, 1971; Lahti et al., 1988) are known to be more diverse towards the nemoral and warmer forest areas. Thus, the pattern of increasing species richness of mycetophilids towards north and west in the region is remarkable, and so is the high species-richness in boreal forests compared to boreonemoral forests. Several parameters that normally are supposed to favour high biodiversity, such as temperature and abundance of broad-leaved trees, are increasing towards southeast in the study area (Rohde, 1992; Stokland et al., 2003). The relatively high diversity found in boreal forests can not be ascribed to methodological differences. On the contrary, the species-richness of the boreal forests could be under-estimated due to smaller samples (one trap sample per site is expected to be less species-rich than two half trap samples per site in the boreonemoral part), shorter sampling period, and smaller geographical extent of the study area compared to the boreonemoral forests (see Section 2). High species numbers of mycetophilids in areas in the boreal zone is not unique for south Norway (Økland, 1996). Previous inventories of mycetophilids in northern regions showed remarkably high species numbers, such as 400 species from the province Lule Lappmark (35,470 km^2) at the Arctic circle of northern Sweden (Hedmark, 1998) and 616 species in Karelia (180,500 km^2) (Polevoi, 2000).

There seems to be some properties that make the boreal forests in the central and northern parts of Fennoscandia especially suitable for mycetophilids. Precipitation (*PREC*) was a strong positive factor for species-richness of mycetophilids, and there was a negative influence of landscapes with higher contents of fields (*FIELD*) and coniferous stands with a low tree density (*IMPCONIF*). All of these results are consistent with previous knowledge about this insect group. Dry forest conditions have been suggested to be unfavourable for mycetophilids (Väisänen, 1984; Økland, 1995, 1996). Mycetophilids are frequently observed in dark and closed forests, and they are often found in moist holes or under root jars, especially during dry periods. Increasing precipitation (*PREC*) was positively correlated with elevation (*ELEV*) and negatively correlated with temperature (*TEMP*). These regional gradients may be regarded as parts of a gradual transition towards boreal forests. A mixture of coniferous and deciduous forest elements seems to favour species-richness of mycetophilids. One might argue that we should have seen a positive effect of the proportion of coniferous forest at landscape level in the boreonemoral study area, which was not the case. The coniferous forests in the Swedish study area include a large proportion of conifer plantations (few stands older than 100 years). These stands are planted in areas that are more suitable for deciduous trees in the boreonemoral zone (see maps in Stokland et al., 2003) and are probably suboptimal for mycetophilids due to their lack of continuity in time (Økland, 1994, 1996).

The strong influence of percentage coverage of woodland key habitats and protected areas with mixed forest agrees with previous results on the preferences of mycetophilids, although the response to forest variables at the landscape level differed somewhat from those of the boreal forest. In boreal forests of southeastern Norway, the percentage coverage of old growth in the surrounding 100 km^2, and the continuity in dead wood and tree cover at the stand level, were the major determinants of high species richness (Økland, 1994, 1996). Woodland key habitats of mixed forests in the current study area share some of these qualities by generally having more continuity in dead wood in different stages of degradation compared to surrounding forest landscapes (NBF, 1999). Since mixed forest includes both coniferous and deciduous forest elements, it probably promotes high species richness by combining mycetophilid habitats from both forest types. The wide range in coverage of oldgrowth in the study of southeastern Norway (from 16.7% to 76%; Økland, 1996) was, however, absent in the present study of boreonemoral forest, where key habitats typically cover only 0–6% of forest landscapes (NBF, 1999; Stokland et al., 2003).

4.1. Conclusions and implications for conservation and management

Mycetophilids is a species rich insect group, also in former open woodland pastures that have been invaded by other tree species. Woodland key habitats and protected areas with mixed forest of conifers and deciduous trees appear to be the forest habitats with highest species-richness of mycetophilids in boreonemoral forests. Future changes in the extent of such key habitats and similar forest stands are probably decisive for the survival of sensitive species of mycetophilids.

Our results also have more general implications for conservation and for monitoring of forest biodiversity. Mycetophilids could be suggested as an indicator group of boreal forests due to their large diversity in such habitats. In many cases, monitoring is done locally in one or a few study areas, e.g., by scientists in long-term studies or by volunteers studying attractive sites. Our results for mycetophilids in boreonemoral forests suggest that climate and geography are very important determinants of species richness. Therefore, if our results are relevant for other taxa, variation in such factors at larger scales should be considered in monitoring and conservation work.

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