

Mycetophilidae (Diptera), an insect group vulnerable to forestry practices? A comparison of clearcut, managed and semi-natural spruce forests in southern Norway

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The mycetophilid fauna and environmental variables were studied at 15 sites within a spruce forest in southern Norway. There were five replications of each of the following categories: semi-natural forests, clearcuts, and managed forests (clearcut 70–120 years ago). Clearcutting seems to induce a long lasting effect on the Mycetophilidae fauna. The semi-natural forests were more species-rich and contained more 'potentially rare' species than the two other categories. Even though managed forests and clearcuts differed in faunal composition, their species richness was not significantly different. Continuity is probably a main factor for maintaining the diversity of Mycetophilidae species. Lumping the 15 sites together, the number of species was strongly correlated with the (temporal) continuity of tree cover and substrates, which may reflect an increased diversity of fungal habitats both in dead wood and on the ground. The degree of continuity was recognized by means of indicator species of fungi, lichen and vascular plants. The amount of dead wood was correlated with the species diversity, but was probably dependent on the continuity factor, since clearcuts with much dead wood had relatively fewer species.

Important elements in a strategy for conservation of the diversity of mycetophilid species seem to be: (i) to identify and protect the remnant patches of forests with long continuity, (ii) as far as possible, to practice timber harvesting in earlier clearcut forests instead of semi-natural forests.

Keywords: Mycetophilidae; diversity; spruce forest; clearcut; continuity

Introduction

Maintaining biological diversity and avoiding extinction of species are official goals for Norwegian forestry (DN-report, 1989). However, basic knowledge about ecological requirements is lacking for several species-rich groups of organisms. Reaching this goal will demand rapid progress in the research on less-studied groups, which may constitute a substantial part of the diversity in forests. Only then will we be able to choose optimal strategies for maintaining diversity. These ideas have motivated the research programme 'Forest Ecology and Multiple Use', which supported the present project.

Mycetophilidae is a diverse family of small to medium-sized dipterous insects. They are numerous in forest environments, but little is known about the impact of forestry practices on this family. The Finnish check list contains more than 450 species of Mycetophilidae (Mycetophilidae s.str.; Hackman, 1980). Norway has no modern check list for Diptera, but the number in Norway is presumed to be on the same order

(Ottesen, 1993). Extensive studies of Mycetophilidae have been carried out in the context of taxonomy (see references in Hackman *et al.*, 1988), as well as host selection and seasonality (Buxton, 1954, 1960; Dely-Draskovits and Babos, 1976; Hackman and Meinander, 1979; Russel-Smith, 1979; Väisänen, 1981; Yakovlev, 1988a; Kurina, 1991). The larvae of most species develop in fungal microhabitats, however, a few species feed on algae, mosses and liverworts or are saprophagous in bird nests (Hackman *et al.*, 1988). Few authors have compared the mycetophilid fauna in different forest types, perhaps due to the time-consuming identification work. One exception is a comparison of the mycetophilid fauna in *Pinus* and *Populus* forests in Karelia (Yakovlev, 1988a,b; Yakovlev and Zaitzev, 1990). Earlier comparisons of mycetophilid fauna in managed and unmanaged forests are not known to the author, but such studies exist for beetles (Gutowski, 1986; Biström and Väisänen, 1988; Väisänen *et al.*, 1993).

In the present paper, the mycetophilid fauna is compared between (i) semi-natural forests (ii) managed forests and (iii) clearcuts. The diversity, the occurrence of 'potentially rare species', and the frequency of the most abundant species, are related to selected environmental variables. The most important factors for maintaining the diversity of Mycetophilidae are discussed in relation to the present results and existing knowledge about habitat requirements.

Materials and methods

Study area

The study was conducted in Østmarka forest (UTM: N 636100, E 148000) about 15 km east of Oslo, Norway. The area is dominated by spruce forest (*Picea abies*) with scattered deciduous trees (*Betula* sp., *Populus tremula*, *Salix caprea*, *Sorbus aucuparia*, *Alnus incana*, *Prunus padus*), except for a dominance of pines (*Pinus sylvestris*) on ridges and hilltops. The bedrock of the whole area consists of gneisses. The landscape is intersected by many small north-south valleys with only slight variation in elevation.

Site descriptions

Mycetophilids were collected at 15 sites, five in semi-natural forests (only selectively cut), five in managed forests (clearcut 70–120 years ago), and five in clearcuts (clearcut 2–3 years ago). All sites were situated within an area of 90 km² in the central part of Østmarka forest. The elevation ranged from 200 to 300 metres above sea level. All sites were confined to varieties of *Eu-Piceetum myrtilletosum* potential vegetation type. However, there were consistent vegetational differences between the forest types.

Four of the semi-natural sites (S-N 2 – S-N 5) were chosen within the Østmarka forest reserve (12.5 km²) in the centre of the forest. According to older forest workers and managers, this area has only been selectively cut (most recently about 60 years ago). Marks after forest fires were found. Measurement of single spruce trees in the reserve has shown ages up to 227 years (Hoel, 1993). During the Second World War (1940–45), the amount of dead wood was considerably reduced by an intense period of firewood cutting (Olav Larsen personal communication). The amount of dead wood has increased considerably during the last decades as a result of the reserve plans, and today the density of dead wood is generally high.

The fifth semi-natural site (S-N 1) was placed in a small area (0.1 km²) of nearly

primaeval forest, completely surrounded by managed forest, about 5 km to the north of the reserve. This site has probably not been cut, due to different access; and may even have avoided fires due to the moist conditions in the valley bottom (Zackrisson and Østlund, 1991).

The sites in managed forests (MAN 1–5), situated in a forest about 4 km to the south of the reserve, were extensively clearcut at the beginning of this century. This forest supplied a pulp industry and match production. The same area contained three of the clearcut sites (CLC 2–4), while the two other clearcut sites (CLC 1 and 5) were situated in a cultivated forest about 2 km to the west of the nature reserve. All clearcuts were relatively small, not exceeding 0.038 km².

Environmental variables were recorded within an area of 1600 m² in each site. Each variable is explained in Table 1. The levels of the continuity variable were:

- (i) No continuity: Indicator species are absent. There are indications of comprehensive silviculture, such as relatively even-aged forest, presence of many stumps after a clearcutting, lack of dead wood, and the structure of forest shows signs of extensive thinning.
- (ii) Low continuity: Indicator species of a low level are present. There is no indication of comprehensive silviculture in recent time. The forest may have been selectively cut, but many stumps after a clearcutting are not found. The forest may show signs of interruptions of the continuity. The forest may be more even-aged, and marks may reveal forest fires during the last 200 years.
- (iii) Medium continuity: Indicator species of a medium level are present. No visible indications on interruptions of the continuity. The age structure of the forest is more heterogenous, and dead wood at different stages of disintegration is present.
- (iv) High continuity: Indicator species of the highest level are present. There is no visible indication of interruptions of the continuity. The age structure of the forest is heterogenous, and dead wood at all stages of disintegration are present.

Table 1. Explanation of environmental variables recorded within 1600 m² at each site

Variable	Registration
Wood	vol. pr. 1000 m ² of dead wood in general
Decid	vol. pr. 1000 m ² of dead deciduous wood
Decay	vol. pr. 1000 m ² of dead wood with decay deeper than 5 cm
Mosscov	vol. pr. 1000 m ² of moss-covered dead wood
Sp-Poly	no. of polypore species within the site
No-Poly	no. of polypore fruiting bodies pr. 1000 m ²
Moss	% area of field layer dominated by moss
Heather	% area of field layer dominated by heather
Grass	% area of field layer dominated by grass
Branch	% area of field layer dominated by branch/logwastes (diam. <10 cm)
Stumps	number of artificial stumps pr. 1000 m ²
Cont	indications of long-time continuity in tree-cover and substrates
Tree age	max. age of single trees in the area
Cutting	clearcut (1), or never clearcut (0)
Relascop	Spiegel relascop

This method of indicator species has been developed by surveys of a large number of forests in northern Sweden (Karström, 1992), and has been modified to the spruce forests of southern Norway (Bredesen *et al.*, 1993). Selected species of fungi, lichens and vascular plants are used to indicate different levels of continuity in the bottom layers, continuity in the tree growth, and the continuity of dead and rotting wood. In the present study, there was a medium continuity in site S-N 1, low continuity in the sites S-N 2–5, and no continuity in the other sites.

Sampling methods and species identification

The mycetophilids were collected with one Malaise trap (Townes, 1962) in each of the sites. The traps were randomly placed within each site, with the collection bottle towards the south, and operated from 22 April to 1 June 1991. All male individuals of Mycetophilidae (s.str.) were determined to species, except for the genus *Mycetophila*. The nomenclature is mainly based on the Catalogue of Palearctic Diptera (Hackman *et al.*, 1988), with additions from Zaitzev (e.g. Zaitzev 1984, 1988). Some species deviated from the given descriptions; they may be new species, but are given numbers until a complete check and description is finished (marked sp.1 in the Appendix). Other species could not be identified to species level, but may be the same as other fully identified species in the list (e.g. *Boletina sciarina* gr., *Dynatosoma* sp.). Species known in only few numbers from collections in Fennoscandia were defined as 'potentially rare species'.

Statistical methods

Differences in species numbers between the forest types were tested with model I ANOVA, with an *a posteriori* multiple range test (Sokal and Rohlf, 1981), and with Pearson's test for goodness of fit (Bhattacharyya and Johnson, 1977).

PCA correlation biplot (centered and standardized) was performed on the numbers of species and the 15 environmental variables from the sites (Jongman *et al.*, 1987), by means of the computer programme Canoco, version 3.1. The data were found to conform well to the model of linearity assumed for this technique (Braak and Prentice, 1988). The two first axes showed relatively high eigenvalues (0.643 and 0.284) and explained a large portion of the variation (92.4%). Multiple regression was not applied because of the high degree of colinearity among the variables. Pearson's moment correlation (Bhattacharyya and Johnson, 1977) was applied on the relation between the environmental variables and the numbers of individuals in the seven most abundant species, while Spearman's Rank Correlation (Rs) was used in the cases of variables in ordinal scale.

A comparison of faunal composition was needed when the numbers of species were equal. The low frequency of most of the species implied an assumption of Poisson distribution. A PD test was derived from the index of percent dissimilarity, which has proved to be a good measure of dissimilarity (named Bray-Curtis in Faith *et al.* 1987; A_i and B_i were the numbers of species i in the forest types A and B, and n was the number of species involved):

$$PD = \frac{\sum_{i=1}^n |A_i - B_i|}{\sum_{i=1}^n A_i + \sum_{i=1}^n B_i} \quad (1)$$

A_i and B_i , and the differences $A_i - B_i$ and the sums $A_i + B_i$, were assumed to be pairwise independent and all Poisson distributed. If the sum $A_i + B_i$ is considered as a constant, then $A_i | A_i + B_i$ has a binominal distribution. Under a null hypothesis of equal A_i and B_i , A_i will be $\text{Bin}(A_i + B_i, 1/2)$.

The mean was estimated by ($[m_i/2]$ rounded to a whole number):

$$\mu_i = \frac{m_i}{m} \binom{m_i - 1}{\left[\frac{m_i}{2} \right]} \left(\frac{1}{2} \right)^{m_i - 1} \quad (2)$$

$$m = \sum_{i=1}^n m_i = \sum_{i=1}^n (A_i + B_i) \quad (3)$$

If $m_i \geq 10$:

$$\mu_i \approx \frac{1}{m} \sqrt{\frac{2m_i}{\pi}} \quad (4)$$

and the variance was estimated by:

$$\sigma^2 = \frac{m_i}{m^2} - \mu_i^2 \quad (5)$$

The sums of means and variances for all of the species were used in a test based on an approximately normal distribution:

$$\mu = \sum_{i=1}^n \mu_i \quad \sigma^2 = \sum_{i=1}^n \sigma_i^2 \quad (6)$$

$$H_0 : \lambda_A = \lambda_B \quad (7)$$

Reject H_0 if:

$$\frac{PD - \mu}{\sigma} > Z_\alpha \quad (8)$$

where α is the significance level of the test, and z_α is given from a table of the standard normal distribution.

Results

On the basis of 2724 individuals, 92 species were identified to species level, which is approximately one-fifth of the estimated number of species of Mycetophilidae (s.str.) in Norway.

The average numbers of species differed significantly among the forest types (ANOVA: $F = 5.37$, $p < 0.022$) (Fig. 1). The multiple range test showed no significant

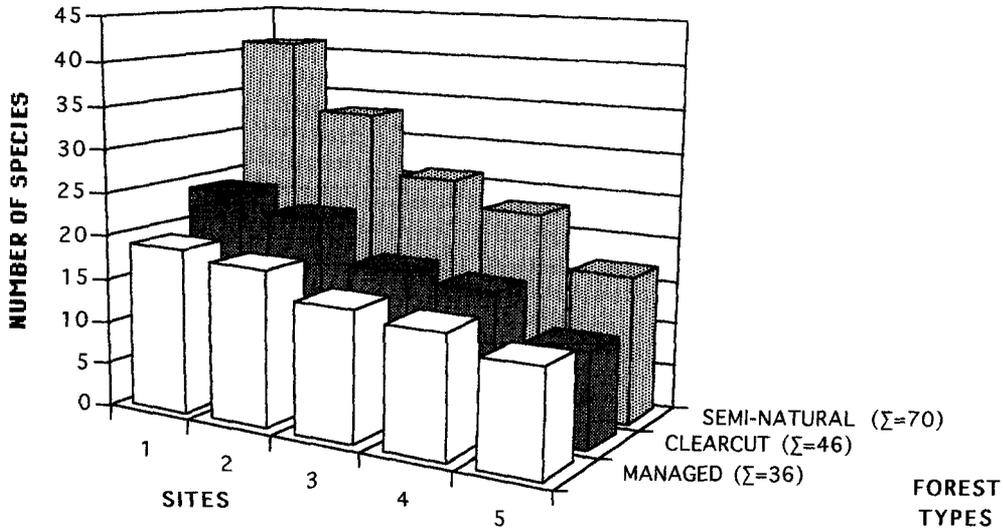


Figure 1. Number of Mycetophilidae species at the different sites and in different forest types. The sites within each forest type are ranked by the number of Mycetophilidae species.

difference between clearcuts (CLC) and managed (MAN) forest sites (mean MAN = 15.6 species, mean CLC = 18 species, confidence interval, $p > 0.05$); however, the average number of species was clearly higher in semi-natural forest compared with both of the other forest types (mean S-N = 28 species, $p < 0.01$). A comparison of the total number of species between the forest types revealed the same pattern. The total number of species was more than 1.5 times higher in semi-natural forest compared with the others (Fig. 1) ($X^2 = 55.5$, d.f. = 1, $p < 0.001$), while clearcuts and managed forests were not significantly different ($X^2 = 1.22$, d.f. = 1, $p > 0.1$). The highest number of

Table 2. Pairwise comparison of faunal composition between the forest types. S-N = semi-natural forest. CLC = clearcuts. MAN = managed forest. Significance levels measured by Z, test indicator of PD-test (see test description under methods)

		S-N against CLC	S-N against MAN	MAN against CLC
species with 1-5 individuals	Z	2.38 ^a	3.72 ^b	0.77 ^c
species with >5 individuals	Z	37.26 ^b	22.37 ^b	52.98 ^b
all species	Z	36.82 ^b	22.48 ^b	52.66 ^b

^a $p < 0.01$

^b $p < 0.001$

^cnon-significant

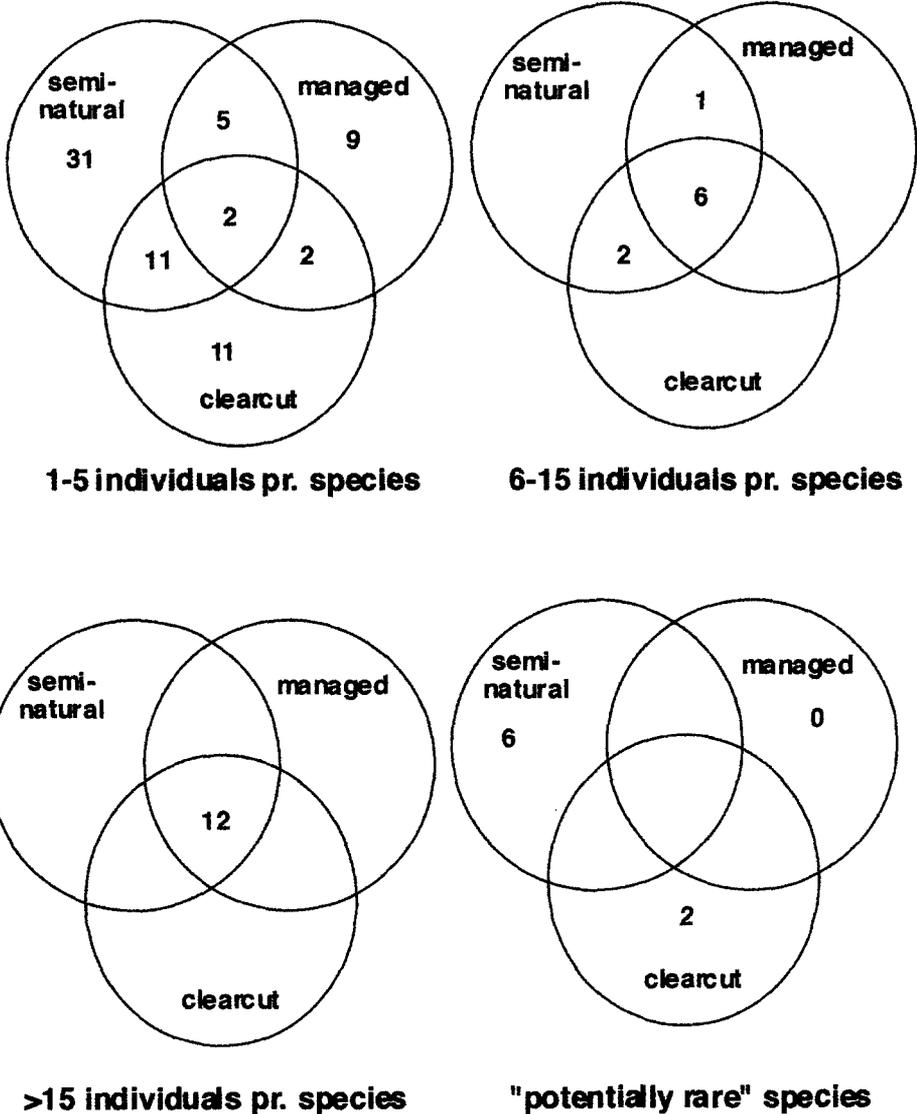


Figure 2. Distribution of mycetophilid species among semi-natural forests, managed forests and clearcuts.

species at a single site (41 species) was recorded at S-N 1, with the number of species about 1.7 times higher than the average of the other semi-natural sites.

Even though the clearcuts and managed forests appeared to be equal in number of species, their faunal composition showed a significant difference. Including all of the species, the faunal composition from all of the forest types were pairwise unequal. However, considering the little occurring species only, the clearcuts and managed forests were not significantly different (PD-test, Table 2).

The semi-natural forest harboured the largest number of 'potentially rare' species

(species which are unknown, or known in only small numbers from Fenno-scandia; Appendix). Among eight 'potentially rare' species, six species were confined to semi-natural forest and two species to clearcuts (Fig. 2).

The frequency distribution was pronouncedly 'few abundant and many infrequent'; and the majority of the infrequent species occurred in the semi-natural forest (Fig. 2). Twelve species occurred in the range of 16–1399 individuals, and nine species in the range of 6–15 individuals. For 71 species, five or fewer individuals were trapped. The number of species in this range was more than double in the semi-natural forest compared with the other types of forest ($X^2 = 12.18$, d.f. = 1, $p < 0.001$).

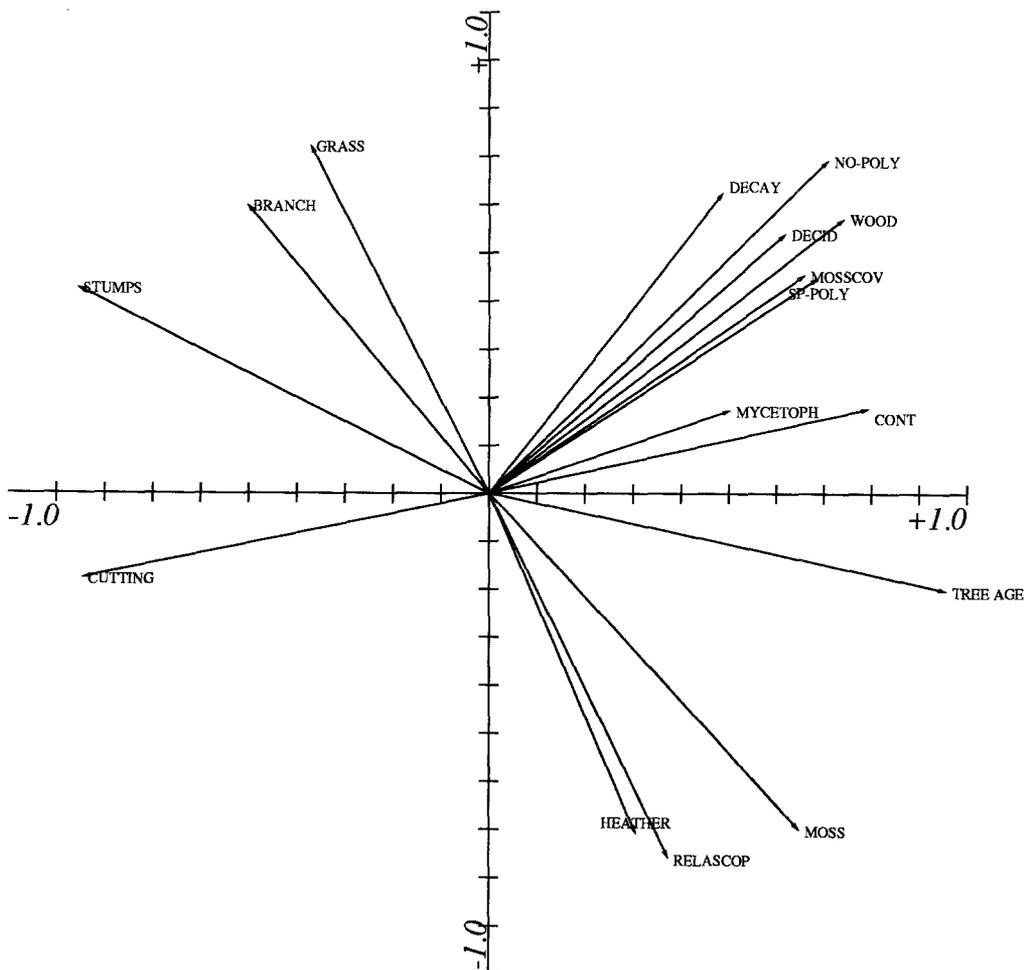


Figure 3. PCA correlation biplot for the numbers of mycetophilid species and environmental variables from all 15 sites (clearcuts, managed and semi-natural forests combined; the variables are explained in Table 1). Variables with vectors pointing in the same direction are positively correlated, variables with vectors in opposite direction are negatively correlated, and vectors perpendicular to each other represent variables that are not correlated.

A correlation biplot (Fig. 3) shows that the number of mycetophilid species was most strongly correlated with the degree of continuity in the forest sites (Spearman $R_s = 0.66$), and had a strongly negative correlation with the cutting regime (clearcut or never clearcut (Spearman $R_s = 0.64$)). Further, several deadwood-related variables (amount of dead wood, dead deciduous wood, decayed dead wood, moss-covered dead wood, polypore fruiting-bodies and polypore species) were intercorrelated, and showed a quite strong correlation with the number of mycetophilid species. Vegetational factors (ground cover of moss, heather and grass), cover of branches/log-wastes, and relascope showed almost no correlation with the number of mycetophilid species, but were clearly intercorrelated. The number of mycetophilid species was only weakly correlated with the distance to a bigger mainland of semi-natural forest (Pearson $R^2 = 0.055$), and the area of semi-natural forest around the site of sampling (Pearson $R^2 = 0.108$).

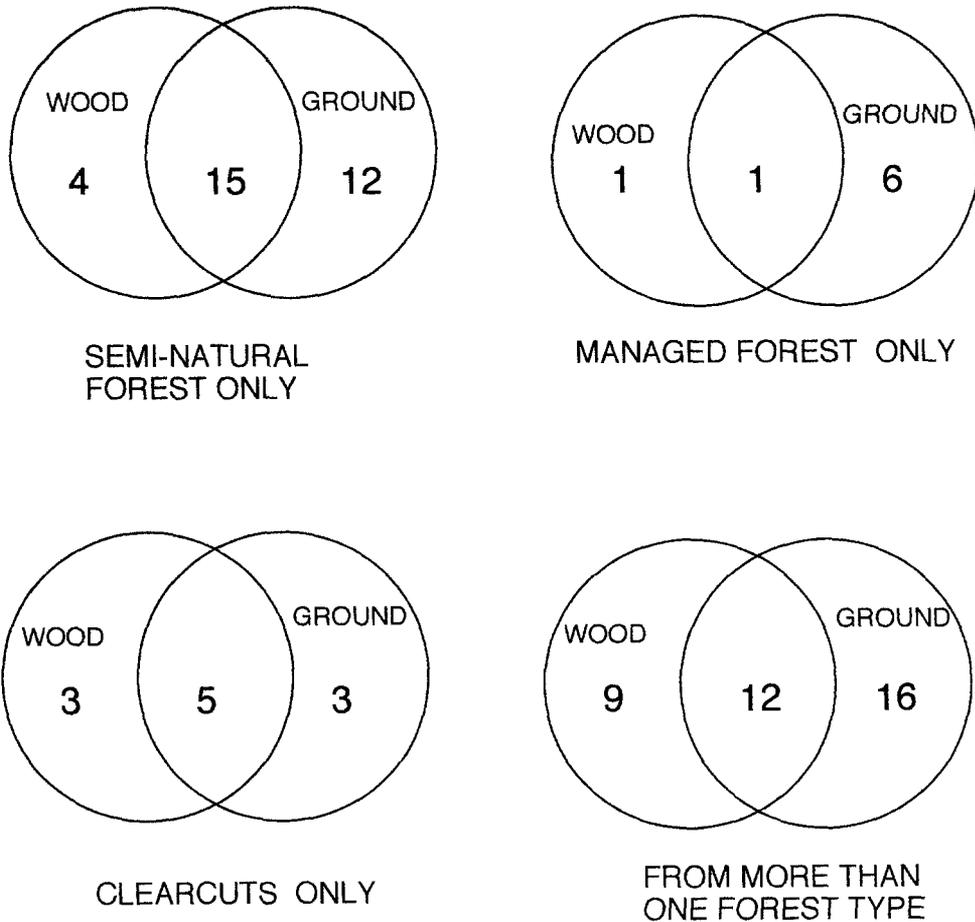


Figure 4. Distribution of mycetophilid species between habitats in dead wood and on the ground in semi-natural forests, managed forests and clearcuts, respectively. Certain species are associated with habitats both in dead wood and on the ground.

Species associated with dead wood did not constitute the major part of the catch, neither among the species only trapped in semi-natural forest, nor in any of the other subgroups (Fig. 4, Appendix). According to the literature, most of the species are described from habits in the soil (e.g. Agaricales) or both habitats in soil and in dead wood.

The relascope and the vegetational variables seemed to be more important for the abundance of the most frequent species. The seven most abundant species constituted 73% of the total number of individuals, and were trapped in the majority of the sites (Table 3). The numbers of individuals in most of these species were most strongly correlated with relascope and the vegetational variables, and are described from habitats on the ground, or both habitats in dead wood or on the ground. Three species in the genus *Cordyla* were most abundant in the managed forest, and showed the strongest

Table 3. Analysis of the most frequent species. Sum = total number of individuals. F% = % of the sites containing the species. Forest type = the forest type with significantly higher or lower numbers of the species. Var = the environmental variables showing strongest correlation with the abundance of the species (see explanations of variables in table 1). Corr = correlation coefficient (Pearson). *p* = significance level. Habitat = rearing habitat according to references (see Appendix)

Species	Sum	F%	Forest type	Var	Corr	<i>p</i>	Habitat
<i>Cordyla nitidula</i>	249	93	most in MAN	heather	0.813	^c	ground
				relascop	0.699	^c	
				grass	-0.642	^c	
<i>Cordyla parvipalpis</i>	67	80	most in MAN	heather	0.807	^c	ground
				relascop	0.78	^c	
				grass	0.621	^a	
<i>Cordyla fusca</i>	79	100	most in MAN	relascop	0.784	^c	ground
				heather	0.758	^c	
				moss	0.564	^a	
<i>Boletina gripha</i>	1399	100	most in CLC	moss	-0.765	^c	ground/wood
				stumps	0.689	^b	
				relascop	-0.611	^a	
<i>Acnemia nitidicollis</i>	63	87	most in CLC	stumps	0.717	^b	ground/wood
				moss	-0.67	^b	
<i>Phronia caliginosa</i>	72	87	fewer in MAN	grass	0.5167	^a	ground/wood
<i>Apolephtisa subincana</i>	65	73	most in S-N	cont	0.616	^a	wood

^a*p* < 0.05

^b*p* < 0.01

^c*p* < 0.001

correlation with heather and relascope. *Boletina gripa* and *Acnemia nitidicollis* were most numerous in the clearcuts, and were negatively correlated with the percent cover of mosses, and positively correlated with the density of artificial stumps. The total number of individuals in clearcuts was about twice the number in semi-natural forests, and three times the number in managed forests. These large differences were solely due to the most abundant species, *Boletina gripa*, with altogether 1399 individuals, of which 1158 were from the clearcuts. Without this species, the total number of individuals was significantly higher at the semi-natural sites ($X^2 = 15.75$, d.f. = 1, $p < 0.01$). *Apolephtisa subincana* differed from the other abundant species: it was described from habitats in dead wood (Appendix), it was most numerous in the semi-natural forest, and it was most strongly considered with the continuity variable.

Discussion

The results of this study indicate that semi-natural forests are more sustaining for mycetophilids, compared with clearcut or managed forests. Both the number of species and the fraction of 'potentially rare' species was much higher in this type of forest. Many of the species were infrequently caught in our traps, which may indicate that their occurrences are more random. However, the same sampling effort in all of the forest types yielded a significantly larger proportion of randomly occurring species in the semi-natural forest. Therefore, the probability that the differences in numbers of species between the forest types can be assigned to chance factors is assumed to be very low.

The local environmental conditions appeared to be more significant for the diversity of Mycetophilidae than the area of semi-natural forest or the distance to potential sources of species. The sites with smallest sizes and longest distances to a bigger mainland of semi-natural forest comprised both the highest and the lowest numbers of mycetophilid species, and the variables area and distance were only weakly correlated with the number of species. However, these landscape variables must be important at some level of the spatial and temporal scales (Kotliar and Wiens, 1990). In other groups of arthropods the area and the distance to 'mainlands of suitable habitat' have proved to be important factors (Rey and Strong, 1983; Hopkins and Webb, 1984; Harrison, 1991). Even though a small and isolated patch showed the highest number of species in the present study, it is not known how long it has been isolated, and how long the species number will persist with the present area and degree of isolation. For the single species, exact information is lacking about how the landscape can be divided into fragments and matrix of suitable and unusable habitats, and it is unknown how the matrix impacts the ecology of the fragments.

The vegetational variables appeared to be important for the abundancies of the most frequent species, but had little influence on the species diversity. Several authors have found a systematic relationship between the flora of green plants and fungi (Gulden, 1982; Arnolds, 1988), but mainly for saprophytic and mycorrhizal fungi in the soil, and to a lesser extent for fungi on substrates above the ground (e.g. dead wood). Probably, the amount of some common host fungi in the soil varies with the amount of certain species of moss, heather or grass at the sites, and therefore has a strong influence on the numbers of individuals in the most abundant mycetophilid species. Most of the abundant species are known from soil-inhabiting fungi, however, existing rearing records

seem to be insufficient for a detailed discussion of the actual host species. The vegetational factor may be more important for the diversity of Mycetophilidae than detected in the present study. The vegetational variables used in this study were rather coarse, and did not consider the composition of plants on the species level. Furthermore, stronger correlation might have been found if the study sites had reflected a marked gradient of vegetational difference (e.g. a gradient from poor to rich flora).

The diversity of Mycetophilidae seems to be linked to more than one local factor, since so many variables were correlated with the number of Mycetophilidae species. All of the variables related to dead wood were clearly correlated with the number of mycetophilid species. The biological interpretations of these correlations may be that many of the species found in this study are associated with dead wood habitats. However, the amount of dead wood in itself is not a sufficient explanation, since the clearcuts with large amounts of dead wood had fewer species. The majority of the species found in this study are not exclusively associated with dead wood, but also utilize habitats in the soil. Therefore, there seems to be some other factor of more fundamental importance. This factor may be the continuity, which showed the strongest correlation and the best fit in a linear regression with the number of Mycetophilidae species.

The importance of continuity in tree-cover and different substrates may be biologically explained by the link to the diversity of fungal habitats. The fungal dimension is assumed to be of major importance for ecosystem function and biodiversity (Hawksworth, 1990). A vast number of plant and animal species have coevolved with fungi (Pirozynski and Hawksworth, 1988). The mycetophilids may have coevolved with the various groups of fungi associated with forest ecosystems, and the imago of several mycetophilid species seem to be adapted to a life in dark and humid habitats under the forest canopy (Ostroverkhova, 1992). Probably, the diversity of Mycetophilidae in a site is directly influenced by the fungal diversity, since most of the species have their larval development in fungal habitats. It is recognized that certain species of fungi are vulnerable to disturbances, and are mainly found in forests with continuity (Karström, 1992), and some of these species were recorded at the semi-natural forest sites. The variables of polypore species and fruiting bodies were clearly correlated with the numbers of mycetophilid species, however, many species of fungi were probably overlooked, or not visible during the registrations (Gulden, 1982; Arnolds, 1988). The interruption of continuity probably reduces the diversity of fungal habitats both in dead wood and in the soil.

The continuity is interrupted by clearcutting. The number of mycetophilid species was clearly lower in the clearcuts studied, despite their small size. Clearcutting makes a marked change in microclimate, which probably can not be tolerated by many species. Ohenoja (1988) summarizes that tens of fungal species disappear, or their fruiting body formation ceases abruptly, after the clearing of a forest. Harvey *et al.* (1980) found that all mycorrhizal fungi associated with the tree roots disappeared within short time after clearcutting. However, some saprophytic species may be favoured and produce even more fruiting bodies on clearings than in the dense forest (Ohenoja, 1988). These findings correspond well with the distribution pattern of the mycetophilids in the present study. Certain species, such as *Boletina gripa*, seemed to be favoured and became numerous under the changed conditions of clearcutting, while several others probably disappeared. However, much is still unknown about the exact habitat preferences of many mycetophilids (Hanski, 1989). For example, *B. gripa* is common in different

kinds of open landscapes (Russel-Smith, 1979; G.E.E. Söli personal communication), but it has only been reared from the mycorrhizal fungus *Suillus bovinus*, which does not tolerate clearcuts (Kurina, 1991). Furthermore, little is known about the impact on species diversity from silvicultural systems other than clearcutting and selection cutting (e.g. shelter wood cuttings).

The method of clearcutting seems to induce a long-lasting effect on the mycetophilid fauna. The managed forests, which were clearcut 70–120 years ago, did not show higher numbers of species than the relatively new clearcuts. The factor of cutting (clearcut or never clearcut) showed a strongly negative correlation with the number of mycetophilid species. Significant changes in the fungal communities during the course of succession in managed spruce forests have been recorded by Bendiksen (1981), however, any comparison of fungal biodiversity between semi-natural forests and secondary-growth forests on former clearings, is not known to the author. Apparently, the restoration of a diverse mycetophilid fauna after a clearcutting requires much more time than 70–120 years. On one hand, this result emphasizes the high value of the forests which have never been clearcut. On the other hand, it is not clear how long the generation time of clearcut forests should be extended to achieve an acceptable restoration of the mycetophilid diversity. If all the species can recolonize a very old stage of a former clearcut forest, it will certainly be a question of how far and scattered the source fragments of semi-natural forest can be for a successful recolonization. The result of this study indicates that such recolonization has not taken place in a 120 year old regrowth of a clearcut, about 4 km from a 'mainland' of semi-natural forest.

Fire may be another cause of discontinuity in spruce forests (Zackrisson and Östlund, 1991; Delin, 1992). Fire marks on old pines, and the structure of the forest, indicate that fire has limited the time of continuity at most of our sites in the semi-natural forest. However, S-N 1 has probably avoided forest fires, and seems to be a site of long continuity and high value with respect to the mycetophilid fauna. Despite its small area, and its surroundings of cultivated forests, this site contained a much higher number of species than the other sites. It is assumed that the identification and protection of the forests with long continuity may be an effective way of conserving mycetophilid species.

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Appendix 1. Frequencies and habitat-associations for all mycetophilid taxa captured in the present study. Sum = total sum of individuals. S-N = sum of individuals within semi-natural forests. MAN = sum of individuals within managed forests. CLC = sum of individuals within clearcuts. Wood = associated with dead wood habitats. Ground = associated with habitats on the ground (fungi on the ground, mycelium in the earth, vole burrows etc.) Ref. = References for habitat associations

Taxa	Sum	S-N	MAN	CLC	Habitat	Ref.
<i>Mycomya prominens</i>	2	0	1	1	Wood/Ground	14
<i>Mycomya tenuis</i>	1	0	1	0	Wood/Ground	14
<i>Mycomya</i> sp.	1	0	1	0	Wood/Ground ^b	14
<i>Acnemia nitidicollis</i>	63	13	9	41	Wood/Ground	6,8
<i>Azana anomala</i> ^a	1	1	0	0		8
<i>Sciophila distincta</i>	3	1	0	2	Wood/Ground ^b	8
<i>Sciophila hirta</i>	1	1	0	0	Wood/Ground ^b	8
<i>Sciophila</i> sp.1	1	0	0	1	Wood/Ground ^b	8
<i>Sciophila</i> sp.2	1	1	0	0	Wood/Ground ^b	8
<i>Sciophila</i> sp.3	1	1	0	0	Wood/Ground ^b	8
<i>Sciophila</i> sp. (fem.)	7	3	1	3	Wood/Ground ^b	8
<i>Apolephtisa subincana</i>	65	37	9	19	Wood	8,R
<i>Boletina basalis</i>	11	7	3	1	Wood/Ground ^b	8,11
<i>Boletina dispecta</i>	1	1	0	0	Wood/Ground ^b	8,11
<i>Boletina erythropyga</i>	2	2	0	0	Wood/Ground ^b	8,11
<i>Boletina gripha</i>	1399	208	33	1158	Wood/Ground	9,R
<i>Boletina lundbecki</i>	3	3	0	0	Wood/Ground ^b	8,11
<i>Boletina lundstromi</i>	1	1	0	0	Wood/Ground ^b	8,11
<i>Boletina maculata</i>	3	2	0	1	Wood/Ground ^b	8,11
<i>Boletina nigrofusca</i>	4	4	0	0	Wood/Ground ^b	8,11
<i>Boletina plana</i>	1	1	0	0	Wood/Ground ^b	8,11
<i>Boletina polaris</i> ^a	1	1	0	0	Wood/Ground ^b	8,11
<i>Boletina trivittata</i>	111	53	19	39	Wood/Ground ^b	8,11
<i>Boletina sciarina</i> gr. (fem.)	85	34	0	51	Wood/Ground ^b	8,11
<i>Coelosia silvatica</i>	1	0	0	1	Wood/Ground ^b	12,13
<i>Hadroneura palmeni</i>	1	0	1	0		8,11
<i>Docosia gilvipes</i>	1	0	0	1	Wood/Ground	13
<i>Docosia fumosa</i>	3	2	1	0		8
<i>Ectrepesthoneura hirta</i>	7	2	0	5	Wood	8
<i>Ectrepesthoneura pubescens</i> ^a	1	0	0	1	Wood ^b	8

Taxa	Sum	S-N	MAN	CLC	Habitat	Ref.
<i>Dynatosoma chochleare</i>	2	1	1	0	Wood ^b	10,11
<i>Dynatosoma reciprocum</i>	15	6	3	6	Wood ^b	10,11
<i>Dynatosoma throacicum</i>	1	1	0	0	Wood ^b	10,11
<i>Dynatosoma</i> sp.	1	0	0	1	Wood ^b	10,11
<i>Epipycta aterrima</i> ^a	2	2	0	0	Wood	3
<i>Phronia bicolor</i>	1	1	0	0	Wood/Ground ^b	4,6,7,11
<i>Phronia caliginosa</i>	72	28	12	32	Wood/Ground ^b	4,6,7,11
<i>Phronia cineracens</i>	4	3	0	1	Wood/Ground ^b	4,6,7,11
<i>Phronia flavicollis</i>	4	3	0	1	Wood	11
<i>Phronia jocos</i>	2	2	0	0	Wood/Ground ^b	4,6,7,11
<i>Phronia mutabilis</i>	1	1	0	0	Wood/Ground ^b	4,6,7,11
<i>Phronia obtusa</i>	2	0	0	2	Wood/Ground ^b	4,6,7,11
<i>Phronia persimilis</i>	1	0	0	1	Wood/Ground ^b	4,6,7,11
<i>Phronia petulans</i>	2	1	0	1	Wood/Ground ^b	4,6,7,11
<i>Phronia willistoni</i>	3	2	1	0	Wood/Ground ^b	4,6,7,11
<i>Phronia</i> sp. (fem.)	116	52	37	27	Wood/Ground ^b	4,6,7,11
<i>Phronia</i> sp. (male)	4	0	1	3	Wood/Ground ^b	4,6,7,11
<i>Platurocypta testata</i> ^a	1	1	0	0	Wood/Ground	2
<i>Sceptonia fuscipalpis</i>	1	0	1	0	Ground ^b	3
<i>Sceptonia nigra</i>	11	6	2	3	Ground ^b	3
<i>Sceptonia tenuis</i>	6	1	1	4	Wood	R
<i>Trichonta aberrans</i>	1	1	0	0	Wood ^b	5
<i>Trichonta comis</i>	4	3	0	1	Wood ^b	5
<i>Trichonta fragilis</i>	1	0	0	1	Wood ^b	5
<i>Trichonta melanura</i>	23	8	9	6	Wood ^b	5
<i>Trichonta vitta</i>	8	1	4	3	Wood	5
<i>Zygomyia humeralis</i>	4	2	0	2		10
<i>Zygomyia notata</i>	10	7	3	0		10
<i>Allodia (Allodia) lugens</i>	2	0	1	1	Ground	6
<i>Allodia (Allodia) lugens</i> gr.	3	2	0	1	Ground ^b	6
<i>Allodia (Allodia) pixydiformis</i>	4	1	1	2	Ground	9
<i>Allodia (Allodia) simplex</i> ^a	2	2	0	0	Ground ^b	6
<i>Allodia (Allodia) truncata</i>	1	0	1	0	Ground ^b	6
<i>Allodia (Brachypeza) czernyi</i>	1	1	0	0	Ground	9
<i>Allodia</i> sp. (fem.)	1	0	0	1	Ground ^b	6
<i>Anatella flavomaculata</i>	1	1	0	0	Wood ^b	1
<i>Anatella gibba</i> ^a	1	0	0	1	Wood ^b	1
<i>Anatella</i> sp.1	1	0	1	0	Wood ^b	1
<i>Anatella</i> sp. (fem.)	2	2	0	0	Wood ^b	1
<i>Brachypeza bisignata</i>	1	1	0	0	Wood/Ground ^b	9
<i>Brevicornu griseolum</i>	1	0	1	0	Ground ^b	6,10
<i>Brevicornu bipartitum</i>	1	1	0	0	Ground ^b	6,10
<i>Brevicornu crassicornis</i>	2	1	0	1	Ground ^b	6,10
<i>Brevicornu disjunctum</i>	2	0	0	2	Ground ^b	6,10
<i>Brevicornu fennicum</i>	4	4	0	0	Ground ^b	6,10
<i>Brevicornu fuscipenne</i>	25	11	6	8	Ground ^b	6,10
<i>Brevicornu kingi</i>	28	15	4	9	Ground ^b	6,10
<i>Brevicornu ruficorne</i>	2	2	0	0	Ground ^b	6,10
<i>Brevicornu sericoma</i>	32	17	12	3	Ground ^b	6,10
<i>Brevicornu sericoma</i> gr. (fem.)	71	43	9	19	Ground ^b	6,10
<i>Brevicornu ruficorne</i> gr. (fem.)	4	4	0	0	Ground ^b	6,10
<i>Brevicornu</i> sp. (fem.)	2	2	0	0	Ground ^b	6,10
<i>Cordyla brevicornis</i>	9	5	0	4	Wood/Ground	R,6

Taxa	Sum	S-N	MAN	CLC	Habitat	Ref.
<i>Cordyla crassicornis</i>	5	3	1	1	Ground	6
<i>Cordyla fissa</i>	3	2	0	1	Ground	7
<i>Cordyla fusca</i>	79	21	50	8	Ground	6
<i>Cordyla nitidula</i>	249	45	170	34	Ground	6
<i>Cordyla parvipalpis</i>	67	9	48	10	Ground ^b	6
<i>Cordyla pusilla</i>	1	1	0	0	Ground ^b	6
<i>Cordyla semiflava</i>	2	2	0	0	Ground ^b	6
<i>Exechia confinis</i>	1	0	1	0	Ground	6
<i>Exechia contaminata</i>	1	1	1	0	Ground	6,9
<i>Exechia dorsalis</i>	7	3	1	3	Ground	6
<i>Exechia indecisa</i>	1	1	0	0	Ground	10
<i>Exechia lucidula</i>	1	1	0	0	Ground	6
<i>Exechia repanda</i>	2	1	0	1	Ground	6
<i>Exechia unimaculata</i>	1	1	0	0	Ground ^b	6
<i>Exechia</i> sp.	6	1	1	4	Ground ^b	6
<i>Exechiopsis (Xenexechia) leptura</i> ^a	1	1	0	0	Ground ^b	6,9
<i>Exechiopsis (s.str.) pseudopulchella</i>	1	0	0	1	Ground ^b	6,9
<i>Exechiopsis (s.str.) intersecta</i>	1	0	0	1	Ground ^b	6,9
<i>Exechiopsis (s.str.) pulchella</i>	2	1	0	1	Ground ^b	6,9
<i>Exechiopsis</i> sp.1	1	1	0	0	Ground ^b	6,9
<i>Rymosia signatipes</i>	1	0	1	0	Ground ^b	6
<i>Rymosia fasciata</i>	2	1	1	0	Ground	7

^a'potentially rare' species in Fennoscandia

^bhabitat association estimated from other members of the genus

1) Chandler, 1977; 2) Chandler, 1981; 3) Edwards, 1925; 4) Gagné, 1975; 5) Gagné, 1981; 6) Hackman and Meinander, 1979; 7) Hackman, 1963; 8) Hutson et al., 1980; 9) Kurina, 1991; 10) Landrock, 1940; 11) Smith, 1989; 12) Söli (in preparation); 13) Väisänen, 1981; 14) Väisänen, 1984; R) own rearing.