

UNLOGGED FORESTS: IMPORTANT SITES FOR PRESERVING THE DIVERSITY OF MYCETOPHILIDS (*Diptera: Sciarioidea*)

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Abstract

The relationship between the mycetophilid fauna and a set of environmental variables was studied in spruce forests of southeastern Norway. At the stand level, the continuous presence of wood in all decay stages combined with a tree cover appeared to be an important factor for increasing the species richness of mycetophilids. However, the spatial representation of suitable stands in the landscape seems to be particularly important, since the % area of old growth in the surrounding 100 km² showed the strongest influence on both species richness and abundance within individual species. The present findings indicate that conservation of a species-rich mycetophilid fauna requires networks of stands within dispersal distances. A reserve network in southern Norway should give special priority to little disturbed forests in the more remote submontane areas, since they appear to be very species-rich, and since their strong populations may provide long-term viability for many mycetophilid species. Copyright © 1996 Elsevier Science Limited.

Keywords: species richness, fungus gnats, spruce forest, disturbance, continuity.

INTRODUCTION

Gradients of species richness and abundances in single species are associated with complex patterns of processes operating at different scales in space and time (Wiens, 1989; Huston, 1994). For poorly studied groups of organisms, studies of such gradients may provide ideas on which processes are important for their populations. Furthermore, such studies may add useful information for more effective reserve selection and management of biodiversity by giving greater priority to those areas which are especially valuable for various groups of organisms (Väisänen & Heliövaara, 1994).

In many groups of forest-dwelling insects, it has been found that a relatively small proportion of the species is dependent on little disturbed forests. For example, most Carabidae species occurring in forests are found in various forest types, or are favoured by the open habitats at clear-cuts and young regrowths, while only few species are seriously affected by logging (Niemelä *et al.*, 1993). A small proportion of species dependent

on little disturbed forests has also been found in other major taxa of Coleoptera, Lepidoptera, Hemiptera and Araneae (Biström & Väisänen, 1988; Väisänen *et al.*, 1993; Pajunen *et al.*, 1995; Økland *et al.*, 1996). However, the environmental requirements of many species-rich insect groups in boreal forests are still unknown, including several families of the insect orders Diptera and Hymenoptera. For example, Diptera may constitute 80–90% of the insects reared from decaying wood (Pfarr & Schrammel, 1991; Hilt & Ammer, 1994).

The mycetophilids (Sciarioidea except Sciariidae) are small to medium-sized dipterous insects, including *c.* 500 species in Norway (Ottesen, 1993). They are numerous in forest environments, and most of the species develop in fungi (Yakovlev, 1994; Zaitzev, 1994). A previous study in the lowlands of southern Norway indicated that increasing continuity of forest environment enhances the species richness (Økland, 1994). Clear-cutting of semi-natural forests seems to induce a long-lasting effect on the mycetophilid fauna, since a marked reduction of species richness was found in forests treated by clear-cutting in the past (70–120 years ago).

In the present study, the mycetophilid fauna of spruce forests was studied at a larger scale in southern Norway. The species richness and abundance of individual species were examined in relation to ecological factors associated with (1) timber productivity; (2) tree species composition; (3) decaying wood and wood-inhabiting fungi; (4) level of disturbance; and (5) climate and geography.

METHODS

Study area and variables

Mycetophilids were sampled from 17 sites in a broad area (33,750 km²) of southeastern Norway in 1993 (Fig. 1). All sites were dominated by Norway spruce *Picea abies* (generally 90–95%). The vegetation of the field layer was dominated by *Vaccinium myrtillus* and a generally poor herb flora, except for some moist sites with somewhat richer vegetation. The sites were selected in oldgrowth forest ranging from unlogged (no stumps) to selectively logged (0.6 stump per living tree) in the recent history.

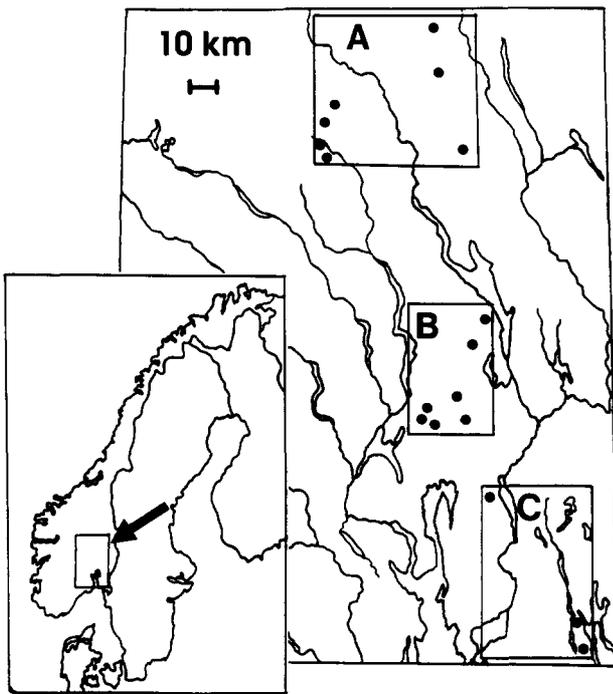


Fig. 1. Map of the whole study area and the smaller study areas A, B and C in southern Norway. ● = sampling sites.

Altogether, 30 ecological variables were recorded in the sites subdivided among five categories (Table 1, Appendix 1). The following six variables require explanation:

STAGES: the decay stages referred to in the variable *STAGES* (Table 1) were: (1) newly dead and with hard surface; (2) initial decomposition, decay less than 5 cm deep; (3) deeply decayed (>5 cm); and (4) nearly disintegrated.

DECAY: the volume of decaying wood in stages 3 and 4.

CONT: continuity in tree layer means that the tree and shrub layers have been closed for a long time, and is important for slow-growing lichen species, as well as wood-inhabiting fungi demanding moisture and a stable supply of dead wood, while continuity of wood in all decay stages is particularly important for wood-inhabiting fungi (Bendiksen, 1994). In Bredeesen *et al.* (1994), each indicator species of lichens and wood-inhabiting fungi was given an increasing value (1, 2 or 3) based on its requirements of continuity of decaying wood and tree layer. The present continuity index (*CONT*) was calculated as a sum of these values for all indicator species found in each site.

LIGHTNIN: the frequency of lightning strikes (*LIGHTNIN*) is assumed to be correlated with the natural frequency of forest fires. This variable was based on electronic registrations in the period 1 January 1981–31 December 1990 (Direktoratet for naturforytning, 1994).

THERM and **HYGR:** the degree of inland climate in the sites:

$$THERM = \frac{d_{0.1} (a - b)}{60(T_{\max} - T_{\min}) \sin(10 + L^{\circ})}$$

where $d_{0.1}$ = number of days >0.1 mm precipitation per year, a = number of days with mean temperature $\geq 0^{\circ}\text{C}$, b = number of days with mean temperature $\geq 10^{\circ}\text{C}$, T_{\max} = mean temperature of warmest month in the year, T_{\min} = mean temperature of coldest month in the year, L° = latitude in degrees; and

$$HYGR = P - 29(7.63T),$$

where P = total annual precipitation, and T = the mean annual temperature.

Most of the analyses were performed with all 17 sites. Since these sites represented environmental variations over a broad geographical area, some of the analyses were repeated within three smaller areas: area A (5000 km²) and area B (1900 km²) including seven sites each, and area C (4100 km²) with three sites (Fig. 1).

Most mycetophilids were identified to species level, using the nomenclature in Soós and Papp (1988), supplemented by more recent revisions and species descriptions (Appendix 2). Species richness was analysed for (1) mycetophilids in general; (2) mycetophilids associated with decaying wood; and (3) mycetophilids developing in soil-inhabiting fungi.

Generally, the number of species tends to increase with the number of individuals in the sample. *Rarefaction* (used in Appendix 3) is a species richness index calculating the number of species expected in each site if all samples were of a standard size (for example 1000 individuals) (Magurran, 1988):

$$E(S) = \sum \left(1 - \frac{\binom{N - N_i}{n}}{\binom{N}{n}} \right)$$

summed over all species in the sample, where $E(S)$ is the expected number of species in the rarefied sample, n is the standardized sample size, N is the total number of individuals in the sample to be rarefied, and N_i is the number of individuals in the i th species in the sample to be rarefied.

Sampling and data treatment

The insects were collected with one Malaise trap (Townes, 1962) in each site. The traps were mounted with the collector bottles directed towards the south, and were operated from mid-June to the end of August 1993. Preserving fluid was a mixture of 60% ethanol, 20% ethylene glycol and 20% water. Malaise traps have proved to be very effective for trapping dipterous insects (Muirhead-Thomson, 1991), especially mycetophilids which sometimes constitute a considerable part of the captures.

Relationships between ecological variables were analysed with Spearman rank correlation (R_s) (Freund, 1992). The level of significance was adjusted for multiple tests by the Bonferroni correction (Weisberg, 1985). The relationships between ecological variables and the

Table 1. Ecological variables used in analyses of species richness and abundance

Variable	Explanation
Forest density and timber productivity	
<i>BASAL</i>	Basal area (m ²) measured with a relascope ^a
<i>PROD</i>	Timber productivity, i.e. tree height (m) at 40 years old ^a
<i>TREES</i>	No. of trees ^a
Tree species composition	
<i>SPRUCE</i>	% spruce trees ^b
<i>PINE</i>	% pine trees ^b
<i>DECID</i>	% deciduous trees ^b
Saproxyllic substrates	
<i>WOOD</i>	Volume of dead wood (estimated from formula for a cone) ^{ac}
<i>LOGS</i>	No. of standing and lying dead trees ^{bc}
<i>LYING</i>	No. of lying dead trees ^{bc}
<i>STANDING</i>	No. of standing dead trees ^{bc}
<i>SPRUCLOG</i>	No. of standing and lying dead spruce trees ^{bc}
<i>PINELOG</i>	No. of standing and lying dead pine trees ^{bc}
<i>DECIDLOG</i>	No. of standing and lying dead deciduous trees ^{bc}
<i>DECAY</i>	Volume of deeply decayed wood (estimated from formula for a cone) ^{ac}
<i>FUNGSP</i>	No. of wood-inhabiting fungi species (based on fruiting bodies) ^a
Forest continuity and disturbance	
<i>CONT</i>	Indications of continuity in dead wood and tree cover (see text) ^a
<i>STUMPS</i>	No. of stumps divided by no. of trees ^a
<i>STAGES</i>	1, all decay stages present; 0, at least one decay stage absent ^a
<i>OLDGRWTH</i>	% area of oldgrowth forest per 100 km ²
<i>LIGHTNIN</i>	Frequency of lightning strikes
Geography and climate	
<i>ELEVAT</i>	Elevation (m) above sea level
<i>LATITUDE</i>	Latitude in UTM values
<i>THERM</i>	Index of thermic continentality (Johannesen, 1977), see text
<i>HYGR</i>	Index of hygric continentality (Tamm, 1959), see text
<i>TEMP93</i>	Mean monthly temperature of sampling season (June–July 1993)
<i>TEMP92</i>	Mean monthly temperature of preceding season (June–Sept. 1992)
<i>TEMP</i>	Mean monthly temperature of June–Sept, 1961–1990
<i>PREC93</i>	Precipitation (total) of sampling season (May–July 1993)
<i>PREC92</i>	Precipitation (total) of preceding season (May–July 1992)
<i>PREC</i>	Precipitation (total) of June–August, mean of 1961–1990.

^a Variables recorded within a quadrat of 40 × 40 m.

^b Variables recorded by four 50 m transects perpendicular to the quadrat edge.

^c Diameter at breast height > 12 cm.

variables of species richness were tested by stepwise multiple regression (Weisberg, 1985). The maximum number of three explanatory variables was used in each regression in the tests of all 17 sites, and two in tests within the areas A and B. Student's *t*-test for two samples with unequal variances (Freund, 1992) was applied to test significant differences in ecological and species richness variables between areas A, B and C (Appendices 1 and 3).

The influence of elevation and distances between sites on the differences in faunal composition was tested by the Mantel statistic using the computer program R-Package (Legendre & Vaudor, 1991). First, this program computes distance matrices for each variable (elevation, distance and faunal composition), including pairwise distances for all combinations of two sites. Then, it computes Mantel *r*, which is a standardized Mantel *Z*:

$$Z = \sum \sum x_{ij}y_{ij}$$

for all pairs of values (*i,j*) of the two matrices, diagonal excluded.

Differences in faunal composition were measured by the index of % dissimilarity ('Bray and Curtis' index in Faith *et al.*, 1987):

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

where *A_i* and *B_i* were the numbers of species *i* in the sites *A* and *B*, and *n* was the number of species involved.

For species present in at least 25% of the sites, a stepwise multiple regression was carried out between the number of individuals in each species and the ecological variables, ending up with a maximum of three ecological variables in each regression. Finally, the total

number of species influenced by each ecological variable in all of the regressions was counted.

RESULTS

The traps collected altogether 260 species of mycetophilids (Sciarioidea), including 34,557 specimens. Most species belonged to the family Mycetophilidae (229), while a smaller number belonged to Bolitophilidae (14), Keroplatidae (14), and Diadocidiidae (3). In this material, 71 species are known from habitats in decaying wood, while 55 have been reared from soil-inhabiting fungi. Many of these species are infrequent in such trapping. In the present data-set, 33.3% of the species were trapped with less than three specimens, and 46.1% occurred in less than three sites.

Despite equal sampling effort in all sites, the site with the highest species richness (A19) had four times as many mycetophilid species as the sites with the lowest species richness (B20, C17) (Appendix 3). Apparently, increasing species richness was associated with a higher production of mycetophilid numbers in the sites or the surrounding area. The number of species was significantly correlated with the number of individuals in the samples (Appendix 3). Furthermore, *Rarefaction* showed a relatively small variation between the sites, and was only weakly correlated with species richness (Appendix 3).

Table 2 shows the correlation between all ecological variables, except for those which did not correlate strongly with any other variable. Among 30 ecological variables (Table 1), the following nine were excluded before regression analysis, since they were strongly correlated with other variables: *SPRUCE*, *PINE*,

LOGS, *SPRUCLOG*, *STUMPS*, *STAGES*, *TEMP*, *TEMP92* and *TEMP93* (Table 2).

In stepwise multiple regression, the variation in species richness between the sites was best explained by the % of oldgrowth forest in the surrounding area of 100 km² (*OLDGRWTH*, ranging from 16.7% to 76%) (Table 3, Fig. 2). The second step selected the level of continuity, based on indicator species of fungi and lichens (*CONT*). This factor showed a strongly negative correlation with the density of stumps (*STUMPS*, Spearman rank correlation $R_s = -0.80$) and a strongly positive correlation with the representation of decay stages (*STAGES*, $R_s = 0.82$) (Table 2). Precipitation during the summer months (*PREC*) was selected as a third factor. A multiple regression combining the three selected variables (*OLDGRWTH*, *CONT* and *PREC*) explained 88% of the variation in species richness (Table 3). When one of the factors *OLDGRWTH* or *CONT* was excluded, the explanation of the multiple regression was reduced to 31% or 59% respectively, indicating that both had a considerable independent influence.

Considering only species associated with decaying wood, the level of continuity (*CONT*) was selected as the first factor, and then the % of oldgrowth (Table 3). In a third step, the number of logs (*LYING*) was selected. These three selected variables accounted for 64% of the variation in species richness (Table 3). By excluding either *OLDGRWTH* or *CONT*, the explanation dropped to 27% or 45%, respectively.

In the test of species associated with soil-inhabiting fungi, the % of oldgrowth was selected in the first step, the number of standing dead trees (*STANDING*) in the second step, and the number of wood-inhabiting fun-

Table 2. Spearman rank correlation between ecological variables

Shading: Strong correlations, $p < 0.001$ after Bonferroni correction.

	(<i>SPRUCE</i>)	(<i>PINE</i>)	<i>DECID</i>	(<i>LOGS</i>)	(<i>SPRUCLOG</i>)	<i>PINELOG</i>	<i>LYING</i>	<i>STANDING</i>	<i>CONT</i>	(<i>STUMPS</i>)	(<i>STAGES</i>)	<i>ELEVAT</i>	<i>LATITUDE</i>	(<i>TEMP</i>)	(<i>TEMP92</i>)	(<i>TEMP93</i>)
(<i>SPRUCE</i>)	*
(<i>PINE</i>)	-0.22	*
<i>DECID</i>		-0.14	*
(<i>LOGS</i>)	-0.25	0.08	0.21	*
(<i>SPRUCLOG</i>)	-0.04	-0.04	0.01		*
<i>PINELOG</i>	-0.19		-0.16	0.14	0.09	*
<i>LYING</i>	-0.39	0.09	0.34		0.74	0.14	*
<i>STANDING</i>	0.06	0.04	-0.07		0.43	0.10	0.49	*
<i>CONT</i>	-0.30	-0.62	0.57	0.25	0.19	-0.60	0.19	0.19	*
(<i>STUMPS</i>)	0.15	0.75	-0.44	-0.07	-0.07	0.74	0.05	-0.18		*
(<i>STAGES</i>)	-0.37	-0.51	0.57	0.08	0.11	-0.48	0.05	0.12			*
<i>ELEVAT</i>	-0.15	-0.55	0.36	-0.38	-0.49	-0.54	-0.36	-0.45	0.45	-0.49	0.46	*
<i>LATITUDE</i>	-0.01	-0.45	0.19	-0.36	-0.44	-0.45	-0.32	-0.46	0.32	-0.29	0.24		*	.	.	.
(<i>TEMP</i>)	0.10	0.50	-0.27	0.46	0.53	0.51	0.40	0.53	-0.33	0.41	-0.37			*	.	.
(<i>TEMP92</i>)	0.10	0.50	-0.27	0.46	0.53	0.51	0.40	0.53	-0.33	0.41	-0.37				*	.
(<i>TEMP93</i>)	0.10	0.53	-0.28	0.42	0.50	0.53	0.38	0.51	-0.39	0.41	-0.40					*

() = Variables which were excluded from regression analysis because of inter-correlations.

Table 3. Multiple regression 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 with soil-inhabiting fungi (Multiple R^2_{adj} =Cumulative R^2 values, adjusted for degrees of freedom.)

Dependent	Predictors	Coefficient	SE	T	p	Multiple R^2_{adj}
(a) Species total	CONSTANT	-52.463	24.736	-2.121	0.054	
	(1) OLDGRWTH	1.261	0.155	8.147	0.000	0.533
	(2) CONT	3.474	0.600	5.789	0.000	0.824
	(3) PREC	0.264	0.264	2.672	0.019	0.878
(b) Species in wood	CONSTANT	2.082	4.610	0.452	0.659	
	(1) CONT	0.680	0.235	2.890	0.013	0.307
	(2) OLDGRWTH	0.231	0.060	3.884	0.002	0.505
	(3) LYING	0.180	0.073	2.472	0.028	0.638
(c) Species in soil	CONSTANT	-6.292	2.245	-2.803	0.015	
	(1) OLDGRWTH	0.269	0.037	7.172	0.000	0.368
	(2) STANDING	0.366	0.078	4.663	0.000	0.641
	(3) FUNGSP	1.054	0.235	4.494	0.001	0.849

gus species (*FUNGSP*) in the third step. These variables explained 85% of the variation in species richness (Table 3). Exclusion of *OLDGRWTH* reduced the explanation to 30%.

Elevation appeared to be the second strongest factor for the species richness of mycetophilids in the stepwise multiple regression ($R^2 = 0.403$ in the first step), but this factor was not significant when *OLDGRWTH* and *CONT* had been selected, and appeared to have a spurious influence when considering the large variation in species richness found at high altitude (Appendix 3). This variable seems to be indirectly explained by the variables *CONT* and *OLDGRWTH*, since the lowest sites (in area C, <250 m) had lower scores of the variable *CONT*, and some of the highest sites (in area A, >750 m) had a much higher % of oldgrowth compared to the other sites (Appendix 1).

No other factors were found that could indirectly explain the influence of elevation in the regression analysis. Even though several species (64) were only captured at high elevation (>750 m), the influence of

elevation could not be explained by the zonal distribution of species, because most of these species are recorded from areas which are warmer and more oceanic than the lowlands (<250 m) in the present study area (Table 4). Furthermore, the influence of elevation was not associated with a more compressed season at high altitude resulting in more species-rich samples there. Most mycetophilid species are present throughout most of the season (Dely-Draskovits & Babos, 1976; Russell-Smith, 1979; Yakovlev & Zaitzev, 1990; E. B. Yakovlev, pers. comm.), and when the trap capture from a lowland site (site 17 at 200 m, 34 species) was pooled with a trap capture from the same site one month earlier, the pooled number of species (52) was still <50% of the number of species found in the most species-rich sites at high altitudes (Appendix 3).

The species composition of mycetophilids was influenced more by geographical position than altitude. The Mantel tests (Table 5) showed that elevation was not significantly correlated with the differences in faunistic composition when the effect of distance between the sites was eliminated. However, the distance between sites was correlated with the differences in faunistic composition, even when the effect of elevation was

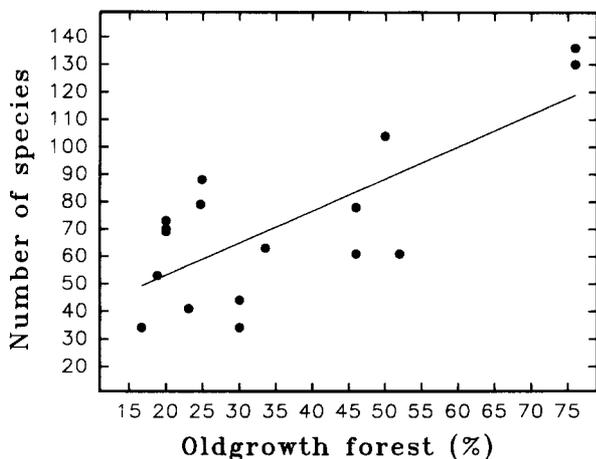


Fig. 2. Linear regression of species richness of mycetophilids on % of oldgrowth forest in the surrounding 100 km² (*OLDGRWTH*); $Y=1.173 X + 29.692$ $R^2=0.533$.

Table 4. The total number of species trapped at different altitudes, and the number of the same species recorded in European countries (a) to the south and west of Fennoscandia, and (b) to the north and east of Fennoscandia (L, 0–250 m; M, 250–750 m; H, > 750 m.)

Height levels	Number of species		
	Total	(a) South/west	(b) North/east
L	9	7	7
LM	7	7	6
LMH	26	21	17
MH	74	56	51
H	64	55	49

Table 5. Mantel statistic between distance matrices of (1) % dissimilarity of fauna (*FAUNA*), (2) differences in elevation (*ELEVATION*), and (3) distance in the landscape (*DISTANCE*). r = standardized Mantel z , t = Mantel's t statistic, p = significance level of t

Test	r	t	p
Mantel between two matrices			
<i>DISTANCE</i> × <i>FAUNA</i>	0.644	6.383	0.00001
<i>ELEVATION</i> × <i>FAUNA</i>	0.578	5.511	0.00001
<i>ELEVATION</i> × <i>DISTANCE</i>	0.794	7.416	0.00001
Partial Mantel tests			
<i>DISTANCE</i> × <i>FAUNA</i> , eliminating effect of <i>ELEVATION</i>	0.372	3.308	0.00047
<i>ELEVATION</i> × <i>FAUNA</i> , eliminating effect of <i>DISTANCE</i>	0.145	1.197	ns

Table 6. Multiple regression between the best explaining predictors and the dependent variables within the areas A and B: (a) total number of species, (b) number of species associated with wood-inhabiting fungi, and (c) number of species associated with soil-inhabiting fungi. (Multiple R^2_{adj} =Cumulative R^2 values, adjusted for degrees of freedom)

Dependent	Predictors	Coefficient	SE	T	p	Multiple R^2_{adj}
Area A						
(a) Species total	<i>CONSTANT</i>	-12.110	6.820	-1.776	0.150	
	(1) <i>CONT</i>	8.538	0.731	11.686	0.000	0.664
	(2) <i>OLDGRWTH</i>	0.898	0.106	8.500	0.001	0.978
(b) Species in wood	<i>CONSTANT</i>	-0.009	5.938	-0.002	0.999	
	(1) <i>CONT</i>	1.953	0.636	3.070	0.037	0.505
	(2) <i>OLDGRWTH</i>	0.219	0.092	2.384	0.076	0.745
(c) Species in soil	<i>CONSTANT</i>	-20.262	9.151	-2.214	0.091	
	(1) <i>OLDGRWTH</i>	0.493	0.104	4.718	0.009	0.600
	(2) <i>FUNGSP</i>	0.323	0.145	2.224	0.090	0.777
Area B						
(a) Species total	<i>CONSTANT</i>	4.730	13.569	0.349	0.745	
	(1) <i>FUNGSP</i>	4.886	1.033	4.728	0.009	0.558
	(2) <i>OLDGRWTH</i>	1.318	0.494	2.665	0.056	0.801
(b) Species in wood	<i>CONSTANT</i>	4.974	5.912	0.841	0.439	
	(1) <i>LYING</i>	0.350	0.122	2.872	0.035	0.547
(c) Species in soil	<i>CONSTANT</i>	7.396	0.967	7.652	0.001	
	(1) <i>FUNGSP</i>	0.886	0.149	5.963	0.002	0.852

eliminated. Furthermore, the number of species differed significantly between the areas A, B and C, and between sites within each area (Appendix 3).

The effect of geographical position motivated a repeated stepwise regression analysis within each of the smaller study areas A and B (Table 6). Many of the same variables were selected as in the analysis of the whole area. The % of oldgrowth and level of continuity were the best predictors though precipitation, number of logs and wood-inhabiting fungi were also important.

Altogether, 93 species were sufficiently frequent for regression analyses of the number of individuals in each species (Fig. 3). The strongest influence was found for the % of oldgrowth forest, which was selected as a significant factor in nearly half of the species. The amount of deeply decayed wood (*DECAY*) and the number of wood-inhabiting fungi (*FUNGSP*) were the next best variables, influencing one-quarter of the species.

DISCUSSION

The present results confirm previous findings that the degree of continuity, based on indicator species of wood-inhabiting fungi and lichens, is an important factor for the mycetophilid fauna (Økland, 1994). In the previous study, the degree of continuity was correlated with dead-wood variables; however, the present regression analyses revealed a considerable independent influence of continuity beyond the effect of the present amount of decaying wood.

The temporal and spatial dynamics of the forest landscapes are important in considering the role of little disturbed forests for flora and fauna. The presence of many indicator species of wood-inhabiting fungi and lichens may indicate that different decay stages of dead wood, combined with a closed tree and shrub layer, have been available for a relatively long time (Karström, 1992; Bendiksen, 1994; Bredesen *et al.*, 1994;

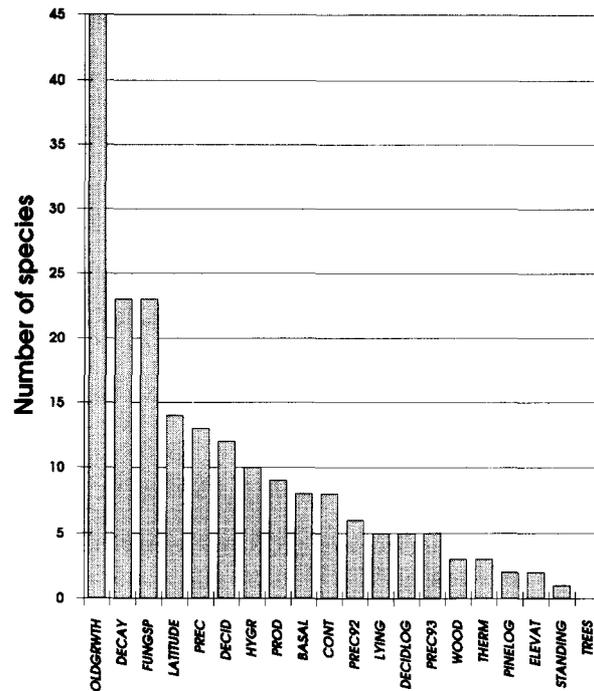


Fig. 3. Test of each species: the total number of species influenced by each ecological variable during stepwise multiple regressions of individual numbers on ecological variables (max. 3 variables selected in each regression).

Lindblad, 1995). However, it is uncertain how long stability of the tree cover in each stand is required in order to find many of these indicator species. A comparison of *Picea abies* swamp-forests of different age, including stands which have avoided forest fires since the arrival of Norway spruce 2000–3000 years BP, indicated that stand continuity beyond 300 years does not lead to a higher species richness of fungi, (Polyporaceae) mosses or lichens (Hörnberg, 1995). However, the methods used in this study (analyses of pollen and macrofossil charcoal) give little or no information about the long-term (>300 years) continuity of dead wood in all decay stages, nor about interruptions of stand continuity by wind-felling and biotic agents of damage. In the present study, the variation in the continuity variable seems to be associated with disturbances of the stands in more recent history, since this variable showed a strongly negative correlation with the density of stumps; however, the ages of the four stands without stumps are unknown.

The spatial component seems to be particularly important, since the % of oldgrowth in a broad surrounding landscape (100 km²) was a major factor for both species richness and abundance within individual species of mycetophilids. This variable is assumed to be correlated with the representation of stands possessing a range of favourable conditions for mycetophilids, in particular continuity of decaying wood and tree cover. Thus, an increasing % of oldgrowth forest in the landscape will be associated with increasing size of favourable patches for mycetophilids, as well as decreasing isolation of each patch. According to general patch occupancy dynamics (Hanski, 1994), such conditions are predicted to increase the species richness as well as the viability of single populations.

The importance of continuity and disturbance for the mycetophilid fauna may be associated with the production of host fungus species (Økland, 1994). Most rearing records of mycetophilids are from soil-inhabiting or wood-inhabiting fungi, while relatively few species have been found in non-fungal habitats (Yakovlev, 1994). Timber removal reduces the density of dead wood in different stages of decay (Linder & Östlund, 1992; Syrjänen *et al.*, 1994), and thereby the amount and species richness of wood-inhabiting fungi (Lindblad, 1995). In the long run, less woody organic material is disintegrated in the forest soil, giving less substrate for the diversity of saprophytic fungi in the ground. Clear-cutting causes a drastic reduction of fungal diversity, especially of mycorrhizal fungi associated with tree roots (Harvey *et al.*, 1980; Ohenoja, 1988). However, most mycorrhizal species may return within 30 years (Bendiksen, 1994). Even though decaying wood may be available on clear-cuts, only few wood-inhabiting fungus species tolerate the new climatic conditions (L. Ryvarden, pers. comm.). Furthermore, little disturbed forest with large amounts of dead wood may be a better winter habitat for species found to be hibernating as adults under loose bark (Plassman, 1975; Ostroverkhova & Isotov, 1986; Yakovlev, 1988).

The production of host fungus species is also an important factor for saproxylic beetles; however, the density of stumps and continuity based on indicator species in each stand were not found to be significant factors for species richness of this group (Stokland, 1994; Økland, *et al.*, 1996). Therefore, it is assumed that other factors in addition to the fungal flora may explain the importance of continuity and disturbance for the mycetophilid fauna.

In many mycetophilid species, the adults have to be present for a long time, until suitable sporophores for oviposition occur in late summer or autumn (Dely-Draskovits & Babos, 1976; Russell-Smith, 1979; Yakovlev & Zaitzev, 1990; E. B. Yakovlev, pers. commun.). Several authors have commented on the tendency of the thin-skinned mycetophilid adults to stay in moist habitats on hot and dry days, such as dark forests, under logs, in moist clefts, in burrows of voles, etc. (Cole & Chandler, 1980; Hutson *et al.*, 1980; Väisänen, 1984; Ostroverkhova, 1992). It is suggested that long periods of drought during this compulsory waiting time may represent a selective force towards a behaviour of remaining in humid places, and to save energy for long-term survival and reproduction purposes. Indirectly, such behaviour may lead to a preference for oldgrowth stands, and a reduced ability of dispersal. The need to save energy is supported by experimental studies of dipteran species showing that increasing flight activity may give significant reductions in egg production (Roff, 1977).

The influence of long-term precipitation (mean of 1961–1990) on species richness of mycetophilids may be associated with the regularity and frequency of periods with high sporophore production. Generally, the sporophores of soil-inhabiting fungi are short-lived, and sporophore production is characterized by considerable variations from year to year, within a season, and between districts (Hanski, 1989). Several mycologists have found that climatic factors, especially precipitation and temperature, account for much of the variation in sporocarp production of soil-inhabiting fungi (Dahlberg, 1991; Ohenoja, 1993). Trapping of mycetophilids in the period 1984–1987 revealed a considerable covariation between the abundance of mycetophilid individuals and the production of sporophores (Yakovlev, 1993).

In many Scandinavian districts, single stands of little disturbed forest may have become increasingly important for species protection during the last 100 years, since no similar stands have been left in a wide surrounding area (Segerström *et al.*, 1994). However, the lesson from the present findings is that protection of a small isolated stand of little disturbed forest may in the long run be insufficient to avoid losses of mycetophilid populations, even when it has a long continuity of decaying wood and tree cover. Over a broad landscape, it may be necessary to secure networks of several stands within dispersal distances, including existing stands with long continuity of wood in all decay stages and unbroken tree cover, as well as stands developing such conditions in the future. A reserve network should not only optimize the number of species, but should also secure the persistence of each species, as advocated for other fauna and flora in Norway (e.g. Sætersdal *et al.*, 1993) and elsewhere (e.g. Pressey & Nicholls, 1989; Lomolino, 1994).

Special priority should be given to 'hot spot' provinces for certain taxa (Väisänen & Heliövaara, 1994), since many species are represented with strong populations here. Generally, the availability of little disturbed forests

increases with altitude in southeastern Norway (Korsmo & Larsen, 1994; Korsmo & Svalastog, 1994). A reserve network for preservation of mycetophilid species in southern Norway should give special priority to these forests at high altitude, especially in the more remote submontane areas, which appear to be particularly valuable. In the present study, such areas had four times as many species as comparable lowland sites, and the populations of many species showed a significantly larger number of individuals here.

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APPENDIX 1

Comparison of the ecological variables between the areas A, B and C

(p = significance level of t -test; ns $p > 0.05$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

Variable	Mean			SD			p		
	A	B	C	A	B	C	A–B	B–C	A–C
Forest density and productivity									
<i>TREES</i>	66.9	73.0	125.0	31.0	24.6	8.7	ns	***	***
<i>BASAL</i>	20.9	33.3	31.7	6.0	8.8	6.0	**	ns	*
<i>PROD</i>	10.8	9.9	12.3	2.9	4.7	3.8	ns	ns	ns
Tree species composition									
<i>SPRUCE</i>	78.5	90.7	82.3	16.8	4.6	3.6	ns	*	ns
<i>PINE</i>	0.9	0.2	6.9	1.9	0.5	9.2	ns	ns	ns
<i>DECID</i>	20.6	9.1	10.8	17.2	4.7	5.9	ns	ns	ns
Saproxylic substrates									
<i>FUNGSP</i>	6.0	6.0	3.7	2.4	2.7	1.2	ns	*	*
<i>WOOD</i>	16.8	7.9	3.0	12.0	3.1	0.7	*	***	***
<i>LOGS</i>	43.9	64.6	69.7	19.8	14.4	37.8	*	ns	ns
<i>DECAY</i>	12.1	3.4	1.7	12.2	2.5	0.5	ns	**	***
<i>SPRUCLOG</i>	31.4	56.7	53.0	13.0	14.6	27.0	**	ns	ns
<i>PINELOG</i>	0.4	0.1	3.0	0.8	0.4	2.0	ns	ns	ns
<i>DECIDLOG</i>	12.0	7.7	13.7	6.1	5.8	12.9	ns	ns	ns
<i>LYING</i>	38.0	47.0	55.7	13.1	12.9	24.0	ns	ns	ns
<i>STANDING</i>	5.9	17.6	14.0	5.6	6.0	13.7	**	ns	ns
Forest continuity and disturbance									
<i>OLDGRWTH</i>	53.0	22.0	27.7	18.1	5.7	4.0	**	ns	***
<i>CONT</i>	6.9	7.4	0.7	2.6	5.2	1.2	ns	***	***
<i>STUMPS</i>	0.2	0.1	0.5	0.2	0.1	0.1	ns	**	**
<i>STAGES</i>	0.6	0.6	0.0	0.5	0.5	0.0	ns	**	**
<i>LIGHTNIN</i>	571.4	1042.9	733.3	95.1	78.7	230.9	***	ns	ns
Geography and climate									
<i>ELEVAT</i>	835.7	585.7	183.3	69.0	90.0	28.9	***	***	***
<i>LATITUDE</i>	68066	66836	65947	224.2	190.5	361.1	***	*	**
<i>PREC</i>	215.1	230.3	210.0	40.7	21.7	3.5	ns	**	ns
<i>PREC92</i>	137.73	164.3	140.3	39.8	19.5	28.3	ns	ns	ns
<i>PREC93</i>	274.3	232.7	181.7	28.4	27.3	8.1	**	***	***
<i>TEMP</i>	9.0	10.9	13.6	0.6	0.9	0.2	***	***	***
<i>TEMP92</i>	9.1	11.3	14.0	0.5	1.0	0.2	***	***	***
<i>TEMP93</i>	8.8	10.7	12.9	0.5	0.7	0.6	***	**	***
<i>THERM</i>	20.8	18.8	19.0	1.3	0.5	2.6	**	ns	ns
<i>HYGR</i>	564.0	506.0	503.1	94.5	72.2	33.5	ns	ns	ns

APPENDIX 2

Frequencies and habitat associations for all mycetophilid species captured in the present study (s = soil-inhabiting fungi; w = wood-inhabiting fungi)

Species name	Sum	Habitat	Species name	Sum	Habitat
Bolitophilidae			<i>M. hacmani</i> Väis.	4	
<i>Bolitophila aperta</i> Lundst.	5	s	<i>M. humida</i> Garrett	20	
<i>B. austriaca</i> (Mayer)	4	s	<i>M. maculata</i> (Meig.)	5	s
<i>B. bimaculata</i> Zett.	2	w/s	<i>M. marginata</i> (Meig.)	2	w
<i>B. cinerea</i> Meig.	5	s	<i>M. mituda</i> Väis.	1	
<i>B. dubia</i> Siebke	1	s	<i>M. nigricornis</i> (Zett.)	4	
<i>B. edwardsiana</i> Stack.	1	s	<i>M. nitida</i> (Zett.)	96	
<i>B. fumida</i> Edw.	2		<i>M. norna</i> Väis.	13	
<i>B. hybrida</i> (Meig.)	9	s	<i>M. penicillata</i> (Dzied.)	1	
<i>B. nigrolineata</i> Landr.	39	s	<i>M. Pseudoapicalis</i> Landr.	1	
<i>B. obscurior</i> Stack.	4	s	<i>M. pulchella</i> (Dzied.)	5	
<i>B. occlusa</i> Edw.	1	w	<i>M. ruficollis</i> (Zett.)	1317	
<i>B. pseudohybrida</i> Landr.	1	s	<i>M. shermani</i> Garrett	611	
<i>B. rossica</i> Landr.	2	s	<i>M. sigma</i> Joh.	2	w
<i>B. saundersi</i> (Curt.)	1	s	<i>M. trivittata</i> (Zett.)	16	
Diadocidiidae			<i>M. tumida</i> (Winn.)	8	w
<i>Diadocidia borealis</i> Coq.	29		<i>M. vittiventris</i> (Zett.)	60	
<i>D. spinosula</i> Toll.	12	w	<i>Neoempheria pictipennis</i> (Hal.)	1	w
<i>D. ferruginosa</i> (Meig.)	12	w	<i>Acnemia falcata</i> Zaitzev	46	
Keroplastidae			<i>A. nitidicollis</i> (Meig.)	120	w
<i>Macrocera grandis</i> Lundst.	2		<i>Allocotocera pulchella</i> (Curt.)	588	
<i>M. parva</i> Lundst.	187		<i>Anaclileia dispar</i> (Winn.)	52	
<i>M. pumilio</i> Leow	1		<i>Azana anomala</i> (Staeg.)	73	
<i>M. stigma</i> Curt.	2	w	<i>Leptomorphus quadrimaculatus</i> (Mats.)	5	w
<i>M. stigmoides</i> Edw.	3		<i>Monoclona furcata</i> Joh.	4	w
<i>M. zetterstedti</i> Lundst.	57		<i>M. rufilatera</i> (Walk.)	2	w
<i>Keroplastus testaceus</i> Dalm.	1	w	<i>Neuratelia nemoralis</i> (Meig.)	24	
<i>Neoplatyura flava</i> (Macq.)	1	w/s	<i>Paratinia sciarina</i> Mik.	1	
<i>Orfelia discoloria</i> (Meig.)	1	w	<i>Phthinia humilis</i> Winn.	4	w
<i>O. falcata</i> A. Zaitzev	2	w	<i>P. mira</i> Ostr.	2	w
<i>O. unicolor</i> (Staeg.)	3	w	<i>P. setosa</i> A. Zaitzev	3	
<i>Pyratula perpusilla</i> (Edw.)	2		<i>Polylepta borealis</i> Lundst.	17	
<i>P. zonata</i> (Zett.)	6		<i>P. guttiventris</i> (Zett.)	46	
<i>Urytalpa ochracea</i> (Meig.)	1	w	<i>Sciophila adamsi</i> Edw.	7	
Mycetophilidae			<i>S. balderi</i> Zaitzev et Økland		
<i>Mycomya annulata</i> (Meig.)	221	w	<i>S. bicuspidata</i> A. Zaitzev	14	
<i>M. bicolor</i> (Dzied.)	3	w	<i>S. exserta</i> A. Zaitzev	3	
<i>M. brunnea</i> (Dzied.)	2		<i>S. fenestella</i> Curt.	2	
<i>M. cinerascens</i> (Macq.)	2	w	<i>S. geniculata</i> Zett.	10	
<i>M. confusa</i> Väis.	1		<i>S. hirta</i> Meig.	27	s
<i>M. dziedickii</i> Väis.	1		<i>S. lutea</i> Macq.	1	s
<i>M. egregia</i> (Dzied.)	2		<i>S. nonnisilva</i> Hutson	3	
<i>M. fasciata</i> (Zett.)	9		<i>S. salassea</i> Mat.	3	
<i>M. festivalis</i> (Väis.)	2		<i>S. spinifera</i> A. Zaitzev	4	
<i>M. fimbriata</i> (Meig.)	74		<i>S. subbicuspidata</i> Zaitzev et Økland		
			<i>Sytemna haagvari</i> Økland	3	
			<i>S. hungarica</i> (Lundst.)	615	w

Appendix 2 — contd

Species name	Sum	Habitat	Species name	Sum	Habitat
<i>S. nittidula</i> Edw.	5		<i>Rondaniella dimidiata</i> (Meig.)	26	w/s
<i>S. penicillia</i> Hutson	14		<i>Tetragoneura sylvatica</i> Curt.	66	w
<i>S. relict</i> a (Lundst.)	16		<i>Dynatosoma fuscicorne</i> (Meig.)	33	w
<i>S. setigera</i> (Lundst.)	190		<i>D. nigromaculatum</i> Lundst.	1	w
<i>S. stylata</i> Hutson	78		<i>D. norwegiense</i> Zaitzev et Økland		
<i>Acomoptera difficilis</i> (Dziedz.)	8		<i>D. reciprocum</i> (Walk.)	5	w
<i>Drepanocercus spinistylus</i> Søli	72		<i>D. rufescens</i> (Zett.)	8	
<i>Apolephthisa subincana</i> (Curt.)	791	w	<i>D. thoracicum</i> (Zett.)	1	
<i>Boletina basalis</i> (Meig.)	469		<i>Mycetophila assimilis</i> Mat.	3	s
<i>B. borealis</i> Zett.	21		<i>M. attonsa</i> (Laf.)	13	w/s
<i>b. brevicornis</i> Zett.	32		<i>M. bohémica</i> (Last.)	8	s
<i>B. cincticornis</i> (Walk.)	23		<i>M. brevitarsata</i> (Last.)	133	
<i>B. cornuta</i> A. Zaitzev	1		<i>M. caudata</i> Staeg.	1	
<i>B. erythrogyga</i> Holm.	25		<i>M. confluens</i> Dziedz.	21	s
<i>B. gripha</i> Dziedz.	12,025	w/s	<i>M. curviseta</i> Lundst.	2	
<i>B. griphoides</i> Edw.	8		<i>M. dentata</i> Lundst.	15	w/s
<i>B. groenlandica</i> Staeg.	320		<i>M. dziedzickii</i> Chand.	1	
<i>B. jamalensis</i> A. Zaitzev	7		<i>M. finlandica</i> Edw.	8	s
<i>B. lundbecki</i> Lundst.	318		<i>M. fungorum</i> (De Geer)	227	s
<i>B. lundstromi</i> Landr.	30		<i>M. hetschkoi</i> Landr.	133	w/s
<i>B. maculata</i> Holm.	26		<i>M. ichneumonea</i> Say	91	s
<i>B. nigricans</i> Dziedz.	1595		<i>M. immaculata</i> (Dziedz.)	1	
<i>B. nigrofusca</i> Dziedz.	4071		<i>M. laeta</i> Walk.	35	w/s
<i>B. pectinunguis</i> Edw.	1		<i>M. lapponica</i> Lundst.	1	
<i>B. plana</i> (Walk.)	295		<i>M. lubomirskii</i> Dziedz.	18	
<i>B. sciarina</i> Staeg.	621		<i>M. luctuosa</i> Meig.	2	w/s
<i>B. silvatica</i> Dziedz.	10		<i>M. marginata</i> Winn.	4	w/s
<i>B. trivittata</i> (Meig.)	22		<i>M. ocellus</i> Walk.	2	w
<i>B. villosa</i> Landr.	3		<i>M. schnablii</i> (Dziedz.)	8	
<i>Coelophthinia thoracica</i> (Winn.)	4	s	<i>M. strigatoides</i> (Landr.)	2	
<i>C. flava</i> (Staeg.)	23	s	<i>M. stylata</i> (Dziedz.)	2	s
<i>C. silvatica</i> Landr.	4		<i>M. unguiculata</i> Lundst.	1	
<i>C. tenella</i> (Zett.)	16	w/s	<i>M. xanthopyga</i> Winn.	2	
<i>C. truncata</i> Lundst.	26		<i>Phronia biarcuata</i> (Beck.)	2	w
<i>Dziedzickia marginata</i> (Dziedz.)	83		<i>P. braueri</i> Dziedz.	117	w
<i>Gnoriste bilineata</i> Zett.	11		<i>P. caliginosa</i> Dziedz.	511	w
<i>G. longirostris</i> Siebke	1		<i>P. cinerascens</i> Winn.	143	w
<i>Grzegorzekia collaris</i> (Meig.)	1	w	<i>P. cordata</i> Lundst.	56	w
<i>Palaeodocosia janickii</i> (Dziedz.)	86	w			
<i>Saigusaia flaviventris</i> (Strobl)	3	w	<i>P. digitata</i> Hack.	4	w
<i>Speolepta leptogaster</i> (Winn.)	2		<i>P. disgrega</i> Dziedz.	4	w
<i>Synapha vitripennis</i> (Meig.)	156		<i>P. dziedzickii</i> Lundst.	1	w
<i>Ectrepesthoneura buccera</i> Plassm.	283		<i>P. elegans</i> Dziedz.	1	
<i>E. colyeri</i> Chand.	3		<i>P. flavicollis</i> Winn.	81	w
<i>E. hirta</i> (Winn.)	629	w	<i>P. forcipata</i> Winn.	81	w
<i>E. nigra</i> A. Zaitzev	5	w	<i>P. fusciventris</i> Van Duzee	7	w
<i>E. pubescens</i> (Zett.)	27		<i>P. nigricornis</i> (Zett.)	14	w
<i>E. referta</i> Plassm.	489	w	<i>P. nigripalpis</i> Lundst.	3412	w
<i>E. tori</i> Zaitzev et Økland			<i>P. peculiaris</i> Dziedz.	3	w
<i>Leia subfasciata</i> (Meig.)	15		<i>P. persimilis</i> Hack.	1	w
<i>L. Winthermi</i> Lehm.	24		<i>P. petulans</i> Dziedz.	1	w

Appendix 2 — contd

Species name	Sum	Habitat	Species name	Sum	Habitat
<i>P. tenuis</i> Winn.	4	w	<i>A. lenis</i> Dzied.	1	s
<i>P. willistoni</i> Dzied.	1		<i>Brachypeza bisignata</i> Winn.	4	w
<i>Sceptonia concolor</i> Winn.	4		<i>Brevicornu arcticum</i> (Lundst.)	2	
<i>S. fumipes</i> Edw.	155		<i>B. bipartitum</i> Last. et Mat.	147	
<i>S. fuscipalpis</i> Edw.	21		<i>B. boreale</i> (Lundst.)	1	
<i>S. regni</i> Chandler	7		<i>B. foliatum</i> (Edw.)	31	
<i>S. tenuis</i> Edw.	5		<i>B. fuscipenne</i> (Staeg.)	6	
<i>Trichonta atricauda</i> (Zett.)	35	w	<i>B. griseicolle</i> (Staeg.)	5	
<i>T. comica</i> Gagné	2		<i>B. griseolum</i> (Zett.)	24	
<i>T. delicata</i> Gagné	4		<i>B. kingi</i> (Edw.)	7	
<i>T. facilis</i> Gagné	1		<i>B. occidentale</i> Zaitz.	2	
<i>T. fissicauda</i> (Zett.)	21		<i>B. ruficorne</i> (Meig.)	113	
<i>T. flavicauda</i> Lundstr.	16		<i>B. sericoma</i> (Meig.)	20	
<i>T. generosa</i> Gagné	2		<i>Cordyla brevicornis</i> (Staeg.)	108	s
<i>T. hamata</i> Mik.	88		<i>C. crassicornis</i> Meig.	10	s
<i>T. melanura</i> (Staeg.)	105		<i>C. flaviceps</i> (Staeg.)	10	s
<i>T. subfusca</i> Lundst.	213		<i>C. fusca</i> Meig.	24	s
<i>T. submaculata</i> (Staeg.)	3		<i>C. murina</i> Winn.	149	s
<i>T. terminalis</i> (Walk.)	2	w	<i>C. nitens</i> Edw.	3	
<i>T. venosa</i> (Staeg.)	10	w/s	<i>C. parvipalpis</i> Edw.	8	s
<i>T. vitta</i> (Meig.)	100	w	<i>C. semiflava</i> (Staeg.)	1	
<i>T. vulgaris</i> Loew	2		<i>C. sixi</i> (Bar.)	13	
<i>Zygomia humeralis</i> (Wied.)	5		<i>Exechia dizona</i> Edw.	1	s
<i>Z. kiddi</i> Chandler	31		<i>E. exigua</i> Lundst.	1	
<i>Z. pictipennis</i> (Staeg.)	2		<i>E. frigida</i> (Boh.)	3	s
<i>Z. pseudohumeralis</i> Casp.	58		<i>E. fusca</i> (Meig.)	1	w/s
<i>Z. semifusca</i> (Meig.)	61		<i>E. lundstroemi</i> Landr.	1	
<i>Z. valida</i> Winn.	2		<i>E. nigra</i> Edw.	1	
<i>Z. vara</i> (Staeg.)	6		<i>E. separata</i> Lundst.	1	s
<i>Allodia anglofennica</i> Edw.	1	s	<i>Exechiopsis clypeata</i> (Lundst.)	1	s
<i>A. lugens</i> (Wied.)	2	s	<i>E. indecisa</i> (Walk.)	1	s
<i>A. lundstroemi</i> Edw.	1	s	<i>E. pulchella</i> (Winn.)	1	
<i>A. septentrionalis</i> Hack.	3		<i>E. subulata</i> (Winn.)	1	s
<i>A. tuomikoskii</i> Hack.	8		<i>Rymosia fasciata</i> (Meig.)	1	w/s
<i>Allodiopsis cristata</i> (Staeg.)	2	s	<i>Tarnania tarnanii</i> (Dzied.)	4	s
<i>Anatella ciliata</i> Winn.	4				

APPENDIX 3

Number of mycetophilid species (Spp.), number of individuals (Ind.) and rarefaction (Rarefact.) in each site; and Spearman rank correlation between these measurements. Comparison of mean values between the areas A, B and C using *t*-test

Site	Elevation	All species			Species in wood			Species in soil		
		Spp.	Ind.	Rarefact.	Spp.	Ind.	Rarefact.	Spp.	Ind.	Rarefact.
Area A										
4	700	78	648	23.9	17	77	9.0	19	46	8.0
7	800	61	520	27.0	20	149	9.3	10	44	5.1
1	850	61	993	18.7	18	627	7.6	8	17	5.7
2	850	104	1523	30.4	31	474	10.0	16	83	6.8
8	850	130	5906	20.8	29	912	8.3	28	154	6.3
5	900	88	952	32.4	22	223	10.1	8	41	5.2
19	900	136	4560	27.7	38	781	10.8	23	264	6.0
Area B										
13	500	73	1497	17.3	21	969	3.4	15	81	5.6
21	500	53	1408	13.6	19	1212	3.7	12	83	5.6
15	550	70	1202	20.5	26	800	5.1	16	48	8.5
18	550	69	713	25.7	23	320	7.6	11	33	5.7
16	600	79	1140	22.1	29	777	5.6	15	46	7.7
14	650	63	447	26.6	21	226	8.1	10	24	6.2
20	750	34	73	33.0	11	26	9.0	10	13	9.0
Area C										
12	150	44	317	21.8	22	91	10.2	11	47	5.7
11	200	41	415	21.2	23	235	7.8	14	43	6.5
17	200	34	218	18.7	13	76	7.0	6	12	6.0
Mean										
Area A		94.0	2157.4	25.8	25.0	463.3	9.3	16.0	92.7	6.1
Area B		63.0	925.7	22.7	21.4	618.6	6.1	12.7	46.9	6.9
Area C		39.7	316.7	20.5	19.3	134.0	8.3	10.3	34.0	6.1
All sites		71.6	1325.4	23.6	22.5	469.1	7.8	13.6	63.5	6.4
<i>p</i> (<i>t</i> -test)										
A against B		0.02	ns	ns	ns	ns	0.003	ns	ns	ns
B against C		0.001	0.001	ns	ns	0.002	ns	ns	ns	ns
A against C		0.0001	0.001	0.004	ns	0.004	ns	ns	0.008	ns
Spearman corr.:										
Spp. × Ind.		$R_s=0.806$			$R_s=0.525$			$R_s=0.838$		
Spp. × Rarefact.		$R_s=0.254$			$R_s=0.195$			$R_s=0.462$		