

# Oak woodland restoration: testing the effects on biodiversity of mycetophilids in southern Sweden

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**Abstract** The effect of harvesting biofuel and woodland restoration on biodiversity is debated. To evaluate the effects of partial cutting on more organism groups, we used pairwise experimental and undisturbed control stands in a large landscape. On average 26% of the basal area including 50–95% of the understorey was harvested at each of 15 oak-rich forest sites. Our earlier results of partial cutting suggested a positive short-term effect for vascular plants and beetles and no or minor negative effects for fungi. Here we analyse the response of mycetophilids (Diptera: Sciaroidea excl. Sciaridae), a neglected but species-rich insect group that was strongly disfavoured by clear-cutting in previous studies. Increased deadwood (slash) caused increase in the number of individuals of mycetophilids associated with wood or wood fungi. The rarefaction species numbers of mycetophilids declined after the treatment, but the absolute number of species was not affected. Our results indicate that a 25% harvest can be compatible with conservation of vascular plants, fungi, saproxylic and herbivorous beetles and mycetophilids in temperate hardwood stands of the type studied. However, more studies are needed to determine what level(s) of stand thinning can be tolerated by different taxa in landscapes with small fragmented conservation stands.

**Keywords** Dead wood · Fungus gnats · Thinning · Biofuel harvesting · Hardwood forest · Temperate forest · Woodland

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## Introduction

As lack of natural disturbances has led to more dense hardwood forests in many regions of North Europe, the optimal strategy for management of biodiversity in the future is debated. Even though the natural history of forests and the focus of conservation debates vary in different countries, it is clear that declining biodiversity due to decreases and changes in broadleaved temperate forests challenges our view of optimal strategies for biodiversity conservation and management (Hannah et al. 1995; Vera 2000; Svenning 2002; Groom et al. 2005). Some ecologists argue that partial cutting can both favour biodiversity and give biofuel that partly replaces the use of fossil fuels; however, the assumption about positive effects on biodiversity is based on few taxa. Many ecologists emphasize natural disturbance regimes as a basis for management actions, but many forests with conservation values have also been strongly disturbed by people for long, mainly through fire (e.g. in North America) and grazing by domestic animals (e.g. in Europe). In many regions, secondary succession has led to changes in tree species composition and denser forests (Vera 2000; Forestry Statistics 2005; Spector and Putz 2006, and references therein), which has inspired the debate about the management alternatives for biodiversity in closed canopy hardwood forests (Sutherland 2002; Birks 2005). A new aspect of this debate is that harvesting and use of biofuel, which potentially could reduce greenhouse gases, is predicted to strongly increase globally (Alcamo et al. 2005; Gustavsson et al. 1995). Forest management systems that can combine goals for biodiversity and CO<sub>2</sub>-emissions are therefore important in the time to come.

Several authors assume that biodiversity in oak-dominated or oak-rich forests of middle and northern Europe (*Quercus robur* and *Q. petraea*) is generally favoured by a semi-open forest structure (Vera 2000; Ranius and Jansson 2000; Nilsson et al. 2001; Svenning 2002; Brudvig and Asbjornsen 2005). From this point of view the development in the Nordic countries is unfavourable because many oak forests that were formerly open and contained large oaks due to grazing in pasture woodland have become dense mixed forest, due to secondary succession following abandonment of grazing or mowing. Partial cutting of small and intermediate-sized trees around large oaks has been recommended for conservation-oriented management in mixed forests with oaks (Dagley et al. 2001; Schuler 2004; Götmark et al. 2005a). Oaks are generally shade-intolerant trees, and light gaps or cutting are needed for regeneration and successful restoration of oak woodland (Vera 2000; Johnson et al. 2002). The interest in partial cutting coincides with growing production of biofuel in Sweden and elsewhere (Lundborg 1998; Johansson 2000; Malinen et al. 2001; Fung et al. 2002). The European Union target is 20% renewable energy of the total energy consumption by 2020, of which two-thirds should come from biofuel (Lins 2004).

It is our concern that the assumptions about favourability of semi-open forest structure build on a limited empirical basis, as the preferences for open or closed canopies are known for relatively few taxa. As far as we have no objective criteria of valuing life forms, management should aim to be based on as many taxa as possible, which is far from the reality in the conservation literature (Clark and May 2002). Furthermore, the knowledge of the requirements should be well-founded, for instance by using controlled and replicated field experiments to evaluate the effects of partial cutting.

Our aim is to expand the knowledge base for future management of temperate dense oak-rich mixed forest by including controlled experiments on more taxa. We use closed canopy stands that remain undisturbed by people as control in the experiments; and study paired experimental (cutting) and control plots before and after cutting. We applied this approach in studies of vascular plants (Götmark et al. 2005a), wood-inhabiting fungi

(Nordén et al. accepted), and saproxylic and herbivorous beetles (Franc 2007), which indicated positive or minor negative effects of partial cutting on biodiversity (see Discussion). In the present study, we include a species-rich insect group known to be sensitive to clear-cutting or canopy-opening; the mycetophilids (Diptera: Sciaroidea excl. Sciaridae).

Mycetophilids are small to medium-sized and non-biting Diptera, including an estimated number of at least 702 species in Sweden (Kjærandsen et al. in print). Most mycetophilids with known habitat requirements develop in fungal substrates in forests (Yakovlev 1994; Zaitzev 1994). Previous studies of mycetophilids in boreal forest revealed significantly lower species richness in clearcut forests compared to uncut oldgrowth forests (Økland 1994). The proportion of oldgrowth forest in the surrounding landscapes (100 km<sup>2</sup>) was positively correlated with mycetophilid species richness and the number of individuals of single species (Økland 1996). Also observations of mycetophilid behaviour (Väisänen 1984; Økland 1996) and the positive effect of precipitation and air humidity on species richness at large spatial scale (Økland et al. 2005) could suggest a negative effect of partial logging.

Based on the results from experimental partial logging, we focus on the following questions: (1) What are the short-term impacts of partial cutting on species richness and species composition of mycetophilids? (2) Do mycetophilids associated with wood-inhabiting fungi and mycetophilids associated with ground-inhabiting fungi react differently to partial cutting? (3) Is there a different effect on species associated with ectomycorrhizal fungi and on saprotrophic fungi? Finally, we summarize our studies of four taxa (vascular plants, wood-inhabiting fungi, saproxylic and herbivorous beetles, mycetophilids) and discuss partial harvesting as management method that may combine biodiversity and production goals in oak-rich temperate forests of conservation value.

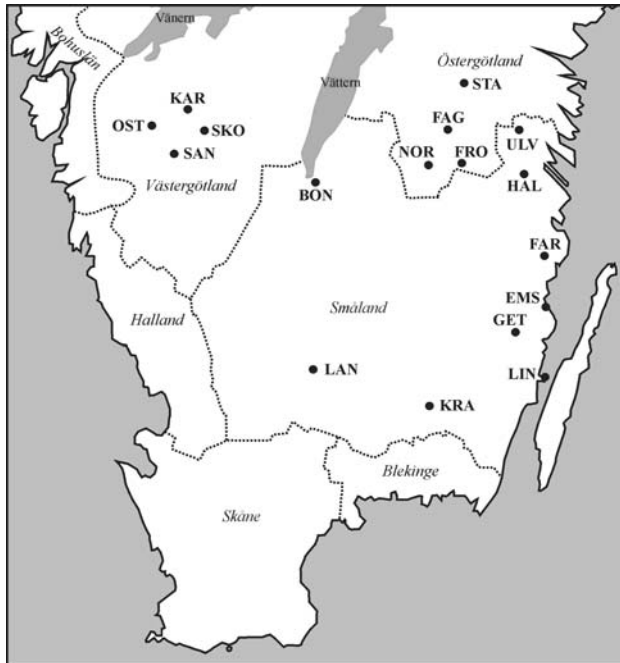
## Methods

### Study area, sites and plots

We selected stands with almost closed canopy within 15 forest sites in southern Sweden (Fig. 1). The sites were located in the boreonemoral zone; a transition between the boreal forest in northern Europe and the temperate (nemoral) forest in the middle parts of Europe (Nilsson 1997). The study sites are located 5–230 m above sea level and the mean monthly precipitation (July) decreases from about 80 mm at the western sites (Fig. 1) to about 55 mm at the eastern coastal sites ([www.smhi.se](http://www.smhi.se)). The mean temperature in July varies from about 14 C in the west to about 17 C in the east. The study sites were relatively level and usually with a bit stony surface on mesic moraine soil.

The forests were mostly dominated by *Quercus robur* and *Q. petraea* (mean basal area before cutting 42%, SD = 14%, range 23–65%,  $n = 15$ ). The oldest oaks at each site were on average 150–200 years old. Younger broadleaved trees of many species, mainly birch *Betula pendula*, ash *Fraxinus excelsior*, trembling aspen *Populus tremula*, maple *Acer platanooides*, lime *Tilia cordata*, beech *Fagus sylvatica*, and goat willow *Salix caprea*, had invaded the study sites, forming dense forest around the oaks with an understorey commonly dominated by the large shrub hazel *Corylus avellana*. Also Norway spruce *Picea abies* occurred at most sites and made up a relatively large part of the canopy at four sites (25–40% of the basal area before cutting). For more information about trees at the sites, see Nordén et al. (2004a, b) and Økland et al. (2005).

The 15 study sites are all of conservation (biodiversity) interest and classified as ‘Woodland Key Habitats’ (12) or Nature Reserves (3). Site information and permissions were



**Fig. 1** Study area in southern Sweden with experimental sites (forests). EMS = Emsfors, FAG = Fagerhults, FRÖ = Fröåsa, FÅR = Färbo, GET = Getebro, HAL = Hallingeberg, KAR = Karla, KRÅ = Kråksjö by, LIN = Lindö, LÅN = Långhults, SAN = Sandviksås, SKÖ = Skölvne, STA = Stafsaäter, ULV = Ulvsdal, ÖST = Östadkulle. All sites are woodland key habitats except for three nature reserves (GET, KAR, KRÅ)

obtained through conservation authorities and forest owners. Each study site consists of two plots of 1 ha, comprising one experimental and one reference plot that were as similar as possible with respect to forest habitat. After plots were established, we selected experimental (cutting) plot randomly from each pair of plots.

Our overall objective is to examine biodiversity of closed canopy (presently undisturbed) and partially harvested (semi-open) stands, without prejudice with respect to 'best' option (forest management or absence of it). One common conservation goal for stands containing large oaks (Löfgren and Andersson 2000) is to favour these trees. Therefore, careful cutting (thinning) was conducted around them, providing space and light. There were few oak saplings, so an additional goal was to favour oak recruitment by cutting conifers (almost all) and other broadleaved trees, but also some oaks of intermediate size. Old (large) individuals of other broadleaved trees were retained. Of the understorey (stems 1–5 cm in diameter at 1.3 m, dbh), 55–95% of all stems were cut and harvested; a higher proportion if there were many stems (this wood fraction is increasingly used for biofuel). Tops and branches of larger trees, and two (cut) oak logs were left in the plots to provide some deadwood. Our partial cutting design has favoured regeneration of oak seedlings (Götmark 2007).

All trees that were to be harvested were marked by us in the summer of 2002. Protocols and detailed instructions were then sent landowners and forestry entrepreneurs, who cut and harvested the stands in October 2002–March 2003. Trees/bushes were cut manually and removed by forwarders from plots. A relatively small proportion of the basal area was

**Table 1** Basal area (m<sup>2</sup>/ha) of trees and canopy (% visible sky) before (2002) and after partial cutting (2003) in experimental plots

Site	Basal area*			Canopy openness**		
	Before	After	% change	Before	After	% change
EMS	22.2	18.7	15.8	11.6	32.2	177
FAG	26.5	20.5	22.8	10.2	31.9	213
FRÖ	35.9	24.2	32.6	18.6	45.9	146
FÅR	31.3	19.6	37.4	18.6	35.6	92
GET	35.9	29.1	18.9	14.2	32.2	127
HAL	28.8	24.1	16.1	12.4	19.9	60
KAR	25.8	18.6	28.0	19.6	35.6	82
KRÅ	30.3	23.1	23.9	9.4	25.0	165
LIN	25.7	21.8	15.2	10.2	29.1	185
LÅN	24.0	17.4	27.3	16.1	28.3	76
SAN	35.8	24.6	31.2	19.4	56.9	194
SKÖ	26.1	20.8	20.3	17.5	42.8	145
STA	19.4	17.2	11.5	9.2	28.1	204
ULV	26.6	20.8	21.6	18.9	33.2	76
ÖST	31.9	23.4	26.5	12.4	31.0	150
Mean	28.4	21.6	23.3	14.6	33.8	139
SD	5.0	3.2	7.3	4.0	9.0	52

\* Based on trees/shrubs >5 cm in diameter at 1.3 m, measured on about 60% of the plot area

\*\* Mean value, based on eight photographs taken from ground level at fixed points

harvested (see below), for two reasons. First, in broadleaved deciduous forest in Sweden and elsewhere (Kittredge et al. 2003) landowners often cut selectively, removing relatively few trees at a time, for fuel or other purposes. Second, our stands had high conservation values, and a small harvest was in line with Precautionary Principles. The proportion of basal area ( $\geq 5$  cm dbh) harvested was on average 23.3% (see Table 1), but because a high proportion of the thin stems (<5 cm dbh) also was removed, the true value is about 25–27%. Based on photographs of the canopy (same positions before–after harvest), the mean canopy openness (proportion of visible sky from ground level) more than doubled after harvest, from 15% to 34% (+139%, Table 1). The increase in light was relatively patchy, and higher e.g. around old oaks, or where spruces had been cut. Harvesting of much of the undergrowth also contributed to increased light levels at ground level.

Each plot had a forested buffer zone of at least 15 m outside the plots to avoid edge effects inside the plots. The 15 study sites contained on average  $14.3 \pm 7.81$  (SD) m<sup>3</sup>/ha coarse dead wood (CWD, diameter >10 cm), and  $11.4 \pm 5.00$  m<sup>3</sup>/ha fine dead wood (FWD, diameter 1–10 cm), which is about two to three times more CWD than in production forest in southern Sweden (Nordén et al. 2004a).

### 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 1994, 1996). We did not sample in the first summer after cutting (2003), since an extra season for response in the insects (e.g. egg-laying and larval development) was considered appropriate. In 2002 (before cutting) and 2004 (after cutting), two traps were used at each site, one in the experimental and one in the reference plot. They were operative

during two periods in each year: in early summer, and in late summer. The periods in 2002 were from 14–18 May (traps started) to 11–14 June (traps emptied), and from 30 July–1 August (started) to 3–6 September (emptied and removed). The periods in 2004 were from 10–17 May (started) to 8–11 June (emptied), and from 27–30 July (started) to 31 August–1 September (emptied and removed; the sampling dates for 2002 apply also for the trapping in Økland et al. (2005), where given dates are incorrect). The two traps at each site were always started on the same date, and emptied on the same date.

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 140–160 m apart near the centre of each plot. 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. The location of traps (with log/branch) was exactly the same in 2002 and 2004. 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<sup>2</sup> 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. The same persons (A. Polevoi and O. Kurina) sorted and identified the specimens in both 2002 and 2004. All specimens were identified to species or genus except for a few destroyed specimens (in several species the female individuals are difficult to identify to the species level). The complete species list is given in Appendix 1. A commented list of species sampled before logging is presented in Kurina et al. (2005).

### Statistical analyses

Experimental and reference plots closely resembled each other. Mean basal areas of trees in experimental ( $n = 15$ ) and reference plots ( $n = 15$ ) before cutting were 28.4 m<sup>2</sup>/ha (SD = 5.0) and 29.7 m<sup>2</sup>/ha (SD = 4.4), respectively, and not significantly different ( $P = 0.42$ ); mean canopy openness before cutting were 14.6% (SD = 4.0) and 14.6% (SD = 4.3), respectively, and not significantly different ( $P = 0.94$ ). Also forest age, structure, deadwood and species content were on average similar in the two plot types. Experimental and reference plots were geographically matched and we used paired Students *t*-test for the data, which were approximately normally distributed. One of the sites (EMS) was omitted from the comparisons because the trap in the partially cut plot was disturbed during sampling after the treatment. The effect of partial harvesting on species richness was assessed as follows: First the number of species in a plot before partial cutting was subtracted from the number of species in the same plot after partial cutting. Thereafter the difference in number of species (after minus before partial cutting) was compared between experimental and reference plots, under a null hypothesis that the average of these differences are equal for experimental and reference plots. The same test procedure was applied for the number of individuals of individual species and in total. Test of individual species was only done for species with minimum five individuals and presence in minimum five sites.

In an attempt to separate the effects of change in microclimate and removal of trees, the above-described test procedure was also applied on species richness and individual numbers within the following sub-categories. A first distinction was made between (1) mycetophilid species associated with wood or wood-inhabiting fungi, and (2) mycetophilid species associated with soil-inhabiting fungi. Secondly, mycetophilids were classified as associated with (3) saprotrophic fungi (fruitbodies found on either wood or soil) or (4) ectomycorrhizal

fungi (fruitbodies found on either wood or soil). Note that saprophytic fungi may be either wood-decayers or decayers of dead organic material in soil. Further, fruitbodies of ectomycorrhizal species may for some species be found on dead wood, although the majority is found on soil. Mycetophilid-fungi associations followed Yakovlev (1994) with additions from Alexander Zaitzev (pers. comm.), and classification of fungi into the above-mentioned classes agrees with the UNITE-database <http://unite.ut.ee/index.php>.

The number of species in an area is usually a function of the number of individuals (Gotelli and Colwell 2001). To check if individual numbers matter for the result of comparing species richness between plots, the number of species in the experimental plots and in the reference plots after partial cutting were compared by average species accumulation curves constructed using EstimateS 7.5 (Colwell 2005). Two curves were plotted, one with number of sites on the  $x$ -axis (species density) and the other with number of individuals on the  $x$ -axis (species richness sensu Gotelli and Colwell 2001). Following Hughes et al. (2001) we did not include confidence envelopes constructed from the variance among the resamples, since they can only be used to compare variation in the richness estimates among samples (shown on the  $x$ -axis) and is not a measure of confidence about the actual richness in the communities. To judge trends, we compared curves visually. For species groups showing a significant difference in mean number of individuals between treatment and reference, the paired  $t$ -test described above was also applied on rarefaction estimates calculated by a web-based rarefaction calculator (Brzustowski 2003).

To analyse if the species composition changed more in the plots subjected to partial cutting than in the reference plots, Sørensen similarity index (Magurran 2004) was calculated for the mycetophilid assemblages before and after the partial cutting. The difference in index value (after minus before partial cutting) was tested with a one-sided paired Students  $t$ -test by comparing experimental plots and reference plots, assuming a null hypothesis that mean changes for the plot types are about equal, and an alternative hypothesis that the species composition changes more and has a higher index value in the experiment plots than in the reference plots.

## Results

The trap material contained altogether 21,982 mycetophilid specimens of which 14,595 were identified to the species level yielding altogether 286 species. The total number of species was about similar before (228) and after the partial logging (226), though the number of individuals was larger after the treatment (6,614 in 2002 and 7,981 in 2004). The experimental plots had higher mean number of individuals after (327 ind.) than before treatment (241 ind.;  $T = 2.63$ ,  $P < 0.01$ , two-sided paired Students  $t$ -test), while the reference plots did not show a significant difference before and after treatment ( $P = 0.63$ ). A corresponding comparison of species number per site showed no significant difference for the treated plots, but a higher number after treatment (48 species) than before treatment (39 species) for the reference plots ( $P = 2.53$ ,  $P < 0.04$  in two-sided paired Students  $t$ -test).

Using both experimental and reference plot in a combined test, we could reduce the effects of between-year variations in population abundances: the differences before and after treatment were compared between experimental and reference plots by paired Students  $t$ -tests (Table 2). The treatment caused no significant change in *number of species* when all species were included ( $P = 0.44$ ), but weak (non-significant) negative tendencies when the species were restricted to sub-groups, i.e. species only associated with wood or wood fungi ( $P = 0.18$ ), species only associated with ground-inhabiting fungi ( $P = 0.12$ ),

**Table 2** Test of treatment effect of partial cutting on mycetophilids in oak-rich forest: change in species richness or individuals in experimental and reference plots (number of species/individuals after minus number of species before treatment)

	No. of species		No. of individuals		Rarefaction (species)	
	Treated	Reference	Treated	Reference	Treated	Reference
<i>All species</i>						
Mean*	7.4	8.4	85.7	11.1		
Range	-47 to 38	-15 to 43	-72 to 326	-240 to 244		
<i>T</i>		0.78		1.52		
<i>P</i>		0.44		0.15		
<i>Wood and wood-fungi</i>						
Mean	-1.0	0.6	28.4	-13.0	-0.4	0.8
Range	-13.0 to 6.0	-5.0 to 8.0	-71 to 145	-139 to 110	-4.5 to 1.8	-2.9 to 3.0
<i>T</i>		1.37		2.53		2.28
<i>P</i>		0.18		0.03		0.03
<i>Saprotrophic fungi</i>						
Mean	-0.4	1.0	20.2	-32.5	0.1	1.4
Range	-12.0 to 6.0	-3.0 to 7.0	-88 to 154	-140 to 96	-3.9 to 3.2	-0.2 to 3.4
<i>T</i>		1.42		2.89		2.82
<i>P</i>		0.17		0.01		0.01
<i>Soil-inhabiting fungi</i>						
Mean	1.5	0.1	-3.6	-1.1		
Range	-4.0 to 7.0	-5.0 to 5.0	-53 to 32	-18 to 43		
<i>T</i>		1.59		0.28		
<i>P</i>		0.12		0.78		
<i>Ectomycorrhizal fungi</i>						
Mean	0.8	-0.5	14.6	22.5		
Range	-1.0 to 3.0	-7.0 to 5.0	-28 to 147	-39 to 181		
<i>T</i>		1.74		1.13		
<i>P</i>		0.09		0.27		

\* Mean based on 14 experimental and 14 reference plots

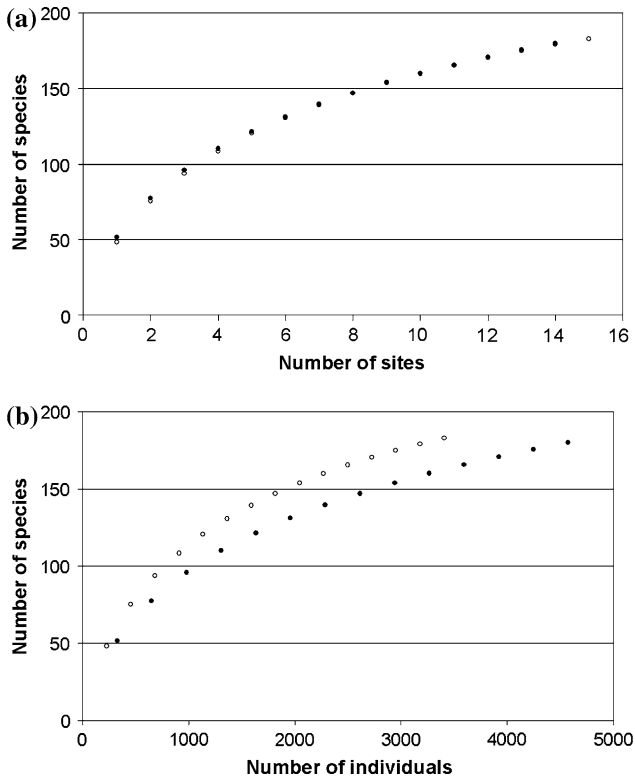
species only associated with ectomycorrhizal fungi ( $P = 0.09$ ), or species only associated with saprotrophic fungi ( $P = 0.09$ ).

The number of individuals was somewhat higher in 2004 (after treatment) than in 2002 (before treatment) both for treated (mean difference 85.7, range -72 to 326) and reference plots (mean difference 11.07, range -156 to 244), though the variation among plots was large (Table 2). The change in number of individuals did not differ significantly between treated and reference plots ( $P = 0.15$ ).

Considering species that are only associated with wood or wood fungi, the average number of individuals increased in the treated plots (28.4) and declined in the reference plots (-13), a significant difference ( $P = 0.013$ ) despite considerable variation among plots (Table 2). Also for species only associated with saprotrophic fungi, the average number of individuals changed differently ( $P < 0.001$ ) with increase in treated plots and decline in reference plots (Table 2). For mycetophilids only associated with ectomycorrhizal fungi and for mycetophilids only associated with soil-inhabiting fungi, there were no significant changes in average number of individuals for treated compared with reference plots (Table 2).

The randomized species accumulation curves for all species (pooled) showed that the species density ( $x$ -axis scaled by the number of sample plots) was about the same for treated and reference plots (Fig. 2a). Species richness (sensu Gotelli and Colwell 2001;



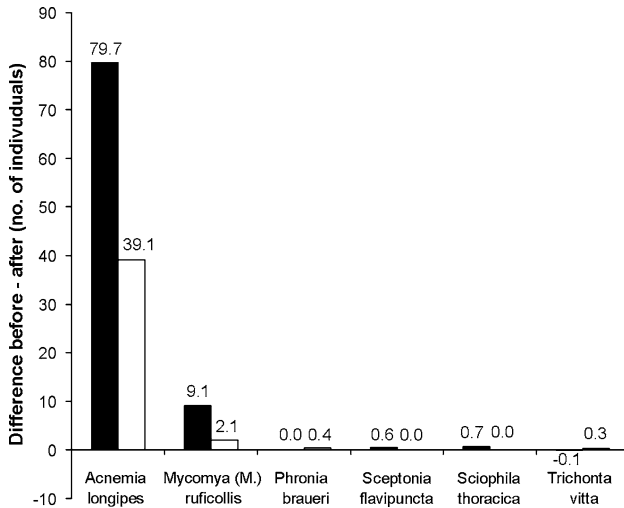


**Fig. 2** Randomized species accumulation curves for mycetophilids after partial cutting, for experimental plots (filled circles) and reference plots (open circles) as a function of site numbers (a; species density) and individual numbers (b; species richness, sensu Gotelli and Colwell 2001)

$x$ -axis scaled by the number of records) tended to be lower in treated than in reference plots, i.e. fewer species for a given number of individuals (Fig. 2b). Since the number individuals differed significantly for some of the sub-groups (Table 2), and since Fig. 2b suggests an effect of individual numbers on species richness, the paired Student  $t$ -tests were repeated on rarefaction values for all mycetophilid species and for species groups with significant difference in abundances (Table 2). We found significant decrease in species richness based on rarefaction values for *species only associated with wood or wood fungi* ( $P < 0.03$ ), and *species only associated with saprotrophic fungi* ( $P < 0.01$ , Table 2).

The change in species composition from 2002 to 2004 analysed by Sørensen's index was similar for experimental plots (mean 1.58, range 1.43–1.75) and reference plots (mean 1.57, range 1.41–1.75), and did not differ significantly between these categories using one-sided paired Students paired  $t$ -test ( $T = 0.91$ ,  $P = 0.37$ ).

We tested in total 114 species one by one (two-sided Students paired  $t$ -test), and found only six species with significantly different change in number of individuals between experimental and reference plots at a 5% level (Fig. 3). Due to multiple tests, only the differences with test significance below 1% can be considered as certain. Large differences were found for *Acnemia longipes* ( $T = 2.49$ ,  $P < 0.02$ ) and *Mycomya (M.) ruficollis* ( $T = 2.17$ ,  $P < 0.04$ ). The other four species *Phronia braueri* ( $T = 2.34$ ,  $P < 0.03$ ), *Sceptonia flavipuncta* ( $T = 2.63$ ,  $P < 0.01$ ), *Sciophila thoracica* ( $T = 2.11$ ,  $P < 0.04$ ), and *Trichonta vitta* ( $T = 2.51$ ,



**Fig. 3** Treatment effect of partial cutting on individual species of mycetophilids in oak-rich forest. The columns represent the average change in number of individuals (number of individuals after minus number of individuals before treatment) for experimental plots (black columns) and reference plots without any treatment (white columns). Only species with a significant difference ( $P < 0.05$ ) between experimental and reference plots are included (pairwise Student's  $t$ -test)

$P < 0.02$ ) exhibited only small negative or positive differences between experimental and reference plots (Fig. 3). All of the significant species are known from wood or wood fungi, or belong to mycetophilid genera that are associated with wood or wood fungi.

## Discussion

### Response of mycetophilids to partial cutting

The most pronounced effect of the present study was an increase in the number of mycetophilid individuals after partial cutting (2004) compared to before (2002). Both between-year variation and the experiment could potentially explain such an effect. Former inventories showed considerable between-year variation in abundances of mycetophilids as well as their major host group, fungi (Yakovlev and Zaitzev 1990; Ohenoja 1993; Yakovlev 1993). However, our strong experimental design indicates that the treatment was the most important factor, because the before-after increase in number of individuals was found in the treated plots and not in the reference plots.

Apparently, the increase of dead wood after partial logging (mainly tops and live and dead branches from removed tree stems) has a slightly positive effect on the abundance of mycetophilids. We found increased number of individuals of mycetophilids associated with wood or wood fungi and mycetophilids associated with saprotrophic fungi, which coincides with an increase (at least fivefold) in total dead wood volume, especially FWD (=fine woody debris with diameter 1–10 cm; records in the same sites in 2003 by Nordén et al. accepted). Alternatively, the abundance of mycetophilids could possibly be favoured by more sheltered microhabitats due to the rapid growth of herbs and other understorey vegetation after the partial logging (Götmark et al. 2005a; Götmark et al. 2005b, p. 232; pers.

obs.). However, this is unlikely, as the increase in individual numbers was only found for mycetophilids associated with wood or wood fungi and saprotrophic fungi, and not for other groups, such as mycetophilids associated with ectomycorrhizal fungi and mycetophilids associated with soil-inhabiting fungi. Furthermore, the degree of grass and bush cover in the experimental sites did not correlate with the individual numbers of mycetophilids associated with wood or wood fungi (Spearman  $r_s \approx 0$ ), mycetophilids associated with saprotrophic fungi ( $r_s = 0.069$ ), or mycetophilids in general ( $r_s = -0.138$ ). The production of mycetophilid individuals may have been favoured by the increase of some early-colonizing fungal species on FWD that started to fructify already in the first year after partial cutting (Nordén et al. accepted), or other fungi on the increased amount of FWD that were available for larval development of mycetophilids.

Despite large samples, the number of recorded species did not change significantly for any of the groups. When rarefaction was used to adjust for the increase in individual numbers, the treatment gave a significant decrease in the number of mycetophilid species associated with wood and wood-fungi, and the number of species associated with saprotrophic fungi (partially overlapping species groups). Nevertheless, the tests based on all individuals collected do not suggest a negative effect of the partial cutting on species richness in the groups. We agree with Gotelli and Colwell (2001, p. 387) that species density (based on all individuals collected) is usually the measure which is most relevant to conservation work.

Previous studies of mycetophilids indicated an immediate and marked reduction in species richness of mycetophilids on clearcuts, which can be associated with the negative effect on ectomycorrhizal fungi and fungi that are sensitive to desiccation (Økland 1994). Fruitbodies of most ectomycorrhizal fungi associated with the tree roots usually disappear shortly after clearcutting; however, some saprophytic fungi may be favoured and produce even more fruitbodies (Harvey et al. 1980; Ohenoja 1988). With a partial cutting of about 26% of the basal area in the present study, a large fraction of the symbiotic partners of the ectomycorrhizal species was still present after the treatment. Species richness of fruitbodies of both saprotrophic and ectotrophic fungi declined slightly, probably due to a combined effect of drier microclimate and removal of trees (Nordén et al. accepted). However, we found no changes in species richness or individual numbers of mycetophilids associated with ectomycorrhizal fungi or mycetophilids associated with soil-inhabiting fungi, presumably because habitats for these mycetophilids were still available within, or close to the plots.

Mycetophilids are believed to contain drought-sensitive species that hide in root jars, holes and crevices to avoid desiccation and that avoid flying into open areas (Vaisänen 1984; Økland 1994, 1996). However, some mycetophilid species might move into semi-open areas under certain conditions; for instance, they have been observed flying at dusk and in moist weather (Vaisänen 1984). Continuously trapping by malaise tents on clearcuts showed that most mycetophilids tend to avoid completely tree-less areas even at night and under moist weather conditions (Økland 1994). Based on the present and earlier results, we hypothesize that many species do not avoid flying into 1 ha plots with partial cutting of about 26% of closed canopy stands. Important questions for future research are: what proportion of the canopy may be removed, and how large forest areas can be cut and tolerated by flying individuals of the various mycetophilid species?

Previous studies have demonstrated that environmental factors acting on large scale are important for species richness of mycetophilids, such as the fragmentation of old growth in the surrounding 100 km<sup>2</sup> and different forest types of Scandinavian vegetation zones (Økland 1996; Økland et al. 2005). The landscapes of the present experimental sites are highly fragmented with respect to old growth forests (about 2% left) and contain forest sites

with relatively few species of mycetophilids (Økland et al. 2005). Possibly, the species pool in the present experiment lack mycetophilid species that are most sensitive to logging and fragmentation of old growth forest. Comparing with less fragmented areas in Scandinavia (Økland et al. 2005), we see that malaise trap captures from sites with at least 40% of old growth forests in the surrounding 100 km<sup>2</sup> in SE Norway contained 180 mycetophilid species that did not occur in the present experimental sites, while only 21 species in the present experimental sites did not occur in the area in SE Norway. Another possibility is that regional climatic differences account for, or contribute to these differences in species richness and composition (Økland et al. 2005).

The population dynamics of the single species have an underlying effect on the patterns of species richness and abundances. In insects, time series analyses of species have revealed a diversity of patterns connected with density dependencies and external factors (Royama 1992). Unfortunately, similar or related studies do not exist for mycetophilids. One may assume that also mycetophilid species have a diversity of population dynamics, and that captures in single years are dependent upon the status of the various populations. On the other hand, if the population dynamics of many species show a similar response to one or more environmental parameters, these parameters may also be determinants of the number of species and/or number of individuals of these species (Økland 1994, 1996; Økland et al. 2005).

#### Partial cutting: effects on biodiversity and suggestions for forest management

Table 3 summarizes our experimental studies of herbaceous vascular plants, wood-living fungi, saproxylic and herbivorous beetles, and mycetophilids. Increased species richness and diversity of herbs due to cutting (Table 3) is probably also beneficial for e.g. fungi and invertebrates using these plants (e.g. parasites, herbivores, nectar-feeders). Partial cutting

**Table 3** Summary of effects of partial cutting on vascular plants, wood-inhabiting fungi, beetles and mycetophilids in the present experimental study in southern Sweden (see also text)

Taxon <sup>a</sup>	No. sites studied <sup>b</sup>	No. species studied <sup>c</sup>	Effects, species richness	Effects, species composition	Effects, overall and longer-term
Vascular plants <sup>d</sup>	6	158	Increase (on average, 18%)	Increase in diversity ( $H'$ )	Positive
Wood- Inhabiting fungi <sup>e</sup>	21	381	Decrease, but minor	No change <sup>f</sup> (Correspondence Analysis)	Mix of negative and positive
Saproxylic beetles <sup>g</sup>	22	267	Increase (NMS)	Change	Positive
Herbivorous beetles <sup>g</sup>	22	222	Increase	Change (NMS)	Positive
Mycetophilids <sup>h</sup>	15	286	No change, except by rarefaction	No, or slight change (Sörenson's Index)	Minor effects

<sup>a</sup> Vascular plants; forbs and grasses, wood-inhabiting fungi; fruitbody inventory of species on dead wood or dying trees (334 basidiomycetes and 47 ascomycetes)

<sup>b</sup> Out of 25 sites selected for the project, see descriptions in Nordén et al. (2004b)

<sup>c</sup> Total number of species recorded and used in analyses

<sup>d</sup> Götmark et al. (2005a)

<sup>e</sup> Nordén et al. accepted

<sup>f</sup> Except that recorded number of red-listed fungi declined, from 10 to 4 species

<sup>g</sup> Franc (2007)

<sup>h</sup> Present study

appeared to favour saproxylic and herbivorous beetles (Franc 2007). Species richness of wood-living fungi (fruit-bodies) decreased, but this decrease was clearly smaller than the between-year variation in non-manipulated plots (sampled two years before cutting) (Nordén et al. accepted). Moreover, we predict increased species richness of fungal fruit-bodies in the future when the new deadwood is colonized, and as the growing vegetation creates more shade and moisture. In addition, several species of ground-living fungi are favoured by openings/gaps in forest. In the perspective of 5–20 years, we hypothesize that partial cutting is positive for herbs, and essentially neutral for overall fungal and mycetophilid diversity.

The present study indicates a suitable compromise of biodiversity conservation and efforts to reduce CO<sub>2</sub>-emissions by biofuel harvesting. A moderate harvest of the basal area (about 25%) seems to be tolerable or even favourable for species-rich taxa in oak-rich forests of southern Sweden. However, more knowledge about the trade-offs involved is needed, including studies of more taxa, studies within other regions with species compositions that differ from southern Sweden, and studies of responses when more than 25% of the woody biomass is harvested. Based on the precautionary principle, we do not recommend harvesting of more than 25% of the woody biomass during restoration of oak-rich stands in northern Europe.

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## Appendix 1

Species names of all mycetophilids in the present study (taxa with incomplete names are excluded)

<i>Acnemia angusta</i> Zaitzev, 1982	<i>Coelosia tenella</i> (Zetterstedt, 1852) <sup>b,c,d</sup>
<i>Acnemia longipes</i> Winnertz, 1863	<i>Cordyla brevicornis</i> (Staeger, 1840) <sup>a,b,c,d</sup>
<i>Acnemia nitidicollis</i> (Meigen, 1818) <sup>a,b,c,d</sup>	<i>Cordyla crassicornis</i> Meigen, 1818 <sup>b,c</sup>
<i>Acomoptera difficilis</i> (Dziedzicki, 1885)	<i>Cordyla fasciata</i> Meigen, 1830 <sup>b,c,d</sup>
<i>Allocotocera pulchella</i> (Curtis, 1837) <sup>a,d</sup>	<i>Cordyla fissa</i> Edwards, 1925 <sup>b,c</sup>
<i>Allodia</i> (B.) <i>czernyi</i> (Landrock, 1912) <sup>b,c,d</sup>	<i>Cordyla flaviceps</i> (Staeger, 1840) <sup>b,c</sup>
<i>Allodia</i> (B.) <i>grata</i> (Meigen, 1830) <sup>b,c,d</sup>	<i>Cordyla fusca</i> Meigen, 1804 <sup>a,b,c</sup>
<i>Allodia silvatica</i> (Landrock, 1912) <sup>b,c,d</sup>	<i>Cordyla insons</i> Lastovka & Matile, 1974
<i>Anatella ankei</i> Plassmann, 1977	<i>Cordyla murina</i> Winnertz, 1863 <sup>b,c,d</sup>
<i>Apolephthisa subincana</i> (Curtis, 1837) <sup>a,d</sup>	<i>Cordyla nitens</i> Winnertz, 1863 <sup>b,c</sup>
<i>Azana anomala</i> (Staeger, 1840)	<i>Cordyla nitidula</i> Edwards, 1925 <sup>b,c</sup>
<i>Boletina basalis</i> (Meigen, 1818)	<i>Cordyla parvipalpis</i> Edwards, 1925 <sup>a,b</sup>
<i>Boletina brevicornis</i> Zetterstedt, 1852	<i>Cordyla pseudomurina</i> Kurina in press
<i>Boletina dispecta</i> Dziedzicki, 1885	<i>Cordyla pusilla</i> Edwards, 1925
<i>Boletina dubia</i> (Meigen, 1804)	<i>Cordyla semiflava</i> (Staeger, 1840)
<i>Boletina gripha</i> Dziedzicki, 1885 <sup>c</sup>	<i>Diadocidia</i> (D.) <i>ferruginosa</i> (Meigen, 1830) <sup>a,d</sup>
<i>Boletina griphoides</i> Edwards, 1925	<i>Diadocidia</i> (D.) <i>spinosula</i> Tolle, 1948
<i>Boletina gusakovae</i> A.Zaitzev, 1994	<i>Docosia fumosa</i> Edwards, 1925
<i>Boletina lundstroemi</i> Landrock, 1912	<i>Docosia fuscipes</i> (Roser, 1840)
<i>Boletina moravica</i> Landrock, 1912	<i>Docosia gilvipes</i> (Walker, 1856) <sup>a,b,c,d</sup>
<i>Boletina nigricans</i> Dziedzicki, 1885	<i>Docosia moravica</i> Landrock, 1928

## Appendix 1 continued

- Boletina nitida* Grzegorzek, 1885  
*Boletina pallidula* Edwards, 1925  
*Boletina plana* (Walker, 1856)  
*Boletina populina* Polevoi, 1995  
*Boletina rejecta* Edwards 1941  
*Boletina sciarina* Staeger, 1840  
*Boletina silvatica* Dziedzicki, 1885  
*Boletina trispinosa* Edwards, 1913  
*Boletina trivittata* (Meigen, 1818)  
*Bolitophila (B.) cinerea* Meigen, 1818<sup>c,d</sup>  
*Bolitophila (C.) glabrata* Loew, 1869<sup>b,d</sup>  
*Bolitophila (C.) hybrida* (Meigen, 1804)<sup>a,b,c</sup>  
*Brachypeza bisignata* Winnertz, 1863<sup>a,b,d</sup>  
*Brevicornu (B.) boreale* (Lundström, 1914)  
*Brevicornu (B.) cognatum* Ostroverchova, 1979  
*Brevicornu (B.) fasciculatum* (Lackschewitz, 1937)  
*Brevicornu (B.) griseicollis* (Staeger, 1840)<sup>b</sup>  
*Brevicornu (B.) improvisum* Zaitzev, 1995  
*Brevicornu (B.) nigrofuscum* (Lundström, 1909)  
*Brevicornu (B.) parafennicum* Zaitzev, 1995  
*Brevicornu (B.) rosmellitum* Chandler, 2001  
*Brevicornu (B.) ruficorne* (Meigen, 1838)  
*Brevicornu (B.) serenum* (Winnertz, 1863)  
*Brevicornu (B.) sericoma* (Meigen, 1830)<sup>b,c</sup>  
*Brevicornu bipartitum* Laštovka et Matile, 1974  
*Brevicornu fennicum* (Landrock, 1927)  
*Brevicornu fuscipenne* (Staeger, 1840)  
*Coelophthimia thoracica* (Winnertz, 1863)<sup>b,c</sup>  
*Coelosia fusca* Bezzi, 1892<sup>c,d</sup>  
*Leia crucigera* Zetterstedt, 1838  
*Leia cylindrica* (Winnertz, 1863)  
*Leia fuscipennis* Meigen, 1818  
*Leia picta* Meigen, 1830  
*Leia subfasciata* (Meigen, 1818)  
*Leia winthemi* Lehmann, 1822<sup>a,b,c,d</sup>  
*Leptomorphus walkeri* Curtis, 1831<sup>a,b,d</sup>  
*Macrocera lutea* Meigen, 1804  
*Macrocera maculata* Meigen, 1818  
*Macrocera parva* Lundström, 1914  
*Macrocera phalerata* Meigen, 1818  
*Macrocera pilosa* Landrock, 1917  
*Macrocera pumilo* Loew, 1869  
*Macrocera stigma* Curtis, 1837<sup>a,d</sup>  
*Macrocera stigmoides* Edwards, 1925  
*Macrocera vittata* Meigen, 1830  
*Megalopelma nigroclavatus* (Strobl, 1909)  
*Megophthalmidia crassicornis* (Curtis, 1837)  
*Monoclona rufilatera* (Walker, 1837)<sup>a,d</sup>  
*Mycetophila abiecta* (Lastovka, 1963)  
*Mycetophila adumbrata* Mik, 1884<sup>a</sup>  
*Mycetophila alea* Laffoon, 1965<sup>b,c</sup>  
*Mycetophila assimilis* Matile, 1967<sup>b,c</sup>  
*Mycetophila attonsa* (Laffoon, 1957)  
*Mycetophila bohémica* (Lastovka, 1963)  
*Mycetophila boreocruator* Sevcik, 2003  
*Docosia sciarina* (Meigen, 1830)  
*Docosia setosa* Landrock, 1916  
*Dynatosoma dihaeta* Polevoi, 1995  
*Dynatosoma fuscicorne* (Meigen, 1818)<sup>a,d</sup>  
*Dynatosoma nigromaculatum* Lundström, 1913<sup>a</sup>  
*Dynatosoma norwegiense* Zaitzev & Okland, 1994  
*Dynatosoma reciprocum* (Walker, 1848)<sup>a,d</sup>  
*Dynatosoma rufescens* (Zetterstedt, 1838)<sup>a,d</sup>  
*Dziedzickia marginata* (Dziedzicki, 1885)  
*Ectrepesthoneura bucera* Plassmann, 1980  
*Ectrepesthoneura colyeri* Chandler, 1980  
*Ectrepesthoneura hirta* (Winnertz, 1846)<sup>d</sup>  
*Ectrepesthoneura pubescens* (Zetterstedt, 1860)  
*Ectrepesthoneura tori* Zaitzev & Okland, 1994  
*Epicrypta aterrima* (Zetterstedt, 1852)<sup>b</sup>  
*Exechia dizona* Edwards, 1924<sup>b,c,d</sup>  
*Exechia parva* Lundström, 1909<sup>b,c,d</sup>  
*Exechia repandoides* Caspers, 1984  
*Exechiopsis (E.) forcipata* (Lackschewitz, 1937)  
*Exechiopsis (X.) seducta* (Plassmann, 1976)  
*Exechiopsis aemula* Plassmann, 1984  
*Exechiopsis leptura* (Meigen, 1830)  
*Exechiopsis membranacea* (Lundström, 1912)  
*Exechiopsis pseudopulchella* (Lundström, 1912)  
*Gnoriste bilineata* Zetterstedt, 1852  
*Grzegorzecchia collaris* (Meigen, 1818)  
*Keroplatus testaceus* (Dalman, 1818)<sup>a,d</sup>  
*Leia bilineata* (Winnertz, 1863)<sup>a,d</sup>  
*Leia bimaculata* (Meigen, 1804)  
*Mycetophila strigatoides* (Landrock, 1927)<sup>a,b</sup>  
*Mycetophila strobli* Lastovka, 1972<sup>a,b</sup>  
*Mycetophila stylata* (Dziedzicki, 1884)<sup>b</sup>  
*Mycetophila subsigillata* Zaitzev, 1999  
*Mycetophila sumavica* (Lastovka, 1963)  
*Mycetophila trinotata* Staeger, 1840<sup>a,d</sup>  
*Mycetophila unipunctata* Meigen, 1818  
*Mycomya (C.) circumdata* (Staeger, 1840)<sup>a,c</sup>  
*Mycomya (M.) affinis* (Staeger, 1840)  
*Mycomya (M.) annulata* (Meigen, 1818)<sup>b,c,d</sup>  
*Mycomya (M.) cinerascens* (Macquart, 1826)<sup>a,b,c,d</sup>  
*Mycomya (M.) festivalis* Väisänen, 1984  
*Mycomya (M.) flavicollis* (Zetterstedt, 1852)  
*Mycomya (M.) insignis* (Winnertz, 1863)<sup>a,d</sup>  
*Mycomya (M.) marginata* (Meigen, 1818)<sup>a,d</sup>  
*Mycomya (M.) nitida* (Zetterstedt, 1852)  
*Mycomya (M.) parva* (Dziedzicki, 1885)  
*Mycomya (M.) permixta* Väisänen, 1984  
*Mycomya (M.) ruficollis* (Zetterstedt, 1852)  
*Mycomya (M.) trilineata* (Zetterstedt, 1838)  
*Mycomya (M.) tumida* (Winnertz, 1963)<sup>a,d</sup>  
*Mycomya (M.) fimbriata* (Meigen, 1818)  
*Mycomya bicolor* (Dziedzicki, 1855)<sup>a,d</sup>  
*Mycomya circumdata* (Staeger, 1840)<sup>b</sup>  
*Mycomya dziedzickii* Väisänen, 1981<sup>a,d</sup>  
*Mycomya maculata* (Meigen, 1804)<sup>b</sup>

## Appendix 1 continued

- Mycetophila brevitarsata* (Lastovka, 1963)  
*Mycetophila caudata* Staeger, 1840  
*Mycetophila confluens* Dziedzicki, 1884<sup>b,c</sup>  
*Mycetophila curviseta* Lundström, 1911  
*Mycetophila dziedzickii* Chandler, 1977  
*Mycetophila edwardsi* Lundström, 1913  
*Mycetophila eppingensis* Chandler, 2001  
*Mycetophila finlandica* Edwards, 1913<sup>a,d</sup>  
*Mycetophila forcipata* Lundström, 1913<sup>a,d</sup>  
*Mycetophila formosa* Lundström, 1911<sup>a,d</sup>  
*Mycetophila fungorum* (De Geer, 1776)<sup>a,b,c,d</sup>  
*Mycetophila gibbula* Edwards, 1925  
*Mycetophila hetschkoi* Landrock, 1918<sup>a,c,d</sup>  
*Mycetophila ichneumonea* Say, 1823<sup>a,b,c,d</sup>  
*Mycetophila immaculata* (Dziedzicki, 1884)  
*Mycetophila laeta* Walker, 1848<sup>a,d</sup>  
*Mycetophila lobulata* A.Zaitzev, 1999  
*Mycetophila luctuosa* Meigen, 1830<sup>a,b,c,d</sup>  
*Mycetophila mitis* (Johannsen, 1912)  
*Mycetophila nigrofusca* Dziedzicki, 1884  
*Mycetophila occultans* Lundström, 1913  
*Mycetophila perpallida* Chandler, 1993  
*Mycetophila pumila* Winnertz, 1863<sup>a,d</sup>  
*Mycetophila pyrenaica* Matile, 1967  
*Mycetophila signatoides* Dziedzicki, 1884<sup>a,b,c</sup>  
*Mycetophila stolida* Walker, 1856  
*Mycetophila stricklandi* (Laffoon, 1957)  
*Phronia forcipata* Winnertz, 1863  
*Phronia forcipula* Winnertz, 1863<sup>a,d</sup>  
*Phronia gagnei* Chandler, 1992  
*Phronia interstincta* Dziedzicki, 1889  
*Phronia longelamellata* Strobl, 1898  
*Phronia maculata* Dziedzicki, 1889  
*Phronia nigripalpis* Lundström, 1909  
*Phronia nitidiventris* (van der Wulp, 1858)  
*Phronia obtusa* Winnertz, 1863  
*Phronia peculiaris* Dziedzicki, 1889  
*Phronia siebeckii* Dziedzicki, 1889<sup>a,d</sup>  
*Phronia strenua* Winnertz, 1863<sup>a,d</sup>  
*Phronia sudetica* Dziedzicki, 1889  
*Phronia unica* Dziedzicki, 1889  
*Phthinia humilis* Winnertz, 1863<sup>d</sup>  
*Phthinia mira* (Ostroverkhova, 1977)  
*Platurocypta punctum* (Stannius, 1831)<sup>a,d</sup>  
*Platurocypta testata* (Edwards, 1925)<sup>a,d</sup>  
*Polylepta guttiventris* (Zetterstedt, 1852)  
*Pseudobrachypeza helvetica* (Walker, 1856)  
*Pyratula zonata* (Zetterstedt, 1855)  
*Rondaniella dimidiata* (Meigen, 1804)<sup>a,b,c,d</sup>  
*Rymosia fasciata* (Meigen, 1804)<sup>a,b,c,d</sup>  
*Saigausia flaviventris* (Strobl, 1894)<sup>a,d</sup>  
*Sceptonia concolor* Winnertz, 1863  
*Sceptonia costata* (van der Wulp, 1858)  
*Sceptonia cryptocauda* Chandler, 1991  
*Sceptonia demeijerei* Bechev, 1997  
*Sceptonia flavipuncta* Edwards, 1925  
*Mycomya paradenata* Väisänen, 1984  
*Mycomya pseudoapicalis* Landrock, 1925  
*Mycomya trivittata* (Zetterstedt, 1838)  
*Mycomya vittiventris* (Zetterstedt, 1852)  
*Mycomya wankowiczii* (Dziedzicki, 1885)<sup>a,b,d</sup>  
*Mycomya winnertzi* (Dziedzicki, 1885)<sup>a,d</sup>  
*Neoempheria pictipennis* (Haliday, 1833)  
*Neoempheria striata* (Meigen, 1818)<sup>a,c,d</sup>  
*Neoempheria tuomikoskii* Väisänen, 1982  
*Neoplatyura flava* (Macquart, 1826)  
*Neoplatyura modesta* (Winnertz, 1863)  
*Neuratelia nemoralis* (Meigen, 1818)  
*Orfelia discoloria* (Meigen, 1818)<sup>a,b,c,d</sup>  
*Orfelia nemoralis* (Meigen, 1818)  
*Orfelia nigricornis* (Fabricius, 1805)<sup>d</sup>  
*Orfelia unicolor* (Staeger, 1840)<sup>a,d</sup>  
*Palaeodocosia janickii* (Dziedzicki, 1923)  
*Phronia basalis* Winnertz, 1963  
*Phronia biarquata* (Becker, 1908)<sup>a,d</sup>  
*Phronia braueri* Dziedzicki, 1889<sup>a,d</sup>  
*Phronia caliginosa* Dziedzicki, 1889  
*Phronia cinerascens* Winnertz, 1863  
*Phronia disgrega* Dziedzicki, 1889  
*Phronia egregia* Dziedzicki, 1889  
*Phronia electa* Dziedzicki, 1889  
*Phronia elegantula* Hackman, 1970  
*Phronia exigua* (Zetterstedt, 1852)  
*Sciophila thoracica* Staeger, 1840  
*Speolepta leptogaster* (Winnertz, 1863)  
*Symmerus annulatus* (Meigen, 1830)  
*Synapha vitripennis* (Meigen, 1818)  
*Sytemna nitidula* Edwards, 1925  
*Sytemna oklandi* Polevoi, in press  
*Sytemna relicta* (Lundström, 1912)  
*Sytemna stylata* Hutson, 1979  
*Sytemna stylatoides* Zaitzev, 1994  
*Tetragoneura obirata* Plassmann, 1990  
*Tetragoneura sylvatica* (Curtis, 1837)<sup>a,d</sup>  
*Trichonta atricauda* (Zetterstedt, 1852)<sup>a,d</sup>  
*Trichonta brevicauda* Lundström, 1906<sup>a,d</sup>  
*Trichonta falcata* Lundström, 1911<sup>a,d</sup>  
*Trichonta fragilis* Gagne, 1981  
*Trichonta hamata* Mik, 1880<sup>a,d</sup>  
*Trichonta melanura* (Staeger, 1840)<sup>a,d</sup>  
*Trichonta subfusca* Lundström, 1909<sup>a,d</sup>  
*Trichonta submaculata* (Staeger, 1840)  
*Trichonta venosa* (Staeger, 1840)<sup>b,d</sup>  
*Trichonta vitta* (Meigen, 1830)<sup>d</sup>  
*Urytalpa ochracea* (Meigen, 1818)<sup>d</sup>  
*Zygomia angusta* Plassmann, 1977  
*Zygomia humeralis* (Wiedeman, 1817)  
*Zygomia kiddi* Chandler, 1991  
*Zygomia pictipennis* (Staeger, 1840)  
*Zygomia pseudohumeralis* Caspers, 1980  
*Zygomia semifusca* (Meigen, 1818)  
*Zygomia valida* Winnertz, 1863

## Appendix 1 continued

<i>Sceptonia fumipes</i> Edwards, 1925	<i>Zygomya vara</i> (Staeger, 1840)
<i>Sceptonia fuscipalpis</i> Edwards, 1925	<i>Zygomya zaitzevi</i> Chandler, 1991
<i>Sceptonia membranacea</i> Edwards, 1925	
<i>Sceptonia nigra</i> (Meigen, 1804)	
<i>Sceptonia pilosa</i> Bukowski, 1934	
<i>Sceptonia pughi</i> Chandler, 1991	
<i>Sceptonia regni</i> Chandler, 1991	
<i>Sceptonia tenuis</i> Edwards, 1925	
<i>Sciophila caesarea</i> Chandler, 2001	
<i>Sciophila fenestella</i> (Curtis, 1837)	
<i>Sciophila hebes</i> Johansen, 1912	
<i>Sciophila hirta</i> Meigen, 18181234	
<i>Sciophila interrupta</i> (Winnertz, 1863) <sup>b,c</sup>	
<i>Sciophila jakutica</i> Blagoderov, 1990	
<i>Sciophila lutea</i> Macquart, 1826 <sup>a,b,c,d</sup>	
<i>Sciophila nigronitida</i> Landrock, 1925	
<i>Sciophila nonnisilva</i> Hutson, 1979	
<i>Sciophila ochracea</i> Walker, 1856 <sup>a</sup>	
<i>Sciophila persubtilis</i> Polevoi, 2001	
<i>Sciophila plurisetosa</i> Edwards, 1921	
<i>Sciophila subbicuspidata</i> Zaitzev & Okland, 1994	

<sup>a</sup> Associated with wood or wood-inhabiting fungi

<sup>b</sup> Associated with soil-inhabiting fungi

<sup>c</sup> Associated with saprotrophic fungi

<sup>d</sup> Associated with ectomycorrhizal fungi

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