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Host diversity and trophic status as determinants of species richness and community composition of fungus gnats

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Abstract

Making generalisations on trophic interactions is often limited because studies mostly focus on only a few target systems. Despite the important role of fungivores in forest ecosystems, the determinants of their communities are poorly known. This study examined, for the first time, on the basis of quantitative data, the diversity of fungivorous insects in relation to that of their hosts. Variation in range, species richness and community composition of associated partners was compared among fungus gnats (Diptera: Mycetophilidae, Bolitophilidae) and their mushroom hosts (Basidiomycota: Agaricomycetes) using rarefaction procedures and permutational analysis of variance. DNA barcoding aided identification of fungus gnat species. In the studied boreal forests, 80% of the 100 fungal species and 74% of 460 fruitbodies were colonised by fungus gnats. Each infested mushroom species hosted 1 to 12 gnat species, with 37 gnat species reared from 1 to 41 fungal species. Mushroom and fungus gnat species were both associated with three partner species at median. While most of the common gnat species could be considered oligo- or polyphagous, this study showed that earlier works have erroneously categorised some ubiquitous species as polyphagous in the absence of quantitative data. Species richness of fungus gnats and mushrooms correlated strongly at the level of host genera. Regarding partners community composition, analysing frequencies of associations between all pairs of partner species revealed no significant differences among fungus gnats but distinguished between the saprotrophic and ectomycorrhizal mushroom genera. Our results provide empirical evidence to substantiate a recent hypothesis that fungal trophic status affects, via fruitbody characteristics, the community structure of associated organisms. Presented evidence suggests oligophages with host preference to prevail among mushroom-feeding fungus gnats, thereby distinguishing these from many other studied insect guilds, largely composed of broad generalists and strict specialists.

Zusammenfassung

Generalisierungen von trophischen Interaktionen können oft nur eingeschränkt vorgenommen werden, da Untersuchungen meist nur wenige Systeme betrachten. Trotz der wichtigen Rolle, die Pilzfresser in Ökosystemen spielen, sind die für ihre

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Gemeinschaften bestimmenden Faktoren wenig bekannt. Die vorliegende Studie untersucht, erstmalig auf der Basis von quantitativen Daten, die Diversität von fungivoren Insekten mit Bezug auf die Diversität ihrer Wirte. Variationsbreite, Artenreichtum und Gemeinschafts-zusammensetzung der assoziierten Partner wurde verglichen für die Pilzmücken (Diptera: Mycetophilidae, Bolitophilidae) und ihre Wirtspilze. Hierfür setzten wir rarefaction und PERMANOVA ein. DNA-barcoding half bei der Identifizierung der Pilzmückenarten. In den untersuchten borealen Wäldern zeigten 80 der 100 Pilzarten und 74% von 460 Fruchtkörpern Befall durch Pilzmücken. Die befallenen Pilzarten beherbergten 1-12 Pilzmückenarten, wobei 37 Mückenarten aus 1-41 Pilzarten gezogen wurden. Pilzarten und Mückenarten waren beide mit im Median drei Partnerarten assoziiert. Während die meisten gemeinen Mückenarten als oligo- oder polyphag angesehen werden konnten, zeigte diese Untersuchung, dass frühere Arbeiten ohne quantitative Daten einige weit verbreitete Arten fälschlicherweise als polyphag eingeordnet hatten. Der Artenreichtum der Pilze und Mücken korrelierte stark auf der Ebene der Wirtsgattungen. Was die Gemeinschaftszusammensetzung der Partner anlangt, erbrachten Frequenzanalysen der Assoziationen zwischen Paaren von Partnerarten, dass es keine signifikanten Unterschiede zwischen den Pilzmücken gab, wohl aber zwischen den saprotrophen Pilzgattungen und den Ectomycorrhiza-Gattungen. Unsere Ergebnisse erbringen den empirischen Nachweis, um die rezente Hypothese zu unterstützen, dass der trophische Status der Pilze, vermittelt über die Eigenschaften des Fruchtkörpers, die Gemeinschaftsstruktur der assoziierten Organismen beeinflusst. Die vorliegenden Befunde legen nahe, dass Oligophage mit Wirtspräferenz unter den fungivoren Pilzmücken vorherrschen, was sie von vielen anderen untersuchten Insektengilden unterscheidet, die hauptsächlich aus breiten Generalisten und engen Spezialisten zusammengesetzt sind.

Keywords: Agaricales; Boletales; Food web; Functional guilds; Host range; Mycophagy; Russulales; Sciaroidea.

Introduction

As a result of the vulnerability of food webs to habitat change and fragmentation, unravelling trophic interactions is considered one of the big scientific challenges (Hedlund et al. 2004; van der Putten et al. 2004). Increasing the number of comprehensive studies which test and quantify individual trophic interactions has been desired for herbivores (Lewinsohn, Novotny, & Bassett, 2005). However, such information is even scarcer for many other associations, much less studied than the plant–insect interactions. Despite the diversity and abundance of fungus-feeding insects in forest ecosystems, studies that describe their local species richness and the role of host diversity in shaping their communities are limited. While a number of herbivore guilds that differ in trophic behaviour have been distinguished (Novotny et al. 2010), delimiting guilds for insects feeding on fungi is complicated due to widely overlapping host ranges (Hanski 1989; Jakovlev 2012; Krivosheina 2008). The most distinct insect groups include fungivores on: (i) tough perennial fruitbodies of polypores and (ii) soft annual fruitbodies referred to as mushrooms. Monophages form a high proportion among the former but are suggested as being rare among mushroom-feeders (Jonsell & Nordlander 2004; Lacy 1984).

Host species richness and abundance have been identified as important determinants of consumer richness amongst herbivores and their parasitoids (e.g. Elizalde & Folgarait 2010; Kelly & Southwood 1999). Fungi differ from plants in several aspects with their emergence and abundance fluctuating at spatial and temporal scales. Mushrooms are thus considered ephemeral and unpredictable food sources similar to carrion, dung or fruits, which tend to support polyphagous feeders (Hanski 1989). Hanski (1989) has categorised fungivores as poly-, oligo- and monophages according to the number of consumed fungal taxa, stating that some fungivore species are considered specialists just because of insufficient sampling. However, the lack of standardisation of sample sizes may conversely have led to some frequent species erroneously being considered polyphagous. Moreover, mushroom-forming fungi can further be divided into functional guilds with distinct ways of obtaining carbohydrates, suggested to affect fruiting phenology and community structure of fungus-associated organisms (Sato, Morimoto, & Hattori, 2012). Neither mushroom–fungivore community relationships nor the distinction of specialist and generalist fungivores have been investigated in any empirical study.

Boreal forests provide excellent sites for studying the diversity and feeding patterns of fungivores. Here a large part of the fungal biomass is comprised by ectomycorrhizal fungi that live in symbiosis with various tree species. Diversity of ectomycorrhizal fungi peaks in northern temperate regions (Tedersoo, May, & Smith, 2010) where fungus gnats form the majority of insects feeding on these and related saprotrophic mushrooms. Mushrooms are consumed by the larval stages of the insect families Mycetophilidae and Bolitophilidae (Sciaroidea, Nematocera, Diptera) most of which are obligatory fungivores (Chandler 2010; Jakovlev 2012; Krivosheina 2008). The egg-to-adult development lasts 1–2 weeks or about 1 month in some genera living mostly in the hymenophore of fruitbodies (Group II in Jakovlev 2012).

Knowledge of local fungus gnat community composition and how mushroom diversity may affect it is limited. The effect could be weak if the extent of polyphagy suggested for unpredictable hosts holds true. However, as persisting spatial fruitbody patterns are known for many mushroom species (Worthen & McGuire 1990; Sato et al. 2012), higher levels of

host specialisation among fungus gnats cannot be excluded. The few ecological studies available that report varying fungus gnat richness or abundance between habitats, years and seasons (Økland 1994; Økland et al. 2005; Yakovlev 1995), lack or do not extrapolate on host data. Although some fungi are known to be hosts for 38% of European mycetophilid species (Jakovlev 2012), making generalisations on fungus gnat-mushroom associations is hampered by lack of frequency information and the extensive changes in defining fungal taxa in recent decades.

This study aims to characterise fungus gnat diversity in relation to their mushroom hosts in boreal forest via analysing quantitative data obtained by rearing gnat adults from mushroom fruitbodies. We compared variations in range, richness and community composition of associated species among fungus gnat as well as mushroom taxa using rarefaction methods and permutational analysis of variance. The focus was on revealing the role of host species richness and fruitbody abundance, plus taxonomic and ecological components, in shaping fungus gnat-mushroom associations. The distinction of the extreme ends in the continuum from mono- to polyphages was also investigated. Results were expected to reveal whether fungus gnats on mushrooms conform to a guild and how this differs with respect to host association patterns from those of other fungivores as well as herbivores.

Materials and methods

Sampling and identification

Field work was carried out at five forests in Southern Estonia, northern Europe, during mid-September 2011. These belonged to the *Vaccinium myrtillus* site type of oligo-mesotrophic boreal forests dominated by Scots pine (*Pinus sylvestris*) and accompanied by Norway spruce (*Picea abies*). The five study areas (Table 1) were selected to represent forests of similar age, composition of understorey and mycobiota. The peak time of mushroom fruitbody formation and larval infestation was chosen for sampling fruitbodies in their mature, not yet decaying stage. In each area four 10-m diameter plots, separated from each other by at least 50 m, were established. We collected one fruitbody per each mushroom species present in each plot and random fruitbodies from the area between plots to complement the taxonomic representation of fruitbodies from the plots. The fruitbodies were individually placed on peat in plastic containers and covered with nylon fabric. Containers were incubated in an open lab facility at outdoor temperatures.

Emerged adults were checked every other day, collected with the help of an aspirator and placed into 70% ethanol in 1.5 or 4 ml vials. Fungus gnats were identified to species and other insects mostly to family level, recording the abundance of all taxa. Species identification relied on several morphological characters, mainly those of genitalia in case of sibling species. As the latter features are obscure in females, a representative of each genus reared from each fruitbody was allocated for DNA sequencing.

DNA was extracted from the abdomen or leg of adult gnats by incubating the material overnight at 56 °C in 10× Reaction Buffer B (Solis Biodyne, Tartu, Estonia) with the addition of 2.5 μl (20 mg/ml) proteinase K (Fermentas, Lithuania). After 15 min at 98 °C, the material was centrifuged and the DNA solution pipetted into a new tube. In 164 specimens, the 658 bp barcode region at the 5′ end of the mitochondrial cytochrome oxidase subunit I (COI) gene was amplified and sequenced with primers Lep-F1 and Lep-R1 (Hebert, Stoeckle, Zemlak, & Francis, 2004). A following region of ca. 790 bp was sequenced in part of the material using primers C1-J-2183 and TL2-N-3014 (Simon et al. 1994). The sequences were edited and assembled with Sequencher 5.1 (Gene Codes, Ann Arbor, MI, USA) and aligned manually using GeneDoc 2.6.0.3.

Combined sequences of both stretches of COI, 1440 bp in length, derived from male voucher specimens and representing most of the gnat species, were deposited in GenBank under accession numbers KM679366–KM679400. These sequences allowed subsequent identification of ambiguous material. For species delimitation sequences from each genus were analysed separately using PAUP (Swofford 2003). The voucher material was deposited at the entomological collection of the Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences (IZBE), Tartu, Estonia.

Statistical analyses

All analyses were done in the Vegan package of R version 2.15.0. (R Development Inc. 2013) and were based on the presence–absence data for individual associations between each mushroom fruitbody and fungus gnat species. The numbers of fruitbodies from each mushroom species from which a particular gnat species was reared were summed up individually for each gnat species. This resulted in a matrix (see Appendix A) showing frequencies of all individual mushroom species–fungus gnat species associations that are referred to as associations pairs throughout the text. Most of the analyses implemented frequency data of these association pairs. Similarly, when analysing gnat richness among higher fungal taxa, numbers of fruitbodies from each mushroom genus, family or order, infested by one gnat species, were counted for each gnat species.

Rarefied species numbers were generated to compare gnat species richness among mushroom orders and the most abundant mushroom genera, as well as for host species richness of the common gnat species. In the lack of an overlap between the 95% confidence intervals (not shown) of rarefaction numbers at the end point of the largest value of the least represented taxon, host or consumer species richness of

Table 1. Sampled forest sites with numbers of mushroom fruitbodies and fungus gnat species and individuals collected from each location.

Sampling			Host		Fungus gnat	
Location	Coordinates	Date	Species	Fruitbodies	Species	Adults
Miti	58.104639°, 26.374694°	14.09	31	62	17	1515
Soontaga	58.028500°, 26.074806°	16.09	36	90	25	1286
Ihamaru	58.100111°, 26.932069°	18.09	47	91	22	2438
Kaiu	58.655667°, 26.878667°	21.09	52	116	29	3811
Järvselja	58.295833°, 27.261583°	23.09	48	100	20	1991

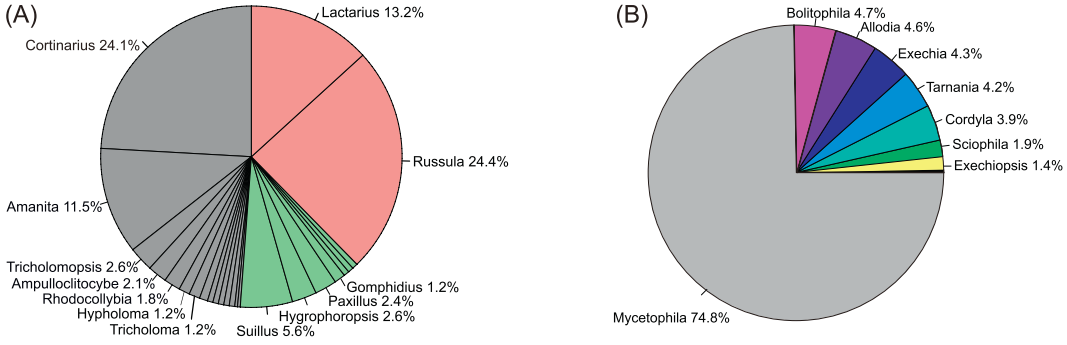

Fig. 1. Proportion of individuals among sampled genera. (A) Fruitbodies with reared fungus gnats in 24 mushroom genera. Colors mark fungal orders: grey–Agaricales, green–Boletales, red–Russulales. (B). Reared adults in 10 fungus gnat genera. In both groups, names of genera with individuals comprising <1% of the total number are not presented.

compared taxa was considered significantly different. Total fungus gnat species richness estimates Chao2 and Jackknife2 were calculated for all sampled mushroom fruitbodies.

Ordination analyses implied calculating the distance matrix of the associations using the Bray-Curtis index. To test the significance of the distinction of predefined fungus gnat and mushroom taxonomic or ecological categories, based on frequencies of individual associations, permutational analysis of variance (PERMANOVA) was performed using the Adonis function in the Vegan package of *R*. Nonmetric multidimensional scaling (NMDS) plots were generated to visualize relative similarities of gnat-mushroom associations among reared fungus gnat species and mushroom host genera. Singletons, i.e. unique association pairs, were omitted from analyses.

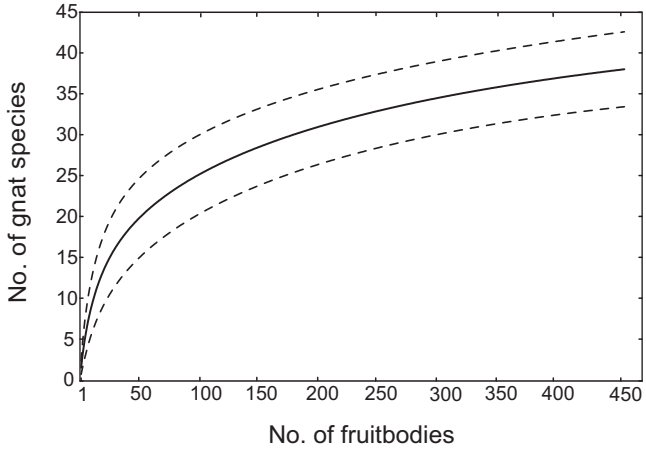

Fig. 2. Rarefaction curve and its ±95% confidence intervals representing fungus gnat species recovery with increasing number of sampled fruitbodies.

Results

Sampled taxa

The 460 collected fruitbodies belonged to 100 identified mushroom species belonging to 28 genera, 14 families and 3 orders (see Appendix B: Table 1). Ectomycorrhizal fungi represented the majority of fungal taxa (84 species/16 genera), the rest (16/12) being saprotrophs. Fungus gnat adults were reared from 340 fruitbodies belonging to 24 mushroom genera (Fig. 1A) and 81 identified species. A quarter of these species were common, with 1–4 fruitbodies sampled in the rest (Appendix B: Table 1). No gnats emerged from any of the fruitbodies of 19 mushroom species and from some of the fruitbodies of 28 mushroom species.

The 11,040 fungus gnat adults reared from the collected fruitbodies were identified to 37 species in 13 genera belonging to two families (Appendix B: Table 2). The seven most abundant gnat species each emerged from >40 mushroom fruitbodies, 11 species were reared from 6 to 31 and 20 species from 1 to 5 fruitbodies (Appendix B: Table 2). Almost one-third of fungus gnat species occurred at all five sites and another third only

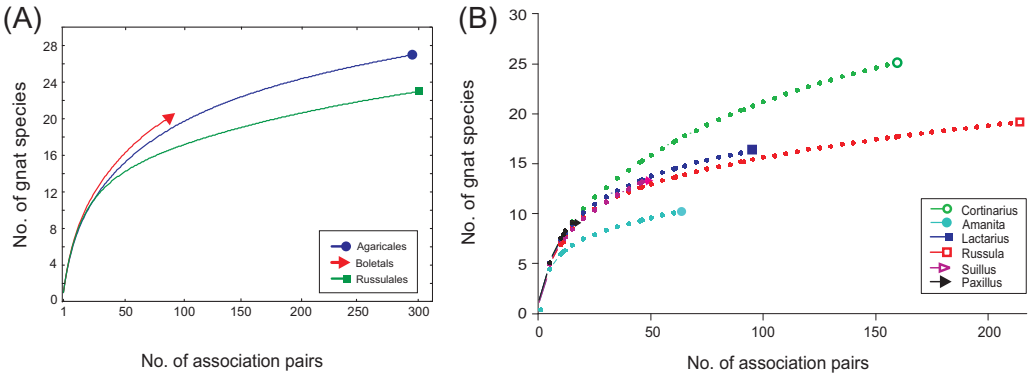

Fig. 3. Rarefaction curves of fungus gnat species reared from mushroom fruitbodies collected at five forest sites. For 'association pairs' at the *x*-axis see 'Materials and methods'. (A) Fungus gnat species richness in three fungal orders. (B) Fungus gnat species richness in the six most abundant fungal genera.

at one of the five sites. The number of reared adults varied considerably among gnat taxa (Appendix B: Table 2). Exhaustiveness of sampling was revealed by: (i) the rarefaction curve of gnat species richness approaching an asymptote with increasing sample size (Fig. 2); (ii) Chao2 and Jackknife2 estimates of the total gnat species richness suggesting only slightly higher values (40 and 45, respectively) than those measured. In addition to fungus gnats, 2375 individuals of six brachycerous and seven nematocerous families of Diptera and parasitic Hymenoptera were reared from the fruitbodies of 60 mushroom species (Appendix B: Table 3).

Fungus gnat richness among fungal taxa

Fungal species from which gnats were reared each hosted 1–12 (mean = 3.6, median = 3, SD = 2.7) gnat species (Appendix B: Table 1). Fungus gnat species richness and abundance of association pairs were highly correlated with species richness of mushroom genera ($R^2 = 0.81$, $P < 0.001$ and $R^2 = 0.77$, $P < 0.001$, respectively). Rarefied gnat species richness was significantly higher in the Agaricales than in the Russulales but Boletales did not significantly differ from either fungal order (Fig. 3A). Among the six best-sampled mushroom genera, gnat species richness was significantly higher in *Cortinarius* and lower in *Amanita* (Fig. 3B). When the frequencies of association pairs, used in previously described analyses, were replaced by frequencies of infested fruitbodies, mushroom taxa did not differ significantly with respect to fungus gnat species richness. Rarefaction curves and their confidence intervals (not shown) estimating gnat species richness with increasing fruitbody numbers overlapped among mushroom genera and orders.

Host richness among fungus gnat species

The larvae of individual fungus gnat species fed on fruitbodies of up to 3 mushroom orders, 8 families, 16 genera and 41 species (mean = 7.9, median = 3, SD = 10.7). Following Hanski (1989), five gnat species reared from >20 host species in >9 genera could be considered as polyphages and 10 gnat species from 2 to 19 host species in 2 to 6 genera as oligophages. Of the seven most abundant gnat species, the oligophages had significantly lower rarefied host richness than the polyphages, except for *Mycetophila fungorum* (Fig. 4). Two of three gnat species regarded as monophages were reared from fruitbodies of one mushroom genus. The remaining 20 gnat species were too rare for inferring their dietary behaviour.

Phylogenetic *vs* ecological component in the fungus gnat–mushroom associations

The fungus gnat communities of the saprotrophic genera of Agaricales appeared significantly different from those of

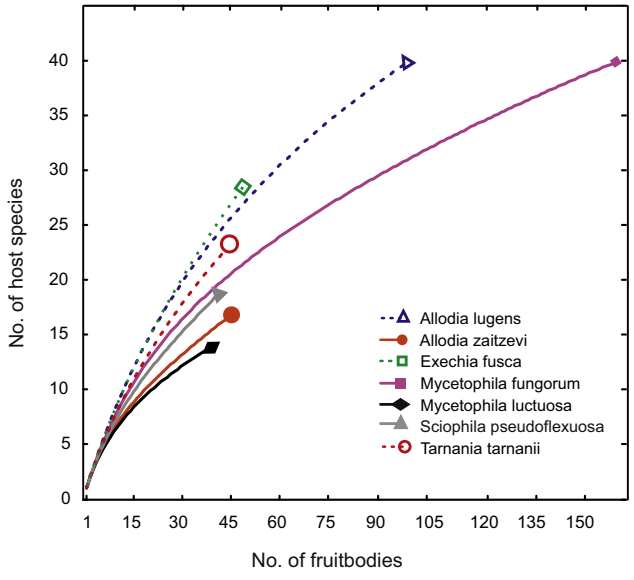

Fig. 4. Rarefaction curves of mushroom host species richness for the seven most abundant fungus gnat species. Oligophages are presented using solid symbols and solid lines and polyphages by open symbols and dashed lines.

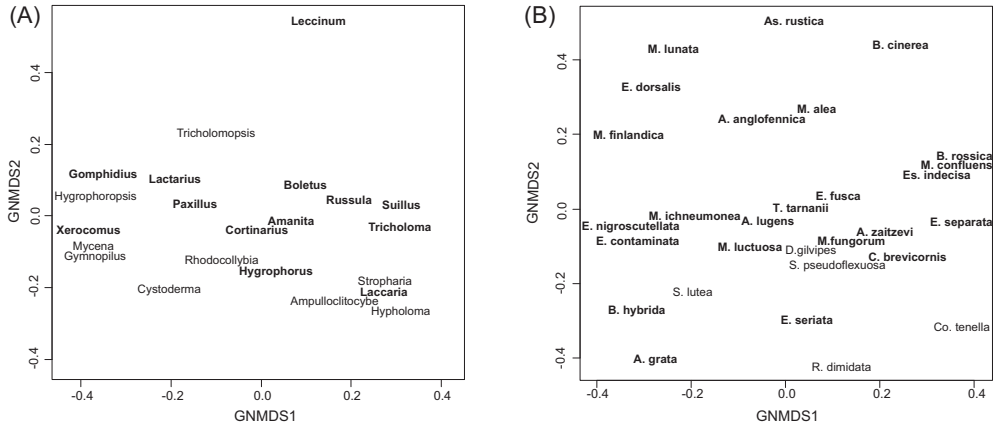

Fig. 5. NMDS plots showing the relative similarities of fungus gnat–mushroom associations among taxa of both partners. (A) Similarities of gnat communities among 22 host genera; ectomycorrhizal genera given in bold. (B) Similarities of host communities among 29 gnat species; gnats with shorter development presented in bold.

ectomycorrhizal genera in all three orders (PERMANOVA: $R^2 = 0.20$, $P = 0.02$). Most of the ectomycorrhizal genera were separated from the saprotrophic Agaricales along the second axis of the NMDS plot (Fig. 5A). Affinities at order level had less distinguishing power among the gnat communities of analysed fungal genera ($R^2 = 0.076$, $P = 0.042$). The NMDS ordination plot showing the relative similarities of association pairs among gnat species (Fig. 5B) revealed no segregation with respect to gnats genus or family affiliations. Although gnats with longer egg-to-adult development, living in the hymenophore of fruitbodies (species of *Coelosia, Docosia, Rondaniella, Sciophila*) were all located below the −0.1 value on the second axis, their host communities were not significantly different from species from the remaining gnat genera (PERMANOVA: $R^2 = 0.02$, $P = 0.7$).

Discussion

This study presents the first attempt to describe local diversity of fungus gnats in the context of their host diversity using quantitative data of their associations. The sampled mushrooms constituted an adequate representation of the mycobiota of the pine dominated boreal forests where the diversity and abundance of ectomycorrhizal fungi exceeds that of saprotrophs. Sampling during the peak time of fruitbody formation and larval development yielded higher mushrooms infestation rates than previously reported (Guevara & Dirzo 1999; Russell-Smith 1979), with observed gnat richness being close to estimated total species numbers.

The community structure of mushrooms and fungus gnats resembled each other in a quarter of species being common. In both groups, species were associated with three partner species at median while species with higher frequency and diversity of associated partners were distributed across the higher taxa. Regarding variation in partner community composition, however, fungus gnats appeared as a rather uniform assemblage of fungivores whereas the two mushroom functional guilds were distinct.

Our results are the first to show that fungus gnat assemblages of saprotrophic and ectomycorrhizal fungi are significantly different. Analysis of frequencies of association pairs between gnat and host species distinguished saprotrophic Agaricales from ectomycorrhizal fungi from all three fungal orders with respect to the composition of their fungus gnat communities. The reasons for ectomycorrhizal and saprotrophic fungi hosting distinct fungus gnat communities likely stem from differences in their nutritional strategies. These apparently cause variation in fruitbodies chemical composition, formation period, duration and seasonal predictability (Sato et al. 2012). The fruitbodies of ectomycorrhizal and saprotrophic fungi differ mostly in carbon (C) and nitrogen (N) isotope ratios, with higher C and lower N content in saprotrophs (Taylor et al. 2003). N content is known to be a limiting factor in the development of herbivorous insects (Mattson 1980) and probably has an impact also on mycophagy.

In contrast to the distinction of the two host guilds with respect to their fungus gnat communities, we found no evidence of segregation of gnats according to their host associations while using permutational analysis of variance of predefined taxonomic and ecological categories. Fungus gnats feeding from mushroom fruitbodies thus conform to the concept of a guild by comprising species exploiting the same resources in a similar way (Simberloff & Dayan 1991). Further niche differentiation, as described for mycophagous *Pegomya* flies (Anthomyiidae, Brachycera) specialising to different mushroom species and or fruitbody parts (Bruns 1984; Hackman & Meinander 1979), is rare among fungus gnats. Further studies are required to establish whether other mushroom-feeding dipteran groups belong to the same guild with fungus gnats or are competing with these, as suggested for drosophilids (Hanski 1989).

Rarefaction analyses, correcting for sampling bias, revealed a stronger impact of host species richness than

abundance on fungus gnat species richness, in contrast to studies of herbivorous insects and their parasitoids (Brändle & Brandl 2003; Elizalde & Folgarait 2010; Kelly & Southwood 1999; Stierman & Singer 2010). Mushroom genera with higher species richness hosted a higher number of fungus gnat species. Significant differences in rarefied fungus gnat species richness were observed among two fungal orders and some common genera based on frequencies of individual gnat species–fungal taxon associations. When these association pairs were replaced by numbers of gnat-infested fruitbodies in each mushroom taxon, the fungal taxa did not differ significantly with respect to their gnat species richness. Fungus gnat host preference is likely the reason why gnat species richness can distinguish among mushroom taxa only when frequencies of association pairs are analysed.

At mushroom order level fungus gnat richness appeared to correspond to the taxonomic and ecological diversity of the three fungal taxa. Namely, the phylogenetic divergence reflected by taxonomic diversity, the proportion of saprotrophic/ectomycorrhizal taxa and the rarefied gnat richness all declined from Agaricales and Boletales to Russulales. The diversity of Agaricales is explained by the inclusion of the most fruitbody- and species-rich host genus *Cortinarius*, but also by numerous small genera comprising most of the saprotrophic hosts sampled. By contrast, Russulales and Boletales both included only or mostly ectomycorrhizal taxa, but differed drastically in their taxonomic diversity. While Russulales had abundant fruitbodies from a few genera, fewer fruitbodies from a larger number of genera were sampled in Boletales.

Our results indicate the importance of analysing quantitative data on host associations for comparing the diet breadth of fungivores. There were no distinct classes with respect to the number of host taxa used in fungus gnats reared from >5 fruitbodies. Among the most abundant gnat species, a lack of overlap in confidence intervals of rarefied host species richness distinguished two groups that could be referred to as oligo- and polyphages. Unexpectedly, the most common gnat species, *Mycetophila fungorum*, had significantly lower rarefied host richness than the other species with high numbers of host taxa. Throughout the literature *M. fungorum* is regarded as a ubiquitous polyphage, but our research has shown this to be erroneous, highlighting the danger of comparing species dietary behaviour without quantitative data.

Reaching a realistic estimation of the proportion of monophages in fungus gnat communities of boreal forests is complicated owing to their rarity. Rare species cannot be considered monophagous as the number of host taxa of a fungus gnat species often increases with sample size (Hanski 1989). While three gnat species were repeatedly reared from fruitbodies of a single host genus, the more rare fungus gnats obviously include a few additional monophages. Even when considering also such rare species, the proportion of monophages was far from reaching half of species in the fungus gnat community on mushrooms as described for insects on polypores (Jonsell & Nordlander 2004), confirming the distinctness of fungivore guilds inhabiting ephemeral and perennial fruitbodies. The presented evidence suggests that also true polyphagy is more rare among mushroom-feeding fungus gnats than considered previously. In this regard, mushroom-feeding fungus gnats appear distinct from many guilds of herbivores and other insects where either broad generalists or strict specialists prevail (e.g. Hulcr, Mogia, Isua, & Novotny, 2007; Murakami, Hirao, & Ichie, 2007; Novotny et al. 2010). Further studies, exploring also the preference-performance linkages, are expected to elaborate on the role of host preference in fungus gnat fitness, diversity and community structure.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.baae.2014.10.004.

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