



Saproxylic Hymenoptera in dead wood retained on clear cuts, relation to wood parameters and their degree of specialisation

Mats Jonsell¹ · Hege Vårdal² · Mattias Forshage² · Julia Stigenberg²

Received: 29 March 2022 / Accepted: 16 February 2023 / Published online: 11 March 2023
© The Author(s) 2023

Abstract

Intensive forestry is a threat to biodiversity, and therefore actions are made to mitigate this loss. The actions are, however, designed based on available knowledge about the requirements of species, and for saproxylic insects this concerns mainly Coleoptera, while the diverse but poorly known Hymenoptera has contributed less. In this paper we therefore asked whether the substrate requirements of Hymenoptera (divided as parasitoids and non-parasitoids) are similar to those of Coleoptera and Diptera. We used an insect material reared from logging residue wood for the comparison. Theoretically parasitoid Hymenoptera should be less specialised than Coleoptera and other host species as they belong to a higher trophic level. However, we found no such difference and even an opposite trend, that parasitoids were more specialised than beetles. Parasitoids had significantly more species in newly dead wood of fine diameter (1–4 cm, compared to coarse wood of 8–15 cm) compared to other groups. This is probably due to that many of them have bark beetles as hosts. The non-parasitoids were less specialised than the other groups and more confined to old wood (4–5 years), which is in line with that many of them are aculeate wasps building nests in emergence holes from other insects.

Implications for insect conservation The habitat requirements of Hymenoptera suggest that the conservation actions designed for the well known groups are also applicable for them. The parasitoids' association to trivial substrates (fine wood) suggest a good supply of breeding habitat, whereas their high specialisation in combination with higher trophic level suggest they contain an even higher proportion of threatened species than Coleoptera. How this is traded off needs further studies.

Keywords Aculeate wasps · Insects · Parasitoids · Substrate associations · Wood living

Introduction

Dead trees harbour an enormous diversity of species, many of which are threatened due to human impact through forestry and other land use (Stokland et al. 2012). The species that during some stage of their development are dependent on dead wood are often termed saproxylic (Dajoz 1966). They are often feeding on the wood or fungi growing in the wood, but may also be predators or parasitoids on wood-living organisms or use the wood as nesting site. Several

actions are undertaken at forest operations to decrease the negative impacts on biodiversity, such as dead-wood retention, creating high-stumps and increasing the share of deciduous trees (Anonymous 2015; Gustafsson and Perhans 2010). However, the actions are, naturally, designed according to available knowledge, which means well known organisms. Poorly known groups have contributed much less. Among saproxylic insects, Coleoptera are comparatively well known, while e.g. Hymenoptera is less known. A key question, if we wish to preserve the full range of the biodiversity, is if the designed actions are fulfilling the requirements also of the less known species. The aim with this paper is to investigate that question for Hymenoptera.

Most saproxylic beetle species are more or less specialised on various characteristics of the wood (Stokland et al. 2012). Factors as tree species, stage of decay, degree of sun exposure, diameter and part of the tree are all important for determining the species composition in a piece of wood (Jonsell et al. 1998; Köhler 2000; Palm 1951,

✉ Mats Jonsell
mats.jonsell@slu.se

Hege Vårdal
hege.vardal@nrm.se

¹ Department of Ecology, Swedish University of Agricultural Sciences, Box 7044, 75007 Uppsala, Sweden

² Department of Zoology, Swedish Museum of Natural History, Box 50007, 10405 Stockholm, Sweden

1959). The fungal flora in the wood is less conspicuous to the human eye, but also very important for which species that could be found (Crowson 1981; Jonsell et al. 2005). Different factors are important to different species, and a species totally specialised to one certain tree species might be indifferent to the level of sun-exposure and vice versa.

It is hard to give an estimate on how many Hymenoptera species that are saproxylic, except for some well known groups as aculeate wasps and Siricidae (Bogusch and Horak 2018). This is true even for the well-studied and species-poor fauna of Fennoscandia. Slightly more than 800 saproxylic Hymenoptera species are known in Fennoscandia, but the real number is estimated to be at least 50% higher (Stokland and Siitonen 2012). That diversity is in level with the number of saproxylic beetles (1450 species) and flies and mosquitoes (around 2000 species) in the same region (Stokland and Siitonen 2012).

Unlike the beetles, most Hymenoptera species are parasitoids (Gauld and Bolton 1988; Hilszczański 2018). This trait implies one level up in the trophic guild compared to species feeding on a primary resource, such as wood or fungi. Higher trophic level increases the risk for extinction (Komonen et al. 2000; LaSalle and Gauld 1993; Shaw and Hochberg 2001; Shaw 2006; Hilszczański 2018). High degree of specialisation is another trait associated with high extinction risks (Clavel et al. 2011), and from an evolutionary perspective it seems likely that risks of a higher trophic level are compensated by lower risk with a less specialized strategy. Specialisation may be defined by many different variables, and among saproxylic species it usually concerns how specific the species is in the choice of wood types. In this paper we measured it as the number of wood types that the species use. For a parasitoid this realized niche is mediated through the use of host species, which at least in part will be dependent on the habitat specificity of the host. In summary, we expected parasitoids to be less specialised in the use of wood types than the basic trophic level.

No comparisons of specialisation among wood types among species of Hymenoptera versus other insect groups exist, to our knowledge. However, it has been shown that species of the families Ichneumonidae and Braconidae much depend on both the forest type and the type of dead wood in the surroundings (Hilszczański et al. 2005; Stenbacka et al. 2010). Thus, there seem to exist specialisation, but whether it is large or small compared to other saproxylic species is difficult to evaluate. This is true especially for the small and even more poorly known species in Pteromalidae and Eurytomidae, which often are more numerous than Ichneumonidae and Braconidae in the wood (Hedgren 2007). Since we expected that the parasitoid life style might affect niche use, we analysed the Hymenoptera in two different groups: parasitoids and non-parasitoids.

Among saproxylic non-parasitoid Hymenoptera, there are wood wasps, ants, digger wasps and bees. Wood wasps feed on the wood (by help of fungi) whereas the other mentioned groups use wood substrates with available holes for nesting, bringing prey or pollen as larval food (Westerfelt et al. 2015; Bogusch and Horak 2018).

Our aim was to test whether Hymenoptera have substrate requirements similar to beetles. If that is supported, the conservation actions designed on knowledge from Coleoptera could be expected to work also for this poorly known species group. If not, actions would need to be revised. Data for the study was obtained by identifying the Hymenoptera material from a previous study of Coleoptera in logging residues (Jonsell 2008; Jonsell et al. 2020; Wedmo 2004). Previous results on Diptera (Jonsell et al. 2020) were also included in the comparison. The questions we asked were:

Are the associations of Hymenoptera (parasitoids and non-parasitoids) to different categories of wood (tree species, age and diameter) similar to the associations of Coleoptera and Diptera?

Is the degree of specialization, measured as niche breadth, of Hymenoptera to various types of dead wood higher than for other insect groups?

Material and methods

Samples of logging residue wood were collected from 40 clear-cut sites (Fig. 1A) in southern Sweden from autumn 2003 to spring 2004. Three main factors were compared: tree species (four species), diameter (three classes), and substrate age (two ages). To ensure that we collected all factor-combinations evenly within the sampled area, it was divided into 14 regions with the same sampling in each region. Suitable clear-cuts in each region were identified by foresters at the Forestry board, Holmen, Sveaskog, Korsnäs and Stora Enso according to our specified criteria: age since cutting and tree-species composition.

From each clear-cut we sampled four tree species: aspen (*Populus tremulae* L.), birch (*Betula pubescens* Ehrh. and *B. verrucosa* Ehrh.), oak (*Quercus robur* L.), and spruce (*Picea abies* (L.) Karst.). If a tree species was missing in a sampling site, that tree species was, if possible, sampled from another clear-cut in the direct vicinities. For each tree species, we took samples from three diameter classes: Thin (1–4 cm), Medium (4–8 cm) and Coarse (8–15 cm). The two thinner classes are usually defined as fine woody debris, whereas the coarsest class is generally defined as coarse woody debris. From each clear-cut, we sampled two bundles of each combination of tree species and diameter class, giving 24 bundles of wood per clear-cut. The substrate age could be compared as the clear-cuts were chosen in pairs of two ages situated between 1 and 3 km from each other, where one

Fig. 1 Pictures of the sampling and rearing: A) a clear cut site from which we sampled B) bundles of wood out of which we reared insects in containers of C) plywood or D) textile sacs



clear-cut was one summer (Young) and the other between 3 and 5 years old (Old), thus giving 20 clear-cuts of each age.

The sampled wood was cut into 50 cm lengths and packed together in 25–35 cm diameter bundles (Fig. 1B). The bundles were brought to the laboratory, where the insects were reared out of the wood in a greenhouse at a temperature of about 20 °C. There were some deviations from this temperature, especially during warm days in the summer, but all samples within the same rearing cohort experienced the same temperature regime. The rearing continued for at least three months. More details on the sampling procedure can be found in Jonsell et al. (2007). That source also includes data on the quantity of wood in the samples.

For practical reasons we had to use two types of rearing containers: wooden boxes (Fig. 1C) and textile sacs (Fig. 1D). To account for the effects of using different rearing containers (Jonsell and Hansson 2007), one of each bundle type (site, tree species and diameter combination) was enclosed in each type of container. For rearing in textile sacs, the bundles of wood were hung from the ceiling by a string, then enclosed in a cotton sac with metal wires on the inside to prevent the wood coming into direct contact with the sac. The insects were collected in a plastic vial

attached to a plastic funnel at the bottom of the cotton sac. The remaining wood bundles were placed in boxes made of plywood. Insects were collected in a glass vial inserted in one gable end. At the end of the rearing period, the remains from the bottom of the wooden box were also inspected for insects, since not all insects were caught in the vials.

To compare the surface areas and volumes of the bundle categories, the number of wood pieces in every bundle was counted and multiplied by the area/volume of a piece representing the median for the class (Jonsell et al. 2007). All bundles had similar bark surface areas (Jonsell et al. 2007). Consequently, the volume of firm wood was largest for the coarsest diameter class. For most saproxylic species, especially in the early stages of wood decay, the surface area is probably a better descriptor of the amount of habitat than wood volume, because such species live in the space between the bark and the wood.

The saproxylic Coleoptera and Diptera were determined to species in earlier studies (Jonsell 2008; Jonsell et al. 2020). The Hymenoptera were first sorted to family-level by the authors MF, JS and HV. JS identified most of the Braconidae to species-level, with some help from MF and Konstantin Samartsev (Russian Academy of Science,

St. Petersburg, Russia) in the subfamilies Doryctinae and Braconinae. HV identified most of the aculeates and the single wood wasp to species-level, with help from Niklas Johansson (Swedish Species Information Centre) and Lars Norén for some Aculeata and William Englund (NHRS) for Formicidae. MF identified most of the Chalcidoidea, the Bethyloidea and the Figitidae to different levels, whereas the Eulophidae were identified by Joseph Berger (Lund University) and Christer Hansson (Biological Museum, Lund, Sweden). Many Hymenoptera were not identified to species-level, partly because the physical state of many of the smaller, weakly sclerotized specimens had significantly deteriorated after more than a decade in suboptimal storage and partly because of the lack of available taxonomic expertise. The Hymenoptera species were analysed in two different groups: parasitoids and non-parasitoids. Data on host use of the parasitoid taxa were extracted from relevant literature (cited in Table 2).

Statistics

In total, 612 samples were used in the analyses. Thus 348 samples are missing compared to the possible total 960, either because they either could not be collected (due to lack of some tree species in some locations) or missing data (see further in Jonsell et al. 2007). Data inspection ensured that all factorial combinations were evenly included and distributed throughout the area, suggesting no risk of bias in the sampling design. Initial preliminary analyses showed that region and rearing method had non-significant effects when they were included as co-variables. Since our main question of the study was wood type affinity, these variables were therefore excluded from further analyses.

Associations with categories of wood type were modelled with generalized linear models (GLM) where the response variable, abundance of a species, was explained by the three explanatory wood type variables (diameter category, age class and tree species). Analyses were done for all species with >9 occurrences (in unique samples). We used the function `glm` in R version 3.5.1 (R Core Team 2018) to fit the models, assuming a Poisson distribution. Using the same distribution for all species was preferred over adjusting to potential deviations from the Poisson distribution for some species as this ensures the comparability of the model coefficients in further analysis (Gelman and Hill 2007). It is not likely to cause any one-directional bias since we are not using significance test for the individual models (Olsson 2002). The outcome of the models was used to define the niches of each species as described below.

Niche breadth was assessed for each species by the share of wood categories that it was associated with, i.e. its niche. It was first calculated for each variable individually, thus given a value between $1/n$ (n = the number of categories for

the variable) and 1 (when there was association to all categories). Those three values were subsequently multiplied into a total niche breadth (as described below). To define the association, we initially tested which variable/-s that could explain a relevant amount of the variation in a forward selection process. We used AIC-informed forward-step selection of the three variables ('step' function within the R statistical package). Variables were included if $k > 2$, i.e. if inclusion of the variable lowered $AIC > 2$ (Venables and Ripley 2002; Burnham and Anderson 2002). Variables not explaining a relevant amount of variation in abundance (i.e. not included by the forward-step selection) were assigned a niche breadth = 1.

For variables that could explain a relevant amount of variation, we assessed which wood categories that belonged to the niche by comparing the abundance in each category relative to the category with highest abundance. For this we used coefficients obtained from species-specific full models (i.e. with all three variables included). Coefficients were calculated by predicting the response variable (i.e. abundance) for all variable combinations (including those variables that did not explain any variation), and for each focal variable we summarized the mean abundance under all other combinations (Gelman and Hill 2007). Categories within a variable that had the highest abundance or a relative abundance ≥ 0.5 of the highest abundance, were defined as a primary niche. Categories with a relative abundance of 0.5–0.1 compared to the highest abundance were defined as a secondary niche. If the relative abundance was lower than 0.1, the category was defined as a non-niche. The niche breadth within a variable was then calculated by dividing the number of used niches with the number of categories, where secondary niches were down-weighted to a half niche. Thus, an association with one of the four tree species gave a niche breadth of 0.25 for that variable. An additional secondary association to another tree species added in that case 0.125, so the niche breadth then summarized to 0.375. The total niche breadth for a species was the multiplication of the three variables' niche breadths.

Mean niche breadth was compared between insect groups with t-tests. We compared the variable-categories with which the species groups are mainly associated, by counting the number of associated species. When a species was associated with no variable it was counted in an additional category as "No association". For Age and Diameter we counted only the categories to which each species had its strongest association, as those variables are ordinal. For Diameter, associations were defined only with the two extreme categories (Thin or Coarse) even though in some cases Medium had the highest value. However, Medium was never the only category that any species used and it is biologically unlikely that a species would have such a narrow diameter association that Medium would in reality be higher than

Table 1 Hymenoptera taxa reared out in frequencies large enough for statistical analyses. Associations are given according to results of GLMs (Appendix 1). The numbers (1, 2 or 3) in front of the variable

categories denotes the order in which they were included in the GLM, with the most explanatory variable included as no

Species	Associations to niches					
	Obs	Inds	Tree species	Diameter	Age	Niche breadth
<i>Parasitoid hymenoptera</i>						
<i>Cephalonomia formiciformis</i>	9	20	2: Bir, Asp, Oak	3: Med (Thin, Coa)	1: Old	0.25
<i>Ecphylylus silesiacus</i>	22	255	1: Spruce	3: Thin (Medium)	2: Young	0.06
<i>Ontsira antica</i>	10	33	1: Oak (Spruce)	3: Thin, Med (Coa)	2: Young	0.16
<i>Entedon</i> spp. ^a	17	535	1: Oak	2: Thin	3: Young	0.04
<i>Eurytoma</i> sp 3	20	68	1: Spruce	3: Thin, Medium	2: Young	0.08
<i>Eurytoma</i> sp 1	10	10	2: Spruce, Oak	No assoc	1: Young	0.25
<i>Trichoplasta</i> n. sp. \"betulae\"	10	53	1: Birch (Aspen)	3: Coarse, Med	2: Young	0.13
<i>Roptrocercus</i> cf <i>xylophagorum</i>	64	1361	1: Spruce	3: Thin, Med (Coa)	2: Young	0.10
<i>Dinotiscus</i> sp ?	39	539	1: Spruce	3: Thin (Coa, Med)	2: Young	0.08
<i>Pteromalidae</i> morfosp. 6	12	31	1: Birch, Oak	2: Thin (Med, Coa)	3: Young (Old)	0.25
<i>Cheiropachus quadrum</i>	11	347	1: Oak	3: Thin (Med, Coa)	2: Young	0.08
<i>Tomicobia</i> sp ?	10	18	1: Spr, Oak (Asp)	2: Coarse, Thin	No assoc	0.42
<i>Non-parasitoid Hymenoptera</i>						
<i>Xiphydria camelus</i>	53	216	1: Birch	3: No assoc	2: Young (Old)	0.19
<i>Leptothorax acervorum</i>	11	59	1: Spruce (Birch)	No assoc	2: Old	0.19
<i>Hylaeus</i> spp. ^b	18	42	2: Spr, As, Oak (Bi)	No assoc	1: Old (Young)	0.66
<i>Mimumesa dahlbomi</i>	13	22	2: Oak (all)	No assoc	1: Old (young)	0.47
<i>Crossocercus</i> spp. ^c	23	74	2: Bir, Asp, Oak	3: No assoc	1: Old	0.38
<i>Passaloecus</i> spp. ^d	9	13	2: Spr, Oak (Bi, As)	No assoc	1: Old (Young)	0.56

“Obs” = the number of samples with occurrence; Inds. = Total no of individuals in those samples;

(a) *Entedon* spp. contain *E. tibialis* & *E. zanara*

(b) *Hylaeus* spp. contain *H. angustatus*, *H. confusus*, *H. incongruus*

(c) *Crossocercus* spp. contain *C. cetratus*, *C. dimidiatus*, *C. leucostoma*, *C. megacephalus*, *C. nigritus*, *C. styrius* and *C. varus*

(d) *Passaloecus* spp. contain *P. borealis*, *P. corniger*, *P. turionum*

both the two extremes (Siitonen and Stokland 2012; Ehnström and Axelsson 2002; Jonsell et al. 2007). Therefore, species estimated to have Medium as their single primary niche and both Coarse and Thin as secondary niches were assigned as “No association” (refining the analyses based on our ecological knowledge as suggested by Gelman and Hill (2007)). Similarly, when Medium was single primary niche and either Coarse or Thin was the secondary niche, species were assigned to that respective secondary niche. The variable Tree species is not ordinal, and therefore all tree species with which an insect species had an association (both primary and secondary) were counted.

We tested if there was a statistically significant difference ($p < 0.05$) between the insect groups in the proportion of species associated with different categories of Age and Diameter with a Chi-square test for contingency tables. For Tree species, the same test was done for each tree species individually, because one insect species may be associated with more than one tree species. JMP Pro 16.0.0 for Mac was used for the t-tests and the Chi-square tests.

Results

A total of 4413 Hymenoptera individuals belonging to 165 different taxa were identified. 19 of those taxa were frequent enough for statistical analyses: 12 of those were parasitoids, and 6 non-parasitoids, of which 5 were aculeate wasps and 1 (*Xiphydria camelus*) a wood-wasp (Xiphydriidae) (Table 1).

The proportion of Hymenoptera species associated with the different diameters of wood deviated from both Coleoptera and Diptera. Parasitoid Hymenoptera were to a higher degree associated with thin wood diameters, whereas the non-parasitoid Hymenoptera had a higher proportion of species with no association (Fig. 2, Pearson Chi-square = 10.0; $p = 0.040$ when only parasitoid Hymenoptera are compared with Coleoptera and Diptera).

Association to age classes of wood showed a higher proportion of parasitoid Hymenoptera in young wood than for the other groups (Fig. 3), whereas the non-parasitoid Hymenoptera had somewhat higher (non-significant)

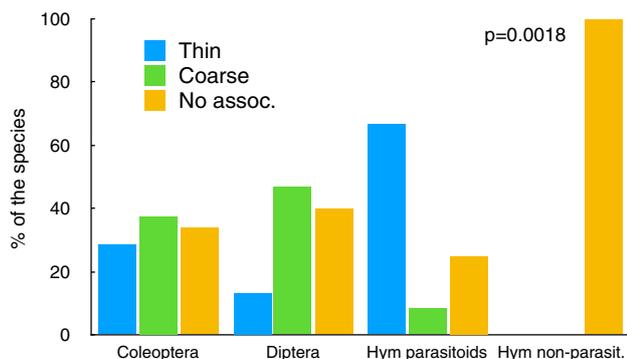


Fig. 2 Proportion of species in different insect groups associated with wood of different diameter categories (thin = 1–4 cm; Coarse = 8–15 cm). Statistical probability for that all groups have the same distribution between diameter categories (Pearson Chi-square $p = 21.1$)

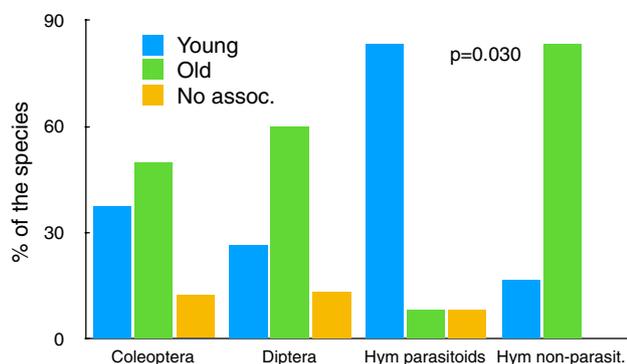


Fig. 3 Proportion of species in different insect groups associated with wood of different age classes (Young = One summer old; Old = 4–5 years old). Statistical probability for that all groups have the same distribution between age categories (Pearson Chi-square $p = 14.0$)

proportion of species in old wood than Coleoptera and Diptera (Fig. 3).

A significantly smaller proportion of species among the parasitoid Hymenoptera used the two tree species aspen and birch, compared to the other groups (Fig. 4; For aspen: Pearson Chi-square = 9.0; $p = 0.028$; for Birch Pearson Chi-square = 10.3; $p = 0.016$). The non-parasitoid Hymenoptera used them in much higher proportion and especially birch. For oak there were no significant differences among the groups in the proportion of species using it (Pearson Chi-square = 2.9; $p = 0.41$). Spruce was used by a comparatively large proportion of species of both groups of Hymenoptera (Fig. 4, Pearson Chi-square = 8.5; $p = 0.037$).

The niche breadth was larger for the non-parasitoids than for the parasitoid Hymenoptera (Fig. 5). For the parasitoid Hymenoptera the tendency was that the niche breadth was narrower than for Coleoptera and Diptera, but the difference was not significant (Fig. 5).

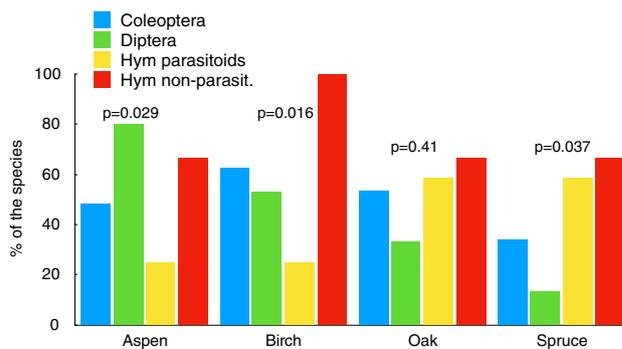


Fig. 4 Proportion of species of different insect groups using wood of different tree species. Statistical probabilities are Pearson Chi-square tests of the probability that all groups have the same distribution within a tree species. An insect species can be associated with more than one tree species explaining why the total share of associated species per group is > 100%

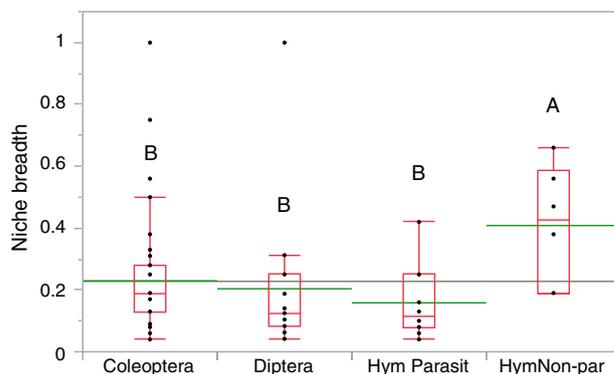


Fig. 5 Niche breadths among four groups of insects reared out from logging residues: Coleoptera, Diptera, Parasitoid Hymenoptera and non-Parasitoid Hymenoptera. Green line = average; Red = boxplot with medians quartiles and extremes. The broadest niche is statistically different (multiple pairwise comparison, Student's *t*) from the others as indicated by letters A and B

Discussion

Our expectation regarding the parasitoids was that their higher trophic level should be compensated by less specificity in host substrate. This was contradicted, as there was no sign of lower specialisation among parasitoid Hymenoptera compared to Coleoptera and Diptera. The insignificant trend actually pointed in the opposite direction to our expectation, indicating that the lack of support for it was not only a statistical Type II-error. A higher specialisation is related to higher extinction risks (Clavel et al. 2011; Shaw and Hochberg 2001; Hilszczański 2018) and adding the higher extinction risk that comes with higher trophic level, it suggests that there should be many threatened species among parasitoid Hymenoptera. This is hardly

reflected in Red Lists as most parasitoid Hymenoptera are so poorly known in terms of life history, distribution and population trends that they usually have not been possible to evaluate. Only 1/8 of the Hymenoptera were evaluated in the most recent revision of the Swedish red-list (Johansson et al. 2020) and even fewer before that. However, the suggested high extinction risk from specialisation may be contradicted by the commonness of the thin wood that many parasitoid Hymenoptera species were associated with (Fig. 2). Thin wood is more common than coarser, and has moreover increased during the last 100 years due to increased amounts of trees (Dahlberg et al. 2011) and we can expect species using the most common wood type to have less risk for extinction. With present knowledge it is not possible to predict how extinction risk is traded off between specialisation and commonness of substrate. That there might be more species sensitive to forestry management among parasitoid Hymenoptera than among Coleoptera, where most species feed on the primary resources fungi and wood, has, however, been suggested in other studies (Hilszczanski et al. 2005; Stenbacka et al. 2010).

The total number of Hymenoptera species found in the wood was very large and included several rare or at least rarely recorded taxa, including species of Aulacidae, Tiphiidae, Sapygidae, undescribed species of Figitidae and rare Braconidae (will be listed in a separate paper). Unfortunately, most species were so scarce in the material that it was not possible to include them in the present analysis. Most of them are parasitoids, suggesting that there is a large diversity of species not encompassed in our analyses which we can expect to be sensitive to modern forest management.

The category of non-parasitoid Hymenoptera was dominated by aculeate wasps that use the wood as nesting site, and not so surprisingly they were not so selective in terms of wood quality. Actually, half of the species within this group in Czech Republic are not even specific on the types of material they use (Bogusch and Horak 2018). They use emergence holes made by other saproxylic species, including longhorn beetles, bark beetles, anobiid beetles, and wood wasps, as nesting sites. For them, hole diameter is the most important factor (Westerfelt et al. 2015), and although different saproxylic species rear out from different types of wood, the right diameter for a particular wasp can be made by many different species and therefore be present in most types of wood (Ehnström and Axelsson 2002). The dependence on the holes also explains why these species were reared from “old” wood as the holes are not formed before some year(-s) has passed. The low specificity suggests a lower extinction risk in relation to supply of dead wood.

Only one of the non-parasitoids in the analysis, the wood-wasp *Xiphydria camelus* is a species that actually feed on wood. Thus, it was not so surprising it was more specialized

than most species using the wood as nest-substrate. The species is a primary colonizer of wood, and consequently associated with young wood. Primary colonizers are usually forced to be restricted in host use (Jonsell and Nordlander 2004; Stokland 2012; Sielbold et al. 2022) and this species only used birch in this study. The ant *Leptothorax acervorum* was specialised to a similar degree as *X. camelus*, although it uses the wood as nesting site. We cannot find any good explanation for this as ants generally are not that specific in what type of wood they use (King et al. 2018).

Especially in the cases where several species were lumped into genus-level taxon units (but also in some more or less uncertain species-level identifications or morphospecies) there may be real specialisations among included taxa that are hidden by the lumping. As long as the units are entire monophyletic groups they are nevertheless meaningful biological units and the process is transparent and reproduceable. Three of the four genus-level units used here are non-parasitoids using available holes, for which such specialisations are less likely to be prominent (Bogusch and Horak 2018).

When it comes to substrate choice in relation to diameter and age of the wood, the two groups of Hymenoptera were the two extremes compared with Diptera and Coleoptera. Especially the parasitoid wasps stood out from the others with a high proportion of species associated with young and thin wood. The parasitoids moreover had low proportion of species using aspen and birch. Both these results are probably largely explained by that many of the parasitoid wasps have bark beetles as one probable host (Table 2). For three of the parasitoids, host use cannot be clearly stated, but only three parasitoids are known from non-bark beetle hosts only (references in Table 2). Thus, at least 10 species out of the total 13, are, or can be, associated with bark beetles (Table 2). As the hosts occur densely in newly dead wood of fine diameters of spruce and oak and less in birch and aspen (Jonsell 2008), our results are logical.

In conclusion, the Hymenoptera deviated mainly from the Coleoptera by being more associated with fine wood diameters. This deviation is usually not a conservation problem since the finest wood usually is overrepresented after forest operations as thin wood is not so efficiently extracted and less profitable than coarser wood (Rudolphi and Gustafsson 2005; Dahlberg et al. 2011). Thus, our results do not suggest any new mitigation actions for forestry. However, the high specialisation of the parasitoids suggest that the amounts of mitigations should be increased as species loss seem to continue (Felton et al. 2020). At stump extraction, insects in the second trophic level seemed to be more sensitive (Victorsson and Jonsell 2013). The large number of parasitoids are double sensitive by being both one trophic level up and being specialised in the choice of wood. Future studies of population

Table 2 The host use and parasitic mode of parasitoid wasp taxa reared out in frequencies large enough for statistical analyses in this study

Taxon	Known hosts	Parasitic mode	Reference
<i>Cephalonomia formiciformis</i> (Bethyliidae)	Saproxylic Coleoptera of Ciidae	Idiobiont gregarious larval or pupal ectoparasitoids	De Santis (1970) and Perkins (1976)
<i>Ecpylus silesiacus</i> (Braconidae)	Saproxylic Coleoptera of at least 66 species in families Curculionidae (Scolytinae) and Bostrichidae	Idiobiont larval ectoparasitoid	Yu et al. (2016) and Hedqvist (1998)
<i>Ontsira antica</i> (Braconidae)	Saproxylic Coleoptera of at least 17 species in families Buprestidae, Cerambycidae, Curculionidae (Scolytinae), Ptinidae, etc	Idiobiont larval ectoparasitoid	Yu et al. (2016) and Hedqvist (1998)
<i>Entedon tibialis</i> (Eulophidae)	Mostly saproxylic Coleoptera in Ptinidae and Curculionidae (Scolytinae), but also non-saproxylic Curculionidae	Koinobiont egg or larval endoparasitoid	Noyes (2019)
<i>Entedon zanara</i> (Eulophidae)	Saproxylic Coleoptera in Buprestidae and Mordellidae, but also non-saproxylic Curculionidae	Koinobiont gregarious egg or larval endoparasitoid	Noyes (2019)
<i>Eurytoma sp 3</i> (Eurytomidae)	Genus uses hosts in a number of insect orders, some species specialised on saproxylic Coleoptera (often Scolytinae), others on gallforming Hymenoptera, or Lepidoptera	Most often idiobiont ectoparasitoid	Noyes (2019) and Hedqvist (1963)
<i>Eurytoma sp 1</i> (Eurytomidae)	Genus uses hosts in a number of insect orders, some species specialised on saproxylic Coleoptera (often Scolytinae), others on gallforming Hymenoptera, or Lepidoptera	Most often idiobiont ectoparasitoid	Noyes (2019) and Hedqvist (1963)
<i>Trichoplasta</i> n.sp. "betulae" (Figitidae)	Genus attacks saproxylic Diptera (Drosophilidae and Lonchaeidae) under tree bark	Koinobiont larval-pupal endoparasitoid	Original data (MF)
<i>Roptrocerus cf xylophagorum</i> (Pteromalidae)	Saproxylic Coleoptera in Scolytinae (at least 64 different species recorded!)	Idiobiont larval or pupal ectoparasitoid	Noyes (2019) and Hedqvist (1963)
<i>Dinotiscus</i> sp. (Pteromalidae)	Saproxylic Coleoptera in Scolytinae (<i>Ips</i> , <i>Phloeosinus</i> and <i>Pityophthorus</i>)	Idiobiont larval-pupal ectoparasitoid	Noyes (2019) and Hedqvist (1963)
Pteromalidae morfospecies 6	Family uses hosts in a number of insect orders	Most often laval or pupal idiobiont ectoparasitoids	Noyes (2019) and Hedqvist (1963)
<i>Cheiropachus quadrum</i> (Pteromalidae)	Mostly saproxylic Coleoptera in Scolytinae, but also other saproxylic Coleoptera and Lepidoptera (of at least 34 species)	Idiobiont larval ectoparasitoid on host larva	Noyes (2019) and Hedqvist (1963)
<i>Tomocobia</i> sp. (Pteromalidae)	Saproxylic Coleoptera in Scolytinae (<i>Ips</i> , <i>Pityophthorus</i> , <i>Pityogenes</i>)	Koinobiont adult endoparasitoid	Noyes (2019) and Hedqvist (1963)

trends and distribution of parasitoid Hymenoptera might reveal that we have larger problems than what is already reflected in red-lists and similar surveys. We should also investigate if those poorly known species can be early

indicators of species losses as they could be expected to be extinct before primary consumers of wood.

Appendix 1

The result of species-wise GLM models used to define the substrate associations of the species.

Variable	Category	Estimate	p-value	Model	AIC
<i>Cephalonomia formiciformis</i>					
Intercept		-3.7	<0.0001	Start	204.9
Age	Young	-19.12	0.992	Age	180.67
Tree sp.	Birch	0.32	0.551	Age + Tree sp.	171
	Oak	-0.24	0.719		
	Spruce	-18.65	0.994		
Diam	Thin	0.24	0.796	Age + Tree sp. + Diam	161.45
	Medium	1.86	0.013		
<i>Ecphyllus silesiacus</i>					
Intercept		-26.08	0.969	Start	2271.75
Tree sp.	Birch	14.44	0.983	Tree sp.	1682.08
	Oak	0.05	1.000		
	Spruce	19.28	0.977		
Age	Young	5.65	<0.0001	Tree sp. + Age	1312.69
Diam	Thin	2.98	<0.0001	Tree sp. + Age + Diam	1047.64
	Medium	1.04	0.006		
<i>Ontsira antica</i>					
Intercept		-24.52	0.989	Start	328.02
Tree sp.	Birch	0.05	1.000	Tree sp.	280.84
	Oak	19.09	0.991		
	Spruce	18.22	0.992		
Age	Young	3.59	0.000	Tree sp. + Age	242.49
Diam	Thin	0.93	0.071	Tree sp. + Age + Diam	242.41
	Medium	0.83	0.116		
<i>Entedon</i> spp.					
Intercept		-26.5	0.951	Start	4886.97
Tree sp.	Birch	15.92	0.971	Tree sp.	3348.68
	Oak	19.5	0.964		
	Spruce	12.83	0.976		
Diam	Thin	6.04	<0.0001	Tree sp. + Diam	2579.42
	Medium	3.72	0.000		
Age	Young	3.99	<0.0001	Tree sp. + Diam. + Age	1879.42
<i>Eurytoma</i> sp. 3					
Intercept		-27.39	0.986	Start	577.68
Tree sp.	Birch	0.02	1.000	Tree sp.	418.6
	Oak	0.04	1.000		
	Spruce	19.7	0.990		
Age	Young	4.34	<0.0001	Tree sp. + Age	328.67
Diam	Thin	3.3	0.001	Tree sp. + Age + Diam	293.84
	Medium	3.36	0.001		
<i>Eurytoma</i> sp. 1					
Intercept		-42.46	0.995	Start	106.39
Age	Young	19.65	0.995	Age	93.75
Tree sp.	Birch	0.07	1.000	Age + Tree sp.	85.07
	Oak	19.67	0.997		
	Spruce	19.65	0.997		
Diam	Thin	0.74	0.376	Not included in model	

Variable	Category	Estimate	p-value	Model	AIC
	Medium	0.27	0.770		
<i>Trichoplasta n. sp. "betulae"</i>					
Intercept		-21.84	0.987	Start	509.81
Tree sp.	Birch	2.02	<0.0001	Tree sp.	416.95
	Oak	-18.09	0.994		
	Spruce	-18.08	0.993		
Age	Young	19.51	0.989	Tree sp. + Age	340.8
Diam	Thin	-3.32	0.001	Tree sp. + Age + Diam	307.38
	Medium	0.05	0.852		
<i>Roptrocerus cf. xylophagorum</i>					
Intercept		-9.39	<0.0001	Start	8095.62
Tree sp.	Birch	2.43	0.019	Tree sp.	4993.95
	Oak	0.16	0.908		
	Spruce	6.93	<0.0001		
Age	Young	4.62	<0.0001	Tree sp. + Age	3111.61
Diam	Thin	0.71	<0.0001	Tree sp. + Age + Diam	3015.84
	Medium	0.51	<0.0001		
<i>Dinotiscus sp?</i>					
Intercept		-10.2	<0.0001	Start	4016.21
Tree sp.	Birch	-0.3	0.765	Tree sp.	2765.12
	Oak	-12.97	0.966		
	Spruce	5.3	<0.0001		
Age	Young	5.02	<0.0001	Tree sp. + Age	2002.4
Diam	Thin	2.29	<0.0001	Tree sp. + Age + Diam	1687.82
	Medium	1.2	<0.0001		
Pteromalidae morphosp. 6					
Intercept		-22.22	0.985	Start	300.35
Tree sp.	Birch	17.56	0.988	Tree sp.	269.25
	Oak	17.87	0.988		
	Spruce	14.79	0.990		
Diam	Thin	2.11	0.004	Tree sp. + Diam	259.07
	Medium	1.34	0.088		
Age	Young	1.01	0.011	Tree sp. + Diam. + Age	253.83
<i>Cheiropachus quadrum</i>					
Intercept		-41.25	0.985	Start	3433.87
Tree sp.	Birch	0.06	1.000	Tree sp.	2296.93
	Oak	22.38	0.992		
	Spruce	0.07	1.000		
Age	Young	19.26	0.967	Tree sp. + Age	1779.77
Diam	Thin	2.13	<0.0001	Tree sp. + Age + Diam	1513.5
	Medium	0.42	0.080		
<i>Tomicobia sp?</i>					
Intercept		-4.69	<0.0001	Start	183.65
Tree sp.	Birch	-16.13	0.992	Tree sp.	169.99
	Oak	2.04	0.057		
	Spruce	1.98	0.060		
Diam	Thin	0.5	0.322	Tree sp. + Diam	157.43
	Medium	-17.56	0.990		
Age	Young	-0.36	0.457	Not included in model	
<i>Xiphydria camelus</i>					

Variable	Category	Estimate	p-value	Model	AIC
Intercept		-21.19	0.986	Start	1440.86
Tree sp.	Birch	20.3	0.987	Tree sp.	922.48
	Oak	0.02	1.000		
	Spruce	0.01	1.000		
Age	Young	0.9	<0.0001	Tree sp. + Age	883.9
Diam	Thin	0.68	0.000	Tree sp. + Age + Diam	873.09
	Medium	0.4	0.041		
<i>Leptothorax acervorum</i>					
Intercept		-18.39	0.977	Start	558.89
Tree sp.	Birch	15.29	0.981	Tree sp.	469.51
	Oak	13.94	0.983		
	Spruce	17.44	0.978		
Diam	Thin	0.02	0.961	Tree sp. + Age	419.43
	Medium	0.4	0.221		
Age	Young	-2.8	<0.0001		
<i>Hylaeus spp.</i>					
Intercept		-1.79	<0.0001	Start	384.26
Age	Young	-2.19	<0.0001	Age	356.99
Tree sp.	Birch	-1.25	0.019	Age + Tree sp.	354.25
	Oak	0.05	0.902		
	Spruce	-0.31	0.445		
Diam	Thin	-0.16	0.672	Not included in model	
	Medium	-0.14	0.702		
<i>Mimumesa dahlbomi</i>					
Intercept		-4.47	<0.0001	Start	214.28
Age	Young	-1.74	0.005	Age	204.5
Tree sp.	Birch	0.5	0.554	Age + Tree sp.	196.53
	Oak	1.81	0.018		
	Spruce	-0.02	0.979		
Diam	Thin	0.9	0.177	Not included in model	
	Medium	1.03	0.118		
<i>Crossocerus spp.</i>					
Intercept		-1.1	<0.0001	Start	619.09
Age	Young	-2.8	<0.0001	Age	554.57
Tree sp.	Birch	0.16	0.587	Age + Tree sp.	515.82
	Oak	0.21	0.510		
	Spruce	-3.31	0.001		
Diam	Thin	-0.31	0.244	Age + Tree sp. + Diam	514.77
	Medium	-0.66	0.027		
<i>Passaloecus spp.</i>					
Intercept		-4.19	<0.0001	Start	138.63
Age	Young	-1.61	0.037	Age	134.44
Tree sp.	Birch	-0.36	0.799	Age + Tree sp.	133.31
	Oak	1.46	0.192		
	Spruce	1.58	0.140		
Diam	Thin	-1.12	0.180	Not included in model	
	Medium	-0.02	0.976		

Acknowledgements We are most thankful for all the experts (listed in Material and Methods) around the country that helped determine the material we sent out to them. Lina Widenfalk and Alejandro Ruete helped with the GLMs. The project was financed through Swedish Energy Agency project no P41926-1.

Funding Open access funding provided by Swedish University of Agricultural Sciences. The project was financed through Swedish Energy Agency project no P41926-1. The authors declare they have no financial interests.

Declarations

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Anonymous (2015) Forests and forestry in Sweden. The Royal Swedish Academy of Agriculture and Forestry, Stockholm.
- Bogusch P, Horak J (2018) Saproxylic bees and wasps. In: Ulyshen MD (ed) Saproxylic insects. Zoological Monographs 1, pp 217–235
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information theoretic approach. Springer, New York
- Clavel J, Julliard R, Devictor V (2011) Worldwide decline of specialist species: toward a global functional homogenization? *Front Ecol Environ* 9:222–228
- Crowson RA (1981) The biology of the coleoptera. Academic Press, London
- Dahlberg A, Thor G, Allmér J, Jonsell M, Jonsson M, Ranius T (2011) Modelled impact of Norway spruce logging residue extraction on biodiversity in Sweden. *Can J for Res* 41:1220–1232
- Dajoz R (1966) Ecologie et biologie des coléoptères xylophages de la hêtraie. *Vie Milieu* 17:525–636
- De Santis L (1970) Las especies argentinas del género *Cephalonomia* (Hymenoptera, Bethyloidea). *Rev Soc Entomol Argent* 32:17–21
- Ehnström B, Axelsson R (2002) Insektsnag i bark och ved. ArtDatabanken, SLU, Uppsala
- Felton A et al (2020) Keeping pace with forestry: Multi-scale conservation in a changing production forest matrix. *Ambio* 49:1050–1064
- Gauld I, Bolton B (1988) The Hymenoptera. Oxford University Press, Oxford
- Gelman A, Hill J (2007) Data analysis using regression and multilevel/hierarchical models. Cambridge University Press, Cambridge
- Gustafsson L, Perhans K (2010) Biodiversity conservation in Swedish forests: ways forward for a 30-year-old multi-scaled approach. *Ambio* 39:546–554
- Hedgren PO (2007) Early arriving saproxylic beetles (Coleoptera) and parasitoids (Hymenoptera) in low and high stumps of Norway spruce. *For Ecol Manage* 241:155–161
- Hedqvist KJ (1963) Die Feinde der Borkenkäfer in Schweden, I. Erzwespen (Chalcidoidea). *Studia Forestalia Suecica* no 11.
- Hedqvist KJ (1998) Bark beetle enemies in Sweden. II. Braconidae (Hymenoptera). *Entomologica Scandinavica Supplement* 52.
- Hilszczański J (2018) Ecology, diversity and conservation of saproxylic hymenopteran parasitoids. In: Ulyshen MD (ed) Saproxylic insects. Zoological Monographs 1, pp 193–216
- Hilszczański J et al (2005) Parasitoids (Hymenoptera, Ichneumonoidea) of Saproxylic beetles are affected by forest successional stage and dead wood characteristics in boreal spruce forest. *Biol Conserv* 126:456–464
- Johansson N, Cederberg B, Hagman A, Larsson A, Stenmark M (2020) Steklar—Hymenoptera. In: Wenche E, et al (eds) Tillstånd och trender för arter och deras livsmiljöer – rödlistade arter i Sverige 2020. SLU, Artdatabanken.
- Jonsell M (2008) Saproxylic beetle species in logging residues: which are they and which residues do they use? *Norwegian J Entomol* 55:109–122
- Jonsell M, Hansson J (2007) Comparison of methods for sampling saproxylic beetles in fine wood. *Ent Fennica* 18:232–241
- Jonsell M, Nordlander G (2004) Host selection patterns in insects breeding in bracket fungi. *Ecol Ent* 29:697–705
- Jonsell M, Weslien J, Ehnström B (1998) Substrate requirements of red-listed saproxylic invertebrates in Sweden. *Biodiv Conserv* 7:749–764
- Jonsell M, Schroeder M, Weslien J (2005) Saproxylic beetles in high stumps of spruce: fungal flora important for determining the species composition. *Scand J for Res* 20:54–62
- Jonsell M, Hansson J, Wedmo L (2007) Diversity of saproxylic beetle species in logging residues in Sweden: comparisons between tree species and diameters. *Biol Conserv* 138:89–99
- Jonsell M, Widenfalk LA, Hellqvist S (2020) Substrate specificity among Diptera in decaying bioenergy wood: can they be conserved by the same measures as are currently applied to beetles? *Biodiv Conserv* 29:2623–2662
- King JR, Warren RJ, Maynard DS, Bradford MA (2018) Ants: ecology and impacts in dead wood. In: Ulyshen MD (ed) Saproxylic insects. Zoological Monographs 1, pp 237–262.
- Köhler F (2000) Totholz Käfer in Naturwaldzellen des nördlichen Rheinlands. Landesanstalt für Ökologie, Bodenordnung und Forsten, Recklinghausen, Germany.
- Komonen A, Penttilä R, Lindgren M, Hanski I (2000) Forest fragmentation truncates a food chain based on an old-growth bracket fungus. *Oikos* 90:119–126
- LaSalle J, Gauld ID (eds) (1993) Hymenoptera and biodiversity. CAB International, Wallingford
- Noyes JS (2019) Universal Chalcidoidea database. World Wide Web electronic publication. <http://www.nhm.ac.uk/chalcidoidea>
- Olsson U (2002) Generalized linear models. An applied approach. Studentlitteratur, Lund.
- Palm T (1951) Die Holz- und Rindenkäfer der nordschwedische Laubbäume. Meddelanden från statens skogsforskningsinstitut, 40, 242 pp.
- Palm T (1959) Die Holz- und Rindenkäfer der süd- und mittelschwedischen Laubbäume. *Opusc Entomol Suppl* 16:1–374
- Perkins JF (1976) Handbooks for the identification of British insects: Hymenoptera Bethyloidea (excluding Chrysididae). Royal Entomological Society, London
- R Core Team (2018) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <https://www.R-project.org/>.

- Rudolphi J, Gustafsson L (2005) Effects of forest-fuel harvesting on the amount of deadwood on clear cuts. *Scand J for Res* 20:235–242
- Seibold S, Weisser WW, Ambarli D, Gossner MM, Mori AS, Cadotte MW, Haggé J, Bässler C, Thorn S (2022) Drivers of community assembly change during succession in wood-decomposing beetle communities. *J Anim Ecol*. <https://doi.org/10.1111/1365-2656.13843>
- Shaw MR (2006) Habitat considerations for parasitic wasps (Hymenoptera). *J Insect Conserv* 10:117–127
- Shaw MR, Hochberg ME (2001) The neglect of parasitic Hymenoptera in insect conservation strategies: the British fauna as a prime example. *J Insect Conserv* 5:253–263
- Siitonen J, Stokland JN (2012) Tree size. In: Stokland JN, Siitonen J, Jonsson BG (eds) *Biodiversity in dead wood*. Cambridge University Press, Cambridge, pp 183–193
- Stenbacka F et al (2010) Saproxylic parasitoid (Hymenoptera, Ichneumonoidea) communities in managed boreal forest landscapes. *Insect Conserv Divers* 3:114–123
- Stokland JN (2012) Host-tree associations. In: Stokland JN, Siitonen J, Jonsson BG (eds) *Biodiversity in dead wood*. Cambridge University Press, Cambridge, pp 82–109
- Stokland JN, Siitonen J (2012) Species diversity of saproxylic organisms. In: Stokland JN, Siitonen J, Jonsson BG (eds) *Biodiversity in dead wood*. Cambridge University Press, Cambridge, pp 248–274
- Stokland JN, Siitonen J, Jonsson BG (2012) *Biodiversity in dead wood*. Cambridge University Press
- Venables WN, Ripley BD (2002) *Modern applied statistics with S*, 4th edn. Springer, New York
- Wedmo L (2004) Saproxylic beetles in logging residuals from *Populus tremula* and *Betula* spp. Examensarbete 2004:3, Dept. of Entomology, SLU, Uppsala
- Westerfelt P, Widenfalk O, Lindelöw Å, Gustafsson L, Weslien J (2015) Nesting of solitary wasps and bees in natural and artificial holes in dead wood in young boreal forest stands. *Insect Conserv Divers* 8:493–504
- Victorsson J, Jonsell M (2013) Effects of stump extraction on saproxylic beetle diversity in Swedish clear-cuts. *Insect Conserv Divers* 6:483–493
- Yu DS, van Achterberg C, Horstmann K (2016) *Taxapad 2016. Ichneumonoidea 2015 (Biological and taxonomical information)*, Taxapad interactive catalogue on flash-drive. Nepean, Ottawa, Canada

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.