Title: Responses of the hyper-diverse community of canopy-dwelling Hymenoptera to oak decline

Running title: Canopy Hymenoptera and oak decline

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ABSTRACT

1. Forest decline and dieback are growing phenomena worldwide, resulting in severe, large-scale degradation of the canopy. This can profoundly alter forest microclimates and the provision of trophic resources and microhabitats for forest arthropods, especially those dwelling in the canopy.

2. In 2019, we assessed the effect of oak decline on the community of canopy-dwelling Hymenoptera. We selected 21 oak stands, and 42 plots, located in three forests in France, presenting contrasting levels of decline. Insects were sampled at the canopy level with green multi-funnel and flight-interception traps.

3. We collected a particularly diverse community of 19,289 insect individuals belonging to 918 taxa, eight larval trophic guilds and five nesting guilds.

4. Oak decline had no effect on the abundance or richness of the overall community, but significantly reshaped the community assemblages. Decline had contrasting effects depending on the taxa and guilds considered. Parasitoids were more abundant at intermediate levels of decline severity. Taxa depending on ground-related resources and microhabitats were promoted. Saproxylic taxa were more diverse while xylophagous insects were negatively impacted.

5. Reduced leaf area index promoted several guilds, and the diversity of the overall community. While an increasing tree mortality rate enhanced the abundance and diversity of deadwood resources, it had negative impacts on Hymenoptera guilds. Our results suggest that micro-environmental changes at the ground-level due to canopy decline have major cascading effects on the communities of canopy-dwelling Hymenoptera.

6. Our study highlights the relevance of studying Hymenoptera communities to investigate the outcomes of disturbances on forest biodiversity.

Keywords: trophic guild, habitat guild, deadwood, canopy openness, temperate forest

INTRODUCTION

Global change is currently increasing the frequency, severity and spatial extent of major forest disturbances in Europe such as droughts, windstorms and wildfires (Seidl et al., 2017; Samaniego et al., 2018; Spinoni et al., 2018). Disturbances can markedly affect the amount, diversity and distribution of key trophic resources and microhabitats for forest arthropods (Cours et al., 2023). One of the main drivers of these changes is the degradation of the forest canopy (Sallé et al., 2021; Cours et al., 2023). A reduction in canopy cover can result from direct disturbance impacts on the trees themselves, but also from subsequent forest dieback or decline, as a progressive loss of tree vigour generally translates into crown dieback (Sallé et al., 2021). Decline and dieback can consequently affect the quality and quantity of foliage, and reduce the production of flowers, fruits and seeds in the crown (Ishii et al., 2004; Günthardt-Goerg et al., 2013; Hu et al., 2013). On the other hand, they may also increase the amount and diversity of deadwood resources and tree-related microhabitats such as fruiting bodies of opportunistic fungi, trunk cavities or perched deadwood (Sallé et al., 2021; Larrieu et al., 2022; Zemlerová et al., 2023). Increased canopy openness also considerably affects microclimates and trophic resources for arthropods in the lower strata of forest ecosystems for instance, by promoting the accumulation and diversification of floral resources in the herbaceous layer, or of deadwood resources on the ground (Cours et al., 2023). Consequently, forest dieback and decline can promote forest biodiversity to a certain extent by increasing structural complexity at multiple scales, as predicted by the pulse dynamics theory (Jentsch and White, 2019; Cours et al., 2022). These modifications can profoundly reshape communities of forest arthropods (Viljur et al., 2022; Cours et al., 2023). The impact of canopy dieback on forest arthropods has been investigated for several taxonomic groups and functional guilds, including some specifically dwelling in the canopy (Martel & Mauffette, 1997; Stone et al., 2010; Sallé et al., 2020; Vincent et al., 2020). While the responses of canopy arthropods is largely mediated by their functional and/or trophic guild (e.g., Sallé et al., 2020), idiosyncratic responses still occur among the taxa of a same guild or taxonomic group (e.g., Vincent et al., 2020). Consequently, the impacts of disturbance-driven changes in canopy structure on arthropod communities are still difficult to predict, especially in the largely under-studied temperate forest canopy (Sallé et al., 2021; Cours et al., 2023). Considering that canopy mortality rate has been on the rise for several decades in Europe (Senf et al., 2018), further studies on how decline and dieback affect canopy-dwelling arthropods are urgently needed, especially for the taxonomic groups that have received limited attention to date, like the Hymenoptera.

Hymenoptera is a hyper-diverse group of insects, sometimes regarded as the most speciose animal order (Forbes et al., 2018). This group plays a wide variety of functional roles in temperate forests. Ants and predatory and parasitic wasps help to regulate forest pests (Hilszczański, 2018). Bees and

102 wasps pollinate forest plants (Motten, 1986; Yumoto, 1987), while ants can disperse seeds (Rico-Gray
103 and Oliveira, 2008). Hymenoptera nests, galleries and galls also provide microhabitats for many
104 species (Stone et al., 2002). Wood-nesting bees and ants, as well as the larvae of xylophagous
105 species, contribute to the decomposition process of wood (Ulyshen, 2016). Phyllophagous and
106 xylophagous species can be major pests for trees (Lyytikäinen-Saarenmaa and Tomppo, 2002;
107 Slippers et al., 2015). The Hymenoptera, especially parasitic wasps, can be used as bioindicators in
108 forest ecosystems (Maleque et al., 2009). Their communities can be largely influenced by stand-
109 related variables such as stand composition (Fraser et al., 2007; Ulyshen et al., 2011a), deadwood
110 resources (Hilszczański et al., 2005; Ulyshen et al., 2011a; Jonsell et al., 2023) and silvicultural
111 practices (Lewis and Whitfield, 1999; Hilszczański et al., 2005; Rappa et al., 2023). Pollinators in
112 particular are sensitive to canopy opening and the subsequent positive impacts on the floral
113 resources in the herbaceous layer and on ground-nesting sites (Wermelinger et al., 2017; Burkle et
114 al., 2019; Viljur et al., 2022; Cours et al., 2023).

115 Many Hymenoptera use the canopy as a hunting ground, a nesting site or a breeding site (Ulyshen,
116 2011). The canopy can also act as a dispersal corridor for species with a preference for open habitats
117 (Pucci, 2008; Di Giovanni et al., 2017). As for other forest insects, the Hymenoptera community
118 exhibits a conspicuous vertical stratification in temperate forests (Smith et al., 2012). Certain
119 ecological guilds like the predatory and parasitic wasps, and the pollinators, differ significantly
120 between the ground level and the canopy (Sobek et al., 2009; Ulyshen et al., 2011b; Urban-Mead et
121 al., 2021), and several taxa are specific to the canopy layer (Ulyshen et al., 2010; Di Giovanni et al.,
122 2017). While some studies have investigated the vertical stratification of certain taxonomic groups or
123 ecological guilds of bees and wasps in temperate forests, few have taken into account the whole
124 Hymenoptera community (e.g., Vance et al., 2007), and none have considered this community's
125 response to forest decline.

126 In the present study, we investigated the impact of oak decline on the community of canopy-dwelling
127 Hymenoptera. We chose to focus on oak forests because they are the dominant forest ecosystem in
128 western Europe; they shelter a diverse entomofauna (Kennedy and Southwood, 1984); finally, they
129 have suffered from historic decline in France (Nageleisen, 2008), and have recently undergone severe
130 summer droughts (in 2018 and 2019) (Saintonge and Goudet, 2020). Our first objective was to
131 characterise the little-known community of canopy-dwelling Hymenoptera in temperate oak forests.
132 Our second objective was to assess how the severity of forest decline affected the richness and
133 taxonomic composition of this community. Our third objective was to evaluate the effects of decline
134 on certain ecological guilds of Hymenoptera, and how changes in stand-related variables drive those
135 effects. We focused on the trophic guilds of larvae and nesting guilds. For these guilds, we

formulated three hypotheses. First (H1), we expected to find positive effects of increasing decline severity on pollinivorous/nectarivorous and phyllophagous species associated with host plants other than oak due to the increased diversity and amount of plant-resources in the herbaceous and shrub layers, commonly observed when canopy closure decreases (Romey et al., 2007; Lu et al., 2019; Cacciatori et al., 2022). Likewise, we expected that soil-nesters would be promoted by more open conditions resulting in warmer soil temperatures. We also hypothesised that xylophagous, saproxylic and wood-nester taxa would benefit from oak dieback and the subsequent increased amount and diversity of deadwood. Conversely (H2), we expected to find negative effects on the guilds that feed on oak foliage, for example, gall-inducing and phyllophagous taxa, due to the decrease in the quality and quantity of leaves. Finally (H3), we hypothesised that decline severity would have contrasted effects on parasitoids and polyphagous taxa, depending on their hosts and trophic resources.

MATERIAL AND METHODS

Study sites

Three oak-dominated (*Quercus petraea* (Matt.) Liebl. and *Quercus robur* L.) French forests were sampled in 2019 (Fig. 1, Tab. S1): one near Orléans (Forêt domaniale d'Orléans, 47°98′97″81N, 1°95′44″E), one near Vierzon (Forêt domaniale de Vierzon, 47°26′89″N, 02°10′74″E) and one near Marcenat (Forêt domaniale de l'Abbaye, 46°21′12″N, 3°36′13″E). All the forests were managed by the French National Forest Service. The Orléans forest covers 35,000 ha and is dominated by oaks (47%) and pines (*Pinus sylvestris* L., 51%). The Vierzon forest covers 7,500 ha and is also dominated by oaks (61%) and pines (*P. sylvestris* and *P. pinaster* Ait., 31%). The Marcenat forest covers 2,100 ha and is dominated by oaks (71%), pines (11%) and Douglas fir (8%). The Vierzon forest suffered the most from decline. Several decline events had been recorded there since 1920, and massive oak mortality had occurred in several stands (Douzon, 2006). In the Marcenat forest, two summer droughts (2018-2019) had led to severe decline in several stands (Saintonge and Goudet, 2020). Conversely, no major decline event had been reported in the Orléans forest.

A total of 21 oak-dominated stands with a minimum surface area of 3 ha were selected in these forests: nine in Orléans, nine in Vierzon and three in Marcenat (Fig. 1). In each forest, we selected healthy, moderately declining or severely declining stands (3 for each category in Orléans and Vierzon, 1 in Marcenat). In each of these stands, we selected one declining and one healthy tree, at least 50 m from each other, in which to hang our traps. In each stand, we recorded average tree height, density and diameter, and the stand tree species composition (Tab. S1). We also evaluated the level of decline according to the DEPERIS protocol (Goudet and Nageleisen, 2019). This protocol

169 makes it possible to quantify decline at the tree level by evaluating the percentage of dead branches
170 and ramification loss in the crown. Based on these criteria, each tree was assigned to a decline class
171 ranging from A (no decline) to F (severe decline). Trees in the A–C classes were considered healthy.
172 Trees in the D–F classes were considered in decline. We used this protocol to describe tree decline at
173 two embedded spatial scales: (i) the ten closest oaks surrounding each trap-bearing tree, hereafter
174 referred as a "*plot*"; and (ii) 30 oaks in the stand where the two plots were located (i.e., the 20 trees
175 in the two monitored plots and ten trees in an additional plot located between the two monitored
176 plots), hereafter referred as a "*stand*". Decline level was evaluated in January or February in 2019
177 and 2020, i.e., before and after Hymenoptera sampling, and we averaged the 2019 and 2020 values
178 for our analyses. We classified our plots and stands into three decline categories depending on the
179 proportion of declining oak trees. When the proportion of declining trees was < 30%, we considered
180 the plot/stand "*healthy*"; when the proportion was between 30% and 60%, the plot/stand was
181 considered "*moderately declining*"; and when the proportion was > 60%, the plot/stand was
182 considered "*severely declining*".

183 In the early summer of 2019, we used a plant canopy analyzer LAI-2200C with a half view cap
184 attached to the optical sensor to quantify the leaf area index (LAI) in the 12 stands in the Orléans and
185 Vierzon forests. More than 50 measurements were carried out at each plot at twilight below the
186 canopy along two diagonal transects; these values were then compared with above-canopy readings
187 taken outside the plot. We applied an ellipsoidal post-processing correction to the first three zenith
188 angles and used the FV2200 software to compute LAI by the gap fraction method. Then, in October
189 2020, we used a Bitterlich relascope with an opening angle corresponding to counting factor n° 1
190 (ratio 1/50) with a mean plot area of about 0.3 ha (Bouget et al., submitted) to characterise the
191 woody resources in each of the 18 plots in the Orléans and Vierzon forests. For each tree, we
192 recorded its status (i.e., living tree, standing dead tree (snag) or downed dead tree (log)), decay
193 stage, tree species and diameter at breast height (DBH). We defined the mortality rate as the basal
194 area of standing and lying deadwood over the total basal area of all the recorded trees (i.e., the sum
195 of both living and dead trees). We calculated the overall volume of living trees and deadwood. For
196 deadwood, we calculated the volume for each status (standing or downed deadwood), decay stage
197 (slightly vs. highly decayed) and diameter class (deadwood DBH < 40 cm vs. ≥ 40 cm). We compiled all
198 this information (i.e., status, species, decay stage and DBH) to calculate deadwood diversity. Finally,
199 we used the dbFD function from the FD R-package to calculate the mean status value of the woody
200 resources and the dispersion value for each plot, based on an ordinal scale (i.e., living trees = 3, snags
201 = 2, logs = 1). For more information, see https://doi.org/10.5281/zenodo.7816954.

202 **Insect sampling**

203 We hung two types of traps in each selected tree: one green multi-funnel trap (ChemTica
204 Internacional, San José, Costa Rica) with 12 fluon-coated funnels, and one cross-vane flight
205 interception trap (Polytrap™). The first type is used to sample borers like *Agrilus* (Rassati et al.,
206 2019); the experiment was initially designed to sample the community of borers along the decline
207 gradient in oak stands (Le Souchu et al., submitted). This type of trap is also efficient for sampling
208 guilds of foliage-associated insects (Sallé et al., 2020). The second type of trap is commonly used in
209 forests to sample saproxylic beetles (Bouget et al., 2008).

210 Both types of traps were suspended among the lower branches in the canopy (i.e., approximately 10
211 - 15m above the ground). The collectors were filled with a 50% (v/v) monopropylene glycol - water
212 solution with a drop of detergent. The traps were in place from the end of March to the beginning of
213 September 2019, during the insects'activite period, and they were emptied every month.

214 **Identification and ecological trait list**

215 All sampled Hymenoptera were sorted and identified to the family or superfamily level, according to
216 the identification key by Goulet and Huber (1993). Then the specimens were sent to taxonomical
217 experts who identified them to the genus, species or morphospecies level. Only the Cynipidae and
218 Figitidae were not identified at a lower taxonomic level.

219 We arranged the taxa into eight larval trophic guilds: gall-inducers, parasitoids, oak-associated
220 phyllophagous larvae, other phyllophagous larvae, phytophagous larvae (i.e. feeding on plant parts
221 other than leaves, for example, seeds), social polyphagous larvae, xylophagous larvae and
222 pollinivorous/nectarivorous larvae. Preferred larval habitat (larval nesting guild) was also considered,
223 when known. Taxa were divided into gall-nesters (gall-inducers and their inquiline parasitoids), soil-
224 nesters, stem-nesters (generally in hollow plant stems) and wood-nesters. For the latter three guilds,
225 we separated the specialists (spe.) from the generalists (gen.), nesting in wood and/or soil and/or
226 stems. Specialist wood-nesters were considered analogous to saproxylic taxa (Jonsell et al., 2023).

227 **Data analysis**

228 All analyses and graphs were performed in R, version 4.1.1 (R Core Team, 2021). We used the ggplot2
229 R-package (Wickham, 2016) to produce the figures. Unless otherwise stated, analyses were realised
230 with the Hymenoptera community collected at the plot level, and the proportion of declining trees at
231 both plot and stand scales. The figures with stand decline levels are included in the body of the
232 present article since they are more informative than the figures with plot decline levels, which are
233 available in the Supplementary Data.

Some specimens of Cynipidae, Figitidae, Halictidae, Andrenidae, Pteromalidae, Encyrtidae and Platygastridae were not identified, either because of a lack of expertise or because the specimens were too damaged for identification. These unidentified specimens were removed from the community analyses.

To extrapolate the species richness for the whole community (i.e., γ-diversity) and for each decline category, we first plotted species rarefaction curves (functions *iNEXT* and *ggiNEXT*, iNEXT R-package; Hsieh et al., 2016) and calculated Chao, Jackknife, Jackknife 2 and Bootstrap diversity indices (function *specpool*, vegan R-package; Oksanen et al., 2022). We used the additive diversity partitioning method (Lande, 1996; Crist et al., 2003) to evaluate the contribution of α- and β-diversity to the γ-diversity of canopy-dwelling Hymenoptera over the entire sampled area (function *adipart*, index = "richness", 1,000 permutations, vegan R-package). We tested whether observed species richness differed from the one we expected by chance (null hypothesis). At the plot scale, we used three levels of differentiation: plot, plot decline category and the whole sampled area. α plot corresponds to the average species diversity per plot, β plot to the diversity among plots and β cat_plot to the diversity among plot decline categories. γ-diversity is the sum of α plot, β plot and β cat_plot (γ = α plot + β plot + β cat_plot). At the stand scale, we used a similar approach except that four levels of differentiation were included: plot, stand, stand decline category and the whole sampled area. In addition, we separated β-diversity (Sorensen dissimilarity index) between plots, stands, decline categories and pairs of decline categories into β-turnover, i.e., species replacement (Simpson dissimilarity index) and β-nestedness (nestedness-resultant fraction of Sorensen dissimilarity) (function *beta.multi*, Sorensen family, betapart R-package; Baselga, 2010; Baselga and Orme, 2012).

We assessed the effect of oak decline on the abundance and species richness of the overall community, of each taxonomic family (when n > 30 ind.), and on the abundance of each taxa (when n > 30 ind.). We also assessed the oak-decline effect on each guild (i.e., larval trophic guilds and nesting guilds). To do this, we used generalised linear mixed-effects models (GLMMs; function *glmer, glmer.nb* or *lmer*, lme4 R-package; Bates et al., 2022) fitted for the Poisson family, the negative binomial family or the log-normal distribution (i.e., log-transformed response). We first selected the best suited family distribution with the fitdistrplus R-package (function *fitdist* and *gofstat*; Delignette-Muller and Dutang, 2015). We then performed GLMMs with either abundance or species richness at both scales (plot and stand). To adjust the decline variable to our dataset, we used linear and equations. We added forest and stand as nested random effects on the intercept in the mixed models to account for repeated measurements and the spatial configuration of the sampling design. Since some traps were not continuously functional, for example, because they fell from the tree, we

also added an offset of the log-number of effective traps across the entrapment season, weighted by the efficacy of each type of trap. To assess model quality, we used marginal R^2 (function *R2*, performance R-package; Lüdecke et al., 2021). We used the differences in AICc scores (function *AICc*, AICCmodavg R-package; Mazerolle, 2023) to compare the fit among models. When the linear and quadratic models were undifferentiated, we show only the results for the simplest one, i.e., the linear model. We also used the indicspecies R-package (function *multipatt*, func = "IndVal.g", 1,000 permutations) to identify indicator species for healthy, moderately-declining and severely-declining stands and plots (Dufrene and Legendre, 1997; De Cáceres and Legendre, 2009; De Cáceres et al., 2010).

In a second step, we implemented Structural Equation Modelling (SEM, piecewiseSEM R-package; Lefcheck et al., 2022) to evaluate the cascading effects of tree decline (i.e., the proportion of declining trees) and tree mortality (i.e., the proportion of dead trees) on taxonomic families and ecological guilds through changes in canopy closure (LAI) and deadwood resources. SEM was used only for the plots located in the Orléans and Vierzon forests. LAI was originally measured in 12 plots in the Orléans and Vierzon forests, and correlated strongly with tree decline rate at the stand scale (Fig. S1). Consequently, in order to avoid excluding additional plots in the SEM analysis, we extrapolated LAI from the tree decline rate in the six remaining plots using the equation of the regression curve (Fig. S1). We studied Hymenoptera responses through (i) the abundance of each taxonomic family, and (ii) the abundance and species richness of each ecological guild (see above). Response variables that did not respect assumptions of residual normality and homoscedasticity for linear regressions were log-transformed. In addition, in a first set of mixed models, we added forest identity (i.e., Orléans or Vierzon) as a random effect in the *lmer* function from lme4 R-package. We finally deleted this random effect since it was redundant with the fixed effects and caused model non-convergence. Finally, we used a linear model with the *lm* function. Several plots were installed close to wetlands, so we added this information to the models as a fixed effect since the characteristic might affect soil-nesters and phyllophagous species associated with plants in the herbaceous and shrub layers. We also added an offset term of the log-number of effective traps across the entrapment season to our models. Finally, since we tested 14 predictors in SEMs to assess the cascading effects of oak decline on each canopy-dwelling Hymenoptera community metric (i.e., multiple tests), we adjusted the p.value to control for an increased risk of type I errors and only considered effects for which p.values were lower than 0.0036 (i.e., 0.05/14).

RESULTS

301 **The community of canopy-dwelling Hymenoptera**

302 We collected 19,289 individuals, belonging to 54 families and 918 taxa (Fig. 2; Tab. S2). The most
303 abundant families were the Ichneumonidae (22% of the specimens), the Cynipidae (22%) and the
304 Perilampidae (14%), while the most diverse were the Ichneumonidae (321 taxa), the Braconidae
305 (121) and the Tenthredinidae (88) (Fig. 2). The dominant species was the chalcid *Perilampus*
306 *ruficornis* (F.) (2,614 individuals), followed by the ant *Dolichoderus quadripunctatus* (L.), the common
307 wasp *Vespula vulgaris* (L.) (647 ind.), and the halictid *Lasioglossum pallens* (Brullé) (605 ind.). Most of
308 the community was composed of singletons (344 taxa) and doubletons (129), and only 198 taxa
309 occurred with more than ten individuals (Tab. S2). Several species cited for the first time in France
310 were sampled, especially members of the Ichneumonidae family (Tab. S2). We also collected 35 bee
311 species registered on Worldwide or European Red Lists (Tab. S2). Among them, three species were
312 near-threatened: *Andrena fulvida* Schenck, *Lasioglossum monstrificum* (Morawitz) and *Lasioglossum*
313 *sexnotatum* (Kirby). The other species were classified as either "data deficient" (13 spp.) or "of least
314 concern" (19 spp.).

315 The activity of most families peaked in the spring (Fig. S2), and the community was the most
316 abundant (64% of total specimens) in April. Species richness was more evenly distributed throughout
317 the sampling period, but also peaked in April (48% of all taxa). Overall, the green multi-funnel traps
318 clearly outperformed the flight interception traps (93% vs. 7% of total abundance, 94% vs. 28% of all
319 taxa) (Fig. S3); for each guild and family, both abundance and species richness were higher in the
320 multi-funnel traps.

321 According to our species-diversity estimators (Tab. 1), there should have been between 1,074 and
322 1,505 species in the entire sampled area. We collected between 61% and 85% of these estimations,
323 and consequently, the rarefaction curve for the whole community barely approached an asymptote
324 (Fig. 3). Both moderately declining and severely declining plots and stands were predicted to shelter
325 slightly more taxa than healthy ones (Tab. 1, Fig. 3, Tab. S3, Fig. S4). The communities in healthy and
326 severely declining stands were clearly distinct, but both were partially similar to those in moderately
327 declining stands (Fig. 4). At the plot scale, a similar pattern was observed, although the divergence
328 was less marked (Fig. S5). Consequently, the differences between decline categories were significant
329 at both the plot (PERMANOVA, $F = 2.49$, $df = 2$, $R^2 = 0.11$, $p = 0.001$) and stand scales (PERMANOVA, F
330 $= 3.76$, $df = 2$, $R^2 = 0.16$, $p = 0.001$).

331 **Contribution of α- and β-diversity to γ-diversity**

332 The additive partitioning of species richness showed that, at the plot scale, *β plot* did not present any
333 significant difference between observed and expected richness (Fig. S6). At the stand scale, the

observed richness of *β plot* was significantly lower than expected (Fig. 5), while observed *β stand* was similar to predicted *β stand*. Conversely, decline categories contributed largely to γ-diversity. Observed *β cat_plot* and *β cat_stand* were significantly higher than expected and respectively represented 39% and 40% of the γ-diversity.

Overall *β*-diversity was mainly due to species turnover, among all plots and stands (Tab. 2), and between each pair of plots (Tab. S4) and stand decline categories (Tab. 2). At the plot scale, *β* nestedness was very low. At the stand scale, however, *β* nestedness was a significant part of the *β*-diversity between moderately declining stands and healthy ones (22%), as well as between moderately and severely declining stands (16%).

Indicator species

One species was associated with healthy plots, 11 with moderately declining plots and 11 with severely declining plots (Tab. S5). At the stand scale, five species were associated with healthy stands, five with moderately declining stands and seventeen with severely declining stands (Tab. S6). Four species were indicators at both plot and stand scales. The majority of the indicators were parasitoids. Several sawflies that feed on non-oak host plants were also indicators of severely declining stands, and a few species with pollinivorous/nectarivorous larvae were indicators of moderately declining plots.

Effect of oak decline on ecological guilds and taxonomic families and taxa

Neither the abundance nor the species richness of the community of canopy-dwelling Hymenoptera was influenced by the extent of the decline. However, contrasting effects were observed among guilds, taxonomic families and taxa (Tabs. 3 & 4, Fig. S7). For larval trophic guilds, the abundance of pollinivorous/nectarivorous and polyphagous species increased with decline severity, while those of xylophagous species decreased (Tab. 3). Parasitoid species were more abundant at intermediate levels of decline (40% of declining trees, Fig. S7). Carnivorous and polyphagous taxa also became more diverse as decline severity increased (Tab. 4). For larval habitat guilds, oak decline only slightly affected the abundance of gall-nesting taxa, while the abundance of both specialist wood-nesters and specialist soil-nesters was promoted (Tab. 3). Decline also promoted the diversity of generalist soil-, wood- and stem-nesters (Tab. 4).

For taxonomic groups, as some guilds were composed of a single family, or sometimes a single species, the effect of oak decline on these families concurred with the effect on the guilds (e.g., Xiphydriidae, *Xiphydria longicollis* (Geoffroy) for xylophagous taxa and Cynipidae for gall-inducers) (Tabs. 3 & 4). Consistent results were also observed for the families making up the majority of a guild,

366 like the Formicidae (polyphagous), the Halictidae (pollinivorous/nectarivorous) and the Vespidae
367 (carnivorous). In addition, the abundance of Evaniidae (*Brachygaster minuta* (Olivier)), Pamphilidae
368 and Tiphiidae (*Tiphia femorata* F.) was promoted with decline severity. This was also true for
369 Pamphilidae diversity. Conversely, the Perilampidae (*P. ruficornis*) were negatively affected by
370 decline, and the abundance of Ichneumonidae peaked at intermediate levels of decline (approx. 50%
371 of declining trees, Tab. 3). At the species level, the abundance of 18 species out of the 83 tested was
372 influenced by oak decline, either positively (5 species), negatively (4) or non-linearly (9). Eleven of
373 them were parasitoids / hyperparasitoids (Tab. 3, Fig. S7). Two species of ants (*D. quadripunctatus*,
374 *Myrmecina graminicola* (Latreille)) were also promoted by intermediate or high levels of decline.

375 The SEM showed that tree mortality promoted the abundance and diversity of deadwood habitats
376 and that tree decline markedly reduced LAI (Figs. 6 & 7). Tree mortality rate negatively affected
377 overall species richness, the abundance of the Eulophidae and, to a lesser extent, that of the
378 Tiphiidae (Fig. 6). Tree decline rate also had direct impacts and promoted both the Halictidae and the
379 Tiphiidae, but reduced Xiphydriidae abundance. Few effects on taxonomic guilds were mediated by
380 changes in forest structure (Fig. 6). The most notable effect was the positive effect of tree decline
381 rate on the overall species richness of Hymenoptera mediated by its negative impact on LAI (Fig. 6).

382 Tree mortality and decline rates also had direct effects on ecological guilds (Fig. 7). An increasing tree
383 mortality rate reduced the abundance and species richness of nectarivorous/pollinivorous species,
384 and the species richness of non-oak phyllophagous, polyphagous and soil-nesting species. As
385 mentioned above, tree decline rate negatively affected the abundance of xylophagous Hymenoptera
386 (Xiphydriidae), but also promoted the species richness of polyphagous species. Nonetheless, the
387 most important impact of tree decline rate was mediated by the reduction in LAI which promoted
388 the species richness of non-oak phyllophagous species, and both the species richness and abundance
389 of nectarivorous/pollinivorous and specialist soil-nesting taxa. LAI impacts on guilds were
390 consistently similar to those of tree mortality, leading to opposite effects of tree decline and tree
391 mortality on ecological guilds (Fig. 7). For the overall community, as well as for
392 nectarivorous/pollinivorous and non-oak phyllophagous taxa, species richness consistently decreased
393 when LAI increased, and was always low when tree mortality rate was high (Fig. S8). Finally, changes
394 in deadwood resources, mediated by tree mortality, only marginally influenced xylophagous taxa and
395 had no impact on the other ecological guilds (Fig. 7).

396

397 **DISCUSSION**

The community of canopy-dwelling Hymenoptera in temperate oak forests

With more than 150,000 species described worldwide, Hymenoptera are one of the most diverse orders of insects (Huber, 2017; Aberlenc, 2020). In our study, we identified 918 taxa, indicating that the community of Hymenoptera dwelling in the canopy of the oak stands was particularly diverse. As a comparison, with the same sampling design, in the same plots and at the same time, we collected approximately 97,000 Coleoptera and 10,000 Hemiptera, and identified 562 and 169 taxa respectively (unpubl. data). In agreement with earlier predictions (Forbes et al., 2018), these results suggest that the community of Hymenoptera could be one of the most diverse, if not the most diverse, community of arthropods in temperate oak forests.

We collected numerous phyllophagous and gall-inducing species (Tab. S2), which supports using green multi-funnel traps to collect foliage-feeding arthropods (Sallé et al., 2020). In the same traps, we also collected a wide diversity of parasitoids and predators, which might have been attracted by the green colour, indicative of potential hunting grounds for their hosts and prey. For example, the most common species in our sampling, *P. ruficornis*, is a hyperparasitoid that frequently parasitises leaf-chewing caterpillars and cynipids (Mitroiu and Koutsoukos, 2023). We also collected several phytophagous species that feed on oak foliage (e.g., *Periclista* spp.) and oak pollen (e.g., *Andrena ferox* Smith, *L. pallens*), and saproxylic taxa known to develop in oak branches (i.e., *X. longicollis*) or to nest in standing deadwood and/or in branches (e.g., *D. quadripunctatus*, *Deuteragenia subintermedia* (Magretti)). We therefore expected to find all of these taxa in the canopy (e.g., Kampichler and Teschner, 2002 for gall-inducers). Conversely, we found several unexpected taxa in the canopy layer. For instance, we collected species that feed on plants in the herbaceous layer (e.g., *Strongylogaster multifasciata* (Geoffroy) a fern-feeder), as well as parasitoids of soil-dwelling grubs (i.e., *T. femorata*) or spiders (i.e., *Aporus unicolor* Spinola). We also sampled several uncommon or even rare species (e.g., *Chrysis equestris* Dahlbom, *Pamphilius balteatus* (Fallén), *Parascleroderma sulcatifrons* (Kieffer), Marhic & Noblecourt, pers. obs.), including three species of bees that are near-threatened at the European level (i.e., *A. fulvida*, *L. monstrificum*, and *L. sexnotatum;* Nieto et al., 2014), and several species new for France (e.g., *Gastrancistrus laticeps* Graham, *Spathius polonicus* Niezabitowski), or even Europe (i.e., *Plastanoxus evansi* Gorbatovsky). This highlights how little we still know about the composition and ecology of canopy-dwelling arthropods in general, and Hymenoptera in particular (Hilszczański, 2018; Sallé et al., 2021), in temperate forests.

Effects of forest decline on the community, guilds and taxa of canopy-dwelling Hymenoptera

430 Oak decline did not directly affect the abundance and richness of the community of canopy-dwelling
431 Hymenoptera. However, it did markedly reshape its composition, which differed significantly along
432 the decline gradient. Species turnover was the main component of these changes, as has been
433 commonly observed (Soininen et al., 2018), while difference among decline categories was the main
434 contributor to global diversity. The significant contribution of nestedness to the *β*-diversity between
435 moderately declining stands and both healthy and severely declining stands is congruent with the
436 NMDS results, and indicates that the community characteristic of an intermediate level of decline is
437 composed of taxa from the other two levels rather than of specific taxa new to the community.
438 Similarly, in a previous study, the species richness of canopy-dwelling beetles was not influenced by
439 oak decline, although both their abundance and their biomass increased (Sallé et al., 2020). Our
440 result is nonetheless surprising since a recent meta-analysis indicates that forest Hymenoptera
441 diversity (excluding ants) is generally promoted by disturbances like wildfires, windstorms and pest
442 outbreaks (Viljur et al., 2022). However, the meta-analysis also found that the magnitude of increase
443 in species richness was quite variable among studies (Viljur et al., 2022). In our case study, the
444 decline effect was generally consistent between the two spatial scales considered (plot vs. stand),
445 but the magnitude of the effects was sometimes different. This might reflect differences in foraging
446 behaviour and habitat use among taxa and/or guilds.

447 Changes in community composition were driven by contrasting responses of taxa and ecological
448 guilds to oak decline, supporting the importance of multi-taxonomic and multitrophic approaches in
449 research on how environmental changes affect community structure (Seibold et al., 2018). As
450 expected from the literature (Gaston, 1991), the parasitoid guild was both the most diverse and the
451 most abundant guild. Since parasitoids, and especially koinobionts, require a diversity of habitats to
452 support the full assemblage of their hosts, they are highly sensitive to changes in habitat (Fraser et
453 al., 2007; Hilszczański, 2018; Jonsell et al., 2023). Overall, in our study, they exhibited quadratic
454 relationships with decline levels, and were more abundant at intermediate levels of decline severity
455 (i.e., 40% of declining oaks). At the taxa level, a majority of species whose abundance was affected by
456 decline also exhibited a similar pattern, with a peak of abundance at low or moderate levels of
457 decline (i.e., 30% to 60% of declining oaks). This suggests that a moderate decline may provide a
458 greater diversity of habitats and trophic resources for parasitoids, as predicted, for instance, by the
459 intermediate disturbance hypothesis (Grime, 1973; Horn, 1975). This overall trend might be further
460 modulated by the host type of the parasitoid. We observed that both Tiphiidae (e.g., *T. femorata*)
461 and Evanidae (e.g., *B. minuta*), which parasitize chafers and cockroaches respectively, benefited from
462 tree decline, while the parasitoids of defoliating or mining moths (e.g., *Agrypon flaveolatum*
463 (Gravenhorst), *Bassus* sp. 1, *Earinus gloriatorius* (Panzer), *Macrocentrus nitidus* (Wesmael), *P.*

464 *ruficornis* (Mitroiu and Koutsoukos, 2023)), were somewhat disadvantaged by high levels of decline.
465 Further studies would be necessary to assess whether these effects depend on host type or are
466 idiosyncratic species responses. It might also be interesting to investigate whether koinobionts are
467 more responsive to forest decline than idiobionts. The other guild belonging to a higher trophic level,
468 the carnivorous taxa, was promoted by oak decline. Disturbances can have highly contrasted effects
469 on predators (Cours et al., 2023). In our study, this guild included several taxonomic families such as
470 Vespidae, Formicidae and Pemphredonidae that prey on a wide range of taxa. The positive decline
471 effect might result either from a higher abundance or accessibility of prey (Cours et al., 2023), or
472 from better habitat conditions. Further studies would be required to identify the factors
473 underpinning this positive effect.

474 As expected, the abundance of pollinivorous/nectarivorous taxa increased with severity of decline.
475 This is in line with previous studies showing that disturbances generally promote pollinators by
476 providing more floral resources and nesting sites (Wermelinger et al., 2017; Viljur et al., 2022; Perlík
477 et al., 2023). Interestingly, however, the dominant family of pollinivorous/nectarivorous bees,
478 Halictidae, was mostly represented by *L. pallens*, a soil-nesting bee which mainly feeds on oak pollen
479 and consequently, does not rely on other floral resources (Hermann et al., 2003). Since the overall
480 abundance of specialist soil-nesters was also promoted by stand decline, this suggests that soil
481 conditions were potentially a more important driver of community change for the guild of
482 pollinivorous/nectarivorous taxa than were floral resources in the herbaceous layer. The abundance
483 and the diversity of polyphagous species were also enhanced by oak decline. This is congruent with
484 the fact that ants, which dominated the guild of polyphagous species, are known to benefit from
485 silvicultural practices leading to more open conditions (Tausan et al., 2017; Grevé et al., 2018; Cours
486 et al., 2023).

487 Oak decline promoted the abundance, but not the diversity, of specialist wood-nesters, i.e. of
488 saproxylic taxa. Yet, the accumulation and diversification of deadwood resources and weakened
489 hosts during forest dieback and decline events generally favour saproxylic taxa abundance and
490 diversity (Beudert et al., 2015; Kozák et al., 2020; Cours et al., 2022, 2023), including those dwelling
491 in the canopy (Stone et al., 2010; Sallé et al., 2020; Le Souchu et al. *subm.*). This overall trend for the
492 guild might be contradicted at the species level, since some saproxylic species can be negatively
493 affected by forest dieback or decline (Vincent et al., 2020). In line with this, the only xylophagous
494 species in our survey i.e., *X. longicollis*, was negatively affected by decline severity. The larvae of this
495 species bore into the branches of weakened broadleaved trees and are sometimes associated with
496 oak decline (Dominik and Starzyk, 1988). Nonetheless, severe decline conditions may have reduced
497 the amount of living branches in the canopy, thereby reducing the amount of breeding substrates for

498 the species, as suggested by both the direct effect of tree decline rate, and the indirect effect of tree
499 mortality on *X. longicollis* abundance.

500 The diversity of generalist stem-, wood- and soil-nesters was promoted by oak decline, while the
501 species richness of the specialist guilds remained unaffected. The decline process may lead to
502 resources pulses, which may be more readily exploited by generalist species (Cours et al., 2023).

503 Contrary to our hypothesis, oak decline did not influence the phyllophagous species typically
504 associated with oaks, and only marginally affected gall-inducers and gall-nesters. Responses of leaf-
505 feeding insects to tree decline can be highly variable, ranging from negative to positive effects
506 (Martel and Mauffette, 1997; Stone et al., 2010; Sallé et al., 2020). Host specificity might modulate
507 the outcome of tree decline on leaf-feeding species, but we did not observe any such tendency in our
508 survey. Interestingly, oak decline had an overall negative effect on the parasitoids of defoliating or
509 mining caterpillars. This suggests a negative impact of decline on leaf-feeding moths, with potential
510 cascading impacts on higher trophic levels. Conversely, the diversity of leaf-feeders associated with
511 other host plants increased with decline severity, and several of them were indicators of high levels
512 of decline (i.e., *S. multifasciata* and *Aneugmenus padi* (L.), both fern-feeders; *Tenthredopsis nassata*
513 (L.) and *Dolerus gonager* (F.), bentgrass-feeders; *Eutomostethus luteiventris* (Klug), a rush-feeder; and
514 *Pachyprotasis simulans* (Klug), a goldenrod-feeder (Lacourt, 2020)). All of the above were
515 "Symphyta" and their increase might reflect the preference of these wasps for open forests (Lehnert
516 et al., 2013), but it might also result from a cascading effect of an increase in plant diversity and
517 biomass along with increased canopy openness (Lehnert et al., 2013; Lu et al., 2019; Cacciatori et al.,
518 2022).

519 **Key parameters of decline-driven changes in Hymenoptera guilds and taxa**

520 The results of the SEMs were consistent with those of the GLMMs, indicating that the effects
521 highlighted by the SEM approach were probably also involved in hymenopteran responses to oak
522 decline over the whole sampling design. Changes in community composition and structure resulted
523 either from the direct effects of tree mortality and tree decline, or from indirect effects mediated by
524 alterations of the forest structure. As dead branches accumulated in the crown of declining trees, an
525 increase in tree decline rate markedly reduced the LAI. Most of the tree decline effects on ecological
526 guilds were mediated by changes in LAI, which was therefore a major driver of community change. In
527 parallel, an increase in tree mortality rate increased the volume and diversity of deadwood
528 resources.

529 An increasing tree decline rate directly promoted the abundance of the Halictidae and Tiphiidae.
530 Both families rely on ground-related trophic resources (floral resources for the Halictidae and soil-

dwelling larvae for the Tiphiidae) and ground habitats since they are soil-nesters (Michez et al., 2019). In declining stands, soil-nesters may benefit from better or warmer micro-environmental conditions but also from better underground resources due to LAI reduction (Cours et al., 2023). In line with this, generalist leaf-feeding weevils, with root-feeding larvae, have been shown to benefit from oak decline (Sallé et al., 2020). The positive effect of a reduction in LAI on nectarivorous/pollinivorous taxa is also congruent with its positive effect on the diversity of non-oak phyllophagous taxa, supporting the above-mentioned hypothesis of a pulse in plant diversity and floral resources when canopy openness increases (Romey et al., 2007; Lu et al., 2019; Cacciatori et al., 2022). In our study, canopy opening promoted the overall diversity of the Hymenoptera taxa, which supports previous observations (Eckerter et al., 2022; Perlík et al., 2023; Rappa et al., 2023). This result also indicates that micro-environmental modifications at the ground level can have critical impacts on the communities dwelling in higher forest strata, especially when species have developmental instars that rely on ground resources or ground micro-habitats.

Surprisingly, while tree mortality rate altered a large array of deadwood resources, we did not observe any effect of these alterations on the taxonomic families and guilds of Hymenoptera, aside from the negative effect of a reduction in the number of living trees on the xylophagous Xiphydriidae. This contradicts several studies where the accumulation and/or diversification of deadwood resources promoted the abundance, species richness or community composition of different Hymenoptera guilds and taxa like bees and wasps (Bogusch and Horák, 2018; Urban-Mead et al., 2021; Rappa et al., 2023), and parasitoid wasps (Hilszczański et al., 2005; Ulyshen et al., 2011a). However, our results are congruent with recent observations where changes in deadwood amounts did not influence the species richness or community composition of either cavity- or non-cavity-nesting Hymenoptera, at least at a local scale (Perlík et al., 2023). Our study plots were located in managed oak forests, and active forest management likely restricted the magnitude of accumulation and diversification of deadwood resources (Bouget et al., *subm.*). This may have limited the potentially beneficial effects of tree mortality and decline on saproxylic Hymenoptera, thus only weakly promoting saproxylic taxa and wood-nesters. It may also be a matter of spatial scale; considering the amount and diversity of deadwood resources over larger spatial scales might be more relevant, especially for taxa with a high dispersal capacity (Cours et al., 2022). In addition, considering more precise parasitoid subguilds, especially those with saproxylic hosts, might also help to unravel the impacts of changes in deadwood on the forest Hymenoptera community (but see below).

In our study, the effects of tree mortality rate on the ecological guilds were consistently opposed to those of the decline rate, and were, overall, negative. The stands with a high tree mortality rate might very well have experienced more severe and frequent droughts in the years before the study, leading to pervasive cascading effects on Hymenoptera through alterations in plant-pollinator or host-parasitoid interactions, for instance (Rouault et al., 2006; Endres et al., 2021). The negative effects could also indicate that canopies with dead trees are avoided by Hymenoptera, thus leading to an overall reduction in abundance and species richness. Stands with high levels of tree mortality might also have experienced critical changes in micro-environmental conditions and trophic resources, but further studies are required to better understand the processes underpinning these deleterious effects.

Forest Hymenoptera and conservation

We have shown that the β-diversity among decline categories at the stand level significantly contributed to the overall γ-diversity, mostly through species turnover. This suggests that, when possible, maintaining a landscape mosaic including stands at different levels of decline or dieback may serve a conservation purpose (Socolar et al., 2016), especially since maintaining high habitat heterogeneity is generally a key goal for the conservation of insect communities (Samways, 2015). There are probably underlying mechanisms linked to resource and habitat supplementation and complementation in the heterogeneous forest landscape (Dunning et al., 1992).

Our results highlight the extreme diversity of the forest Hymenoptera community, and the relevance of Hymenoptera in studying changes in global community structure and forest functional processes. Our results also support their value as forest bioindicators, as previously proposed by Maleque *et al.* (2009). Nonetheless, our study also underlines the relative lack of knowledge of this group in temperate forests (Hilszczański, 2018; Jonsell et al., 2023). Except for a few well-known species, it was difficult to obtain information on the biology and ecology of the taxa we collected. We therefore had to limit the number of ecological traits in our analyses, and our current list of traits is still partially incomplete. This is unfortunate since databases of ecological traits have proven to be useful tools for ecological studies and conservation purposes (e.g., Bouget et al., 2013; 2019). Consequently, considering the growing threats to biodiversity in general, and to insect communities in particular (Wagner, 2020), we call for thorough investigations on the diversity and ecology of Hymenoptera to make better use of their potential as bioindicators (Maleque et al., 2009), understand their ecological services, and better evaluate their conservation value.

CONCLUSION

Oak decline had mixed effects on canopy-dwelling Hymenoptera in our study. We found contrasting responses for some taxa and ecological guilds, which profoundly reshaped the species assemblage but did not affect the overall abundance or diversity of the community. Although tree mortality rate influenced several guilds and taxa, local changes in deadwood resources only had marginal effects on forest Hymenoptera. However, we confirmed the critical role of canopy openness on the ecological guilds and taxa dependant on ground-related resources and microhabitats (floral resources, herbaceous layer and soil conditions). This suggests that micro-environmental changes at the ground level strongly influence changes in canopy communities. We call for a thorough investigation of the changes in ecological processes and community structure at the ground level following forest decline and dieback.

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SUPPLEMENTARY INFORMATION

Representative specimens of Braconidae, Ichneumonidae, Halictidae, Andrenidae, Crabronidae and Pemphredonidae are housed at the Orleans Museum for Biodiversity and the Environment (MOBE, Orléans, France). R scripts, the list of species traits and the list of plot and stand characteristics can be found at: https://doi.org/10.57745/H8CBG1

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913 **Tables**

914

915 Table 1. Species diversity estimators for the overall community and for each category of stand
916 decline in three temperate oak forests (21 stands and 42 plots).

Stand status	Observed species richness	Number of plots	Chao	Jackknife 1	Jackknife 2	Bootstrap	Range
All stands	918	42	1,407 ± 70	1,279 ± 65	1,505	1,074 ± 32	1,074 - 1,505
Healthy	501	14	943 ± 79	742 ± 76	909	604 ± 37	604 – 943
Moderately declining	629	16	943 ± 51	891 ± 76	1,041	745 ± 39	745 - 1,041
Severely declining	532	12	898 ± 61	783 ± 78	940	641 ± 35	641 - 940

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919 Table 2. Overall β-diversity, β turnover and β nestedness between pairs of stand-decline category.
920 Overall β-diversity corresponds to Sorensen dissimilarity, β turnover to Simpson dissimilarity and β
921 nestedness to the difference between Sorensen and Simpson dissimilarity. H = healthy stands, MD =
922 moderately declining stands, SD = severely declining stands.

	Overall *β*-diversity	*β* turnover	*β* nestedness
Among plots	0.95	0.93 (97.89%)	0.02 (2.11%)
Among stands	0.89	0.85 (95.51%)	0.04 (4.49%)
Among categories of stand decline	0.47	0.41 (87.23%)	0.06 (12.77%)
Between H and MD stands	0.37	0.29 (78.38%)	0.08 (21.62%)
Between MD and SD stands	0.38	0.32 (84.21%)	0.06 (15.79%)
Between H and SD stands	0.42	0.40 (95.24%)	0.02 (4.76%)

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Table 3. Effect of the proportion of declining oak trees (plot or stand decline) on the abundance of oak-dwelling Hymenoptera, and on the abundance of guilds (larval trophic guilds, larval nesting guild, saproxylic guild), families (abundance > 30 ind.) and taxa (abundance > 30 ind.). GLMMs were fitted for the negative binomial family (NB), the Poisson family (P) or the log-normal family (Log), with forest and stand as random effects. Models with either linear or quadratic decline variables were tested. ΔAICc = AICc (decline model) – AICc (null model). The best model between plot and stand scales is highlighted in bold. Only significant relationships are shown.

Community / taxa	Abund.	Dist. fam.	Plot decline					Stand decline				
			Delta AICc	Estimate	S. E.	z or t value	Marginal R^2	Delta AICc	Estimate	S. E.	z or t value	Marginal R^2
Overall community	19,282	Log	2.72	-	-	-	-	2.09	-	-	-	-
Larval trophic guilds												
Gall-inducer	4,199	Log	**-4.29**	**d1. 1.74 ns**	**1.7**	**1.01**	**0.20**	**-5.15**	**d1. 2.44 ns**	**2.0**	**1.22**	**0.24**
				d2. -3.06 ns	**1.9**	**-1.65**			**d2. -4.06 .**	**2.2**	**-1.85**	
Parasitoid	9,904	Log	1.75	-	-	-	-	**-6.35**	**d1. 1.49 ***	**0.7**	**2.23**	**0.12**
									d2. -2.25 **	**0.7**	**-3.12**	
Pollinivorous/Nectarivorous	1,246	Log	**-3.05**	**d1. 3.19 ***	**1.5**	**2.13**	**0.07**	**-4.30**	**1.56 ***	**0.6**	**2.63**	**0.15**
				d2. - 2.74 .	**1.6**	**-1.72**						
Polyphagous	1,281	NB	**-9.35**	**1.29 *****	**0.1**	**113.57**	**0.19**	-3.99	1.22 ***	0.1	112.82	0.14
Xylophagous	149	NB	**-3.51**	**-3.47 ***	**1.5**	**-2.33**	**0.35**	2.57	-	-	-	-
Larval nesting guilds												
Gall nest	5,090	Log	0.72	-	-	-	-	**-5.24**	**d1. 3.05 ns**	**2.0**	**1.55**	**0.25**
									d2.-4.55 *	**2.2**	**-2.12**	
Spe. Soil nesters	1,384	NB	0.16					**-4.60**	**0.75 *****	**0.01**	**101.35**	**0.04**
Spe. Wood nesters	1,866	Log	**-3.07**	**0.74 ***	**0.3**	**2.59**	**0.10**	**-2.67**	**0.85 ***	**0.3**	**2.49**	**0.11**
Families												
Cynipidae	4,199	Log	**-4.29**	**d1. 1.74 ns**	**1.7**	**1.01**	**0.20**	**-5.15**	**d1. 2.44 ns**	**2.0**	**1.22**	**0.24**
				d2. -3.06 ns	**1.9**	**-1.65**			**d2. -4.06 .**	**2.2**	**-1.85**	
Evanidae	33	P	-3.13	2.87 **	1.1	2.74	0.15	**-11.88**	**5.03 *****	**1.3**	**3.97**	**0.35**
Formicidae	1,339	NB	**-8.98**	**1.23 *****	**0.1**	**113.00**	**0.18**	-3.35	1.14 **	0.1	109.721	0.13

Tab. 3 continued

Community / taxa	Abund.	Dist. fam.	Plot decline					Stand decline				
			Delta AICc	Estimate	S. E.	z or t value	Marginal R^2	Delta AICc	Estimate	S. E.	z or t value	Marginal R^2
Halictidae	924	Log	**-3.94**	**d1. 3.81 ***	**0.6**	**2.17**	**0.06**	**-4.90**	**1.82 ***	**0.7**	**2.70**	**0.12**
				d2. -3.25 .	**0.6**	**-1.75**						
Ichneumonidae	4,242	Log	3.89	-	-	-	-	**-4.46**	**d1. 2.24 ****	**0.7**	**3.40**	**0.11**
				-	-	-	-		**d2. -2.37 ****	**0.7**	**-3.33**	
Pamphiliidae	38	NB	-1.55	-	-	-	-	**-4.77**	**3 ***	**1.1**	**2.66**	**0.21**
Perilampidae	2,614	NB	-6.30	-1.72 **	0.5	-3.24	0.38	**-9.87**	**-2.67 ***	**0.8**	**-3.45**	**0.42**
Tiphiidae	92	P	**-2.44**	**2.39 ***	**1.1**	**2.21**	**0.05**	**-2.17**	**4.24 ***	**1.9**	**2.29**	**0.12**
Xiphydriidae	149	NB	**-3.51**	**-3.47 ***	**1.5**	**-2.33**	**0.35**	2.57	-	-	-	-
Taxa												
Agrypon flaveolatum	32	P	**-2.63**	**-2.18 ***	**1.1**	**-2.00**	**0.11**	2.32	-	-	-	-
Bassus sp.1	38	NB	**-4.54**	**d1. 9.06 ***	**3.5**	**2.58**	**0.36**	0.07	-	-	-	-
				d2. -12.59 **	**4.7**	**-2.67**						
Brachygaster minuta	33	P	-3.13	2.87 *	1.1	2.74	0.15	**-11.88**	**5.03 *****	**1.3**	**3.97**	**0.35**
Ctenopelmatinae sp.1	88	P	**-86.47**	**d1. 41.56 *****	**8.3**	**4.99**	**0.53**	1.88	-	-	-	-
				d2. -51.48 ***	**11.3**	**-4.55**						
Ctenopelmatinae sp.7	73	P	**-20.70**	**2.92 *****	**0.7**	**4.45**	**0.18**	2.41	-	-	-	-
Deuteragenia vechti	44	P	**-6.11**	**-3.05 ***	**1.2**	**-2.62**	**0.14**	0.11	-	-	-	-
Dolichoderus quadripunctatus	718	NB	**-6.30**	**1.49 ***	**0.5**	**3.06**	**0.18**	-3.30	1.34 *	0.6	2.38	0.12
Earinus elator	180	NB	2.53	-	-	-	-	2.56	-	-	-	-
Earinus gloriatorius	43	NB	**-4.19**	**d1. 7.77 *****	**1.7**	**4.50**	**0.21**	2.57	-	-	-	-
				d2. -9.29 ***	**2.0**	**-4.73**						
Empria tridens	30	P	**-2.72**	**-2.18 ***	**0.9**	**-2.33**	**0.11**	1.07	-	-	-	-
Macrocentrus nitidus	42	NB	**-3.08**	**d1. 5.12 *****	**1.2**	**4.15**	**0.24**	-0.01	-	-	-	-
				d2. -7.78 ***	**1.6**	**-4.98**						

Tab. 3 continued

Community / taxa	Abund.	Dist. fam.	Plot decline					Stand decline				
			Delta AICc	Estimate	S. E.	z or t value	Marginal R^2	Delta AICc	Estimate	S. E.	z or t value	Marginal R^2
Myrmecina graminicola	39	P	**-10.86**	**d1. 12.48 ****	**3.8**	**3.29**	**0.30**	-3.03	d1. 9.87 **	3.7	2.64	0.21
				d2. -12.13 **	**4.0**	**-3.04**			d2. -9.68 *	4.1	-2.39	
Perilampus ruficornis	2,614	NB	-8.50	d1. 2.00 ***	0.1	131.40	0.38	**-22.79**	**d1. 3.53 *****	**0.1**	**124.97**	**0.67**
				d2. -4.36 ***	0.1	-287.19			**d2. -7.43 *****	**0.1**	**-262.53**	
Priocnemis perturbator	38	P	**-4.30**	**d1. 9.73 ***	**3.9**	**2.47**	**0.17**	1.33	-	-	-	-
				d2. -8.37 *	**3.9**	**-2.16**						
Strongylogaster multifasciata	52	P	**-12.98**	**d1. 15.97 ****	**4.7**	**3.40**	**0.31**	-1.43	-	-	-	-
				d2. -11.87 **	**3.5**	**-3.39**						
Tiphia femorata	92	P	**-2.44**	**2.39 ***	**1.1**	**2.21**	**0.04**	**-2.17**	**4.24 ***	**1.9**	**2.29**	**0.12**
Vespa crabro	240	NB	**-3.70**	**1.61 ***	**0.7**	**2.43**	**0.10**	-0.27	-	-	-	-
Xiphydria longicollis	149	NB	**-3.51**	**-3.47 ***	**1.5**	**-2.33**	**0.35**	2.57	-	-	-	-
Xorides praecatorius	30	P	1.37	-	-	-	-	**-3.07**	**d1. 9.88 ***	**3.9**	**2.53**	**0.22**
									d2. -9.82 *	**4.0**	**-2.46**	

Table 4. Effect of the proportion of declining oak trees (plot or stand decline) on the species richness of oak-dwelling Hymenoptera, and on the species richness of guilds (larval trophic guilds, larval nesting guild, saproxylic guild) and families (abundance > 30 ind.). Only significant relationships are shown. See the caption for Table 3 for more information.

Community / taxa	Species richness	Dist. fam.	Plot decline					Stand decline				
			Delta AICc	Estimate	S. E.	z or t value	Marginal R^2	Delta AICc	Estimate	S. E.	z or t value	Marginal R^2
Overall community	918	Log	0.75	-	-	-	-	-0.97	-	-	-	-
Larval trophic guilds												
Carnivorous	70	P	-3.60	0.57 *	0.23	2.54	0.05	-3.23	0.63 *	0.25	2.56	0.05
Non-oak phyllophagous	86	Log	1.62	-	-	-	-	-3.16	0.89 *	0.64	2.6	0.11
Polyphagous	25	P	-2.66	0.56 *	0.25	2.79	0.04	-3.24	0.66 *	0.28	2.40	0.05
Larval nesting guilds												
Gen. Soil nesters	28	P	-2.13	0.53*	0.24	2.19	0.03	-0.68				
Gen. Stem nesters	32	P	-2.92	0.58 *	0.24	2.39	0.04	-3.65	0.67 *	0.27	2.53	0.04
Gen. Wood nesters	40	P	-3,89	0.55 *	0.22	2.57	0.04	-2,72	0.55 *	0.24	2.32	0.03
Families												
Formicidae	29	P	-2.08	0.49 *	0.23	2.15	0.03	-1.54	-	-	-	-
Pamphiliidae	9	P	-4.51	2.00 **	0.69	2.89	0.12	-7.45	2.58 **	0.79	3.29	0.17

Figures

Figure 1

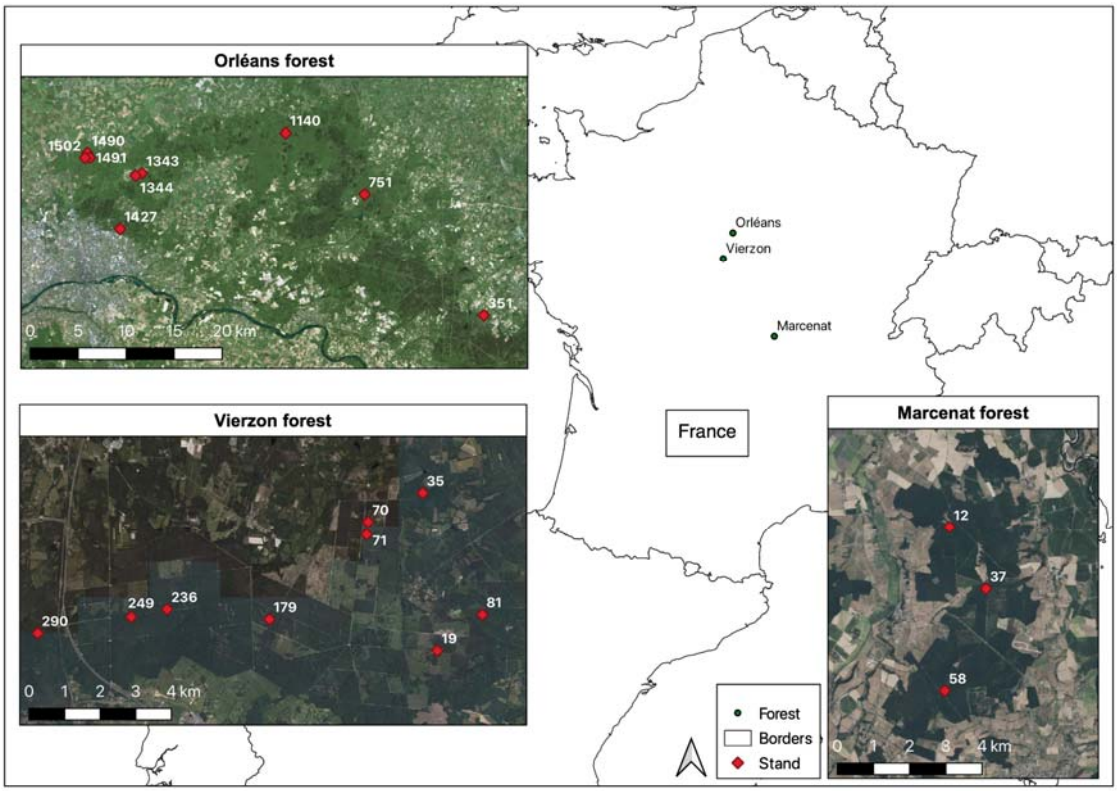

Figure 1. Map of France showing the location of the three oak forests studied, and the 21 stands sampled. Details on the stands can be found in Tab. S1.

Figure 2

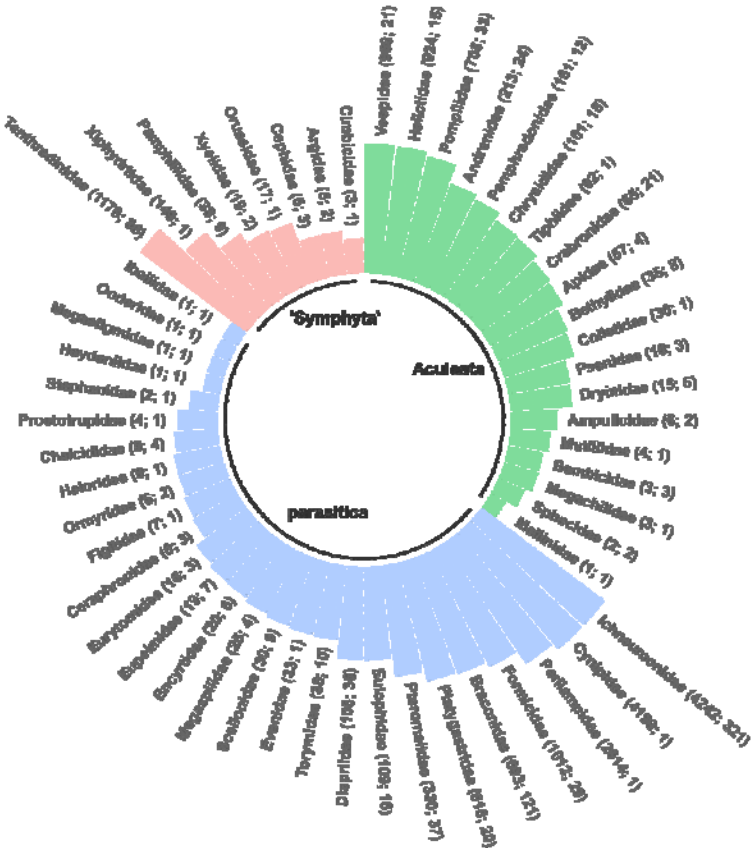

Figure 2. Overview of the abundances (log-transformed) of the Hymenoptera families sampled in oak canopies. Families are arranged in three taxonomic groups: “Symphyta”, Apocrita Aculeata and Apocrita parasitica. Numbers between brackets indicate the number of individuals and the number of taxa identified for each family.

Figure 3

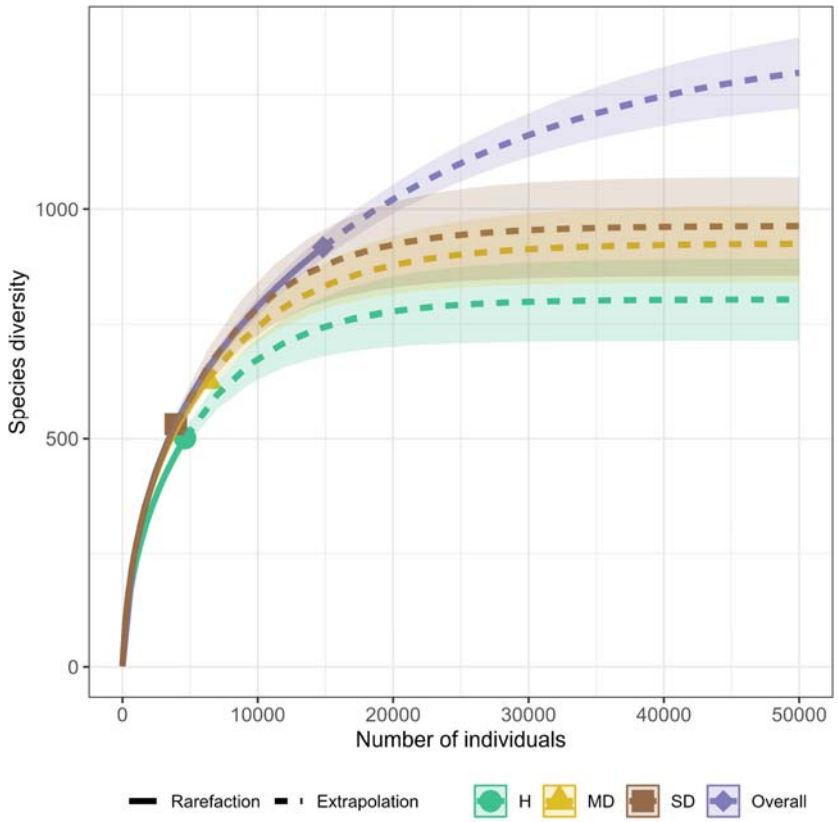

Figure 3. Rarefaction curves for canopy-dwelling Hymenoptera from the three forests, 21 stands and 42 plots. H = healthy stands, MD = moderately declining stands, SD = severely declining stands, Overall = all stands. See main text for details on stand decline categories.

Figure 4

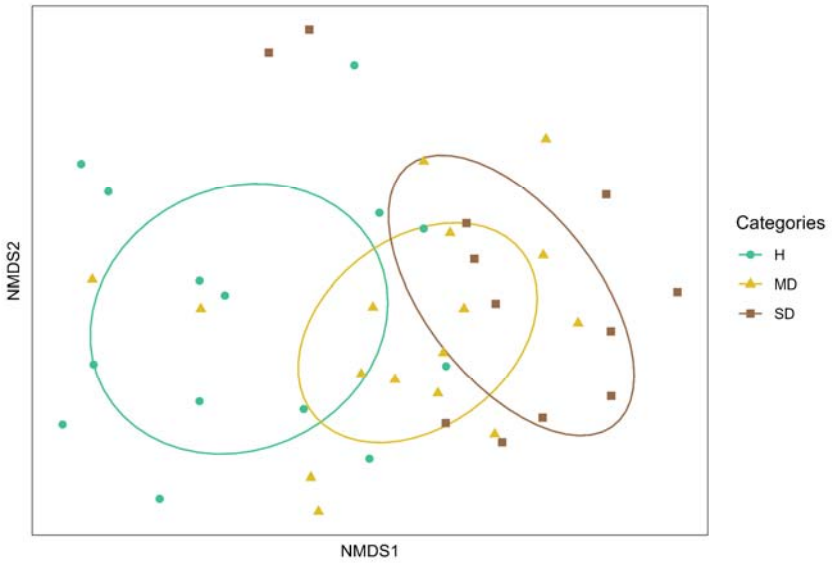

Figure 4. NMDS ordination (k=3, stress=0.18) of species composition per plot, grouped by stand decline category. H = healthy stands, MD = moderately declining stands, SD = severely declining stands. Species with fewer than 10 individuals were removed from the analysis. See main text for details on stand decline categories.

Figure 5

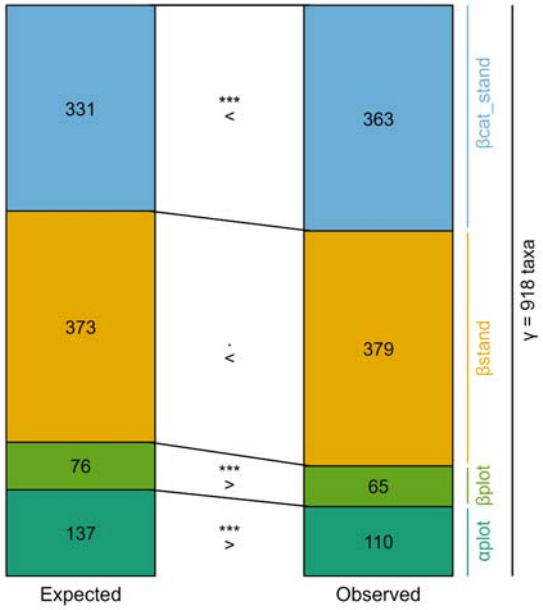

Figure 5. Global additive partitioning of species richness of the canopy-dwelling Hymenoptera in the three oak forests, at plot and stand scales. Four levels are represented: α plot (within plot), β plot (among plots), β stand (among stands) and β cat_stand (among levels of stand decline). Significance levels correspond to the difference between expected and observed values, with ***: $p < 0.001$; . : $p < 0.1$.

Figure 6

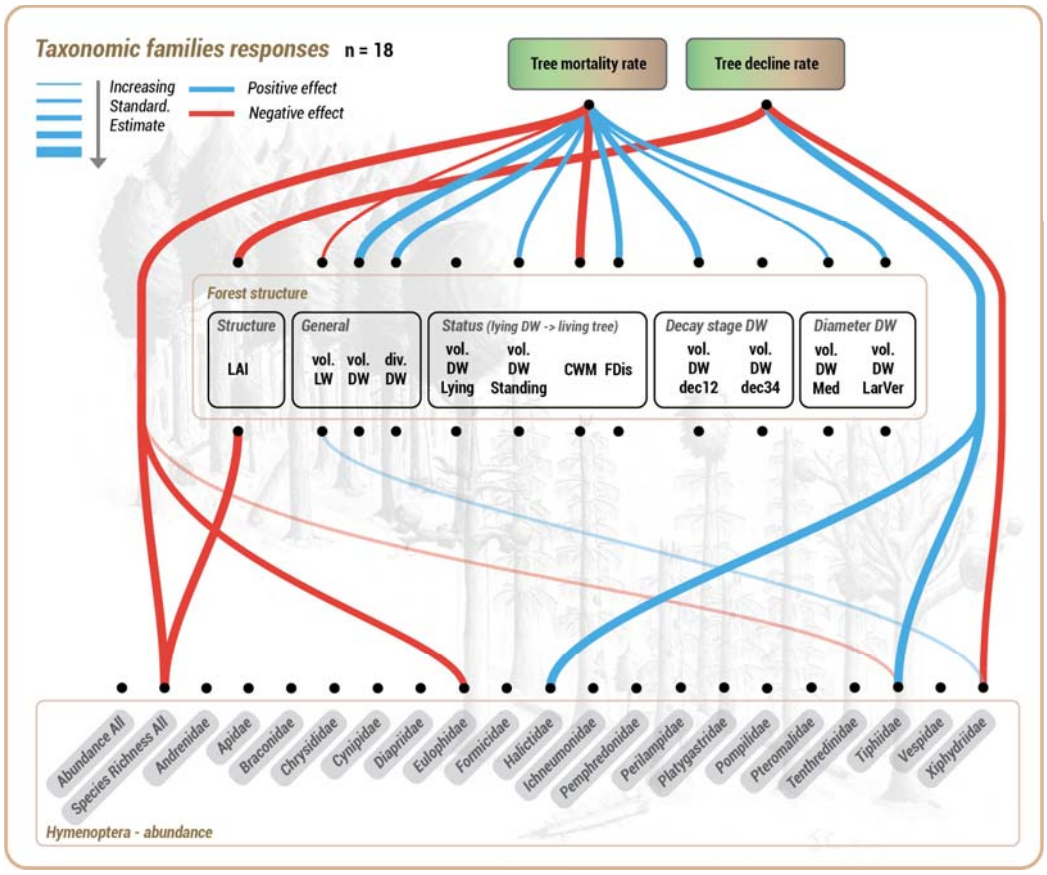

Figure 6. Results of the Structural Equation Modelling (SEM) for the effects of oak decline on the abundance of the main Hymenoptera taxonomic families through changes in forest structure. Since we tested 14 predictors, we used 0.0036 as the p.value (0.05/14). The transparent lines had a p.value below 0.05 but above 0.0036 and help to explain the response variables in the multiple regression models. LAI: leaf area index, vol.: volume, DW: deadwood, LW: living wood, CWM: community-weighted mean trait value, FDis: functional diversity, Med: medium-sized, LarVer: large and very large, dec12: low level of decay, dec34: high level of decay.

Figure 7

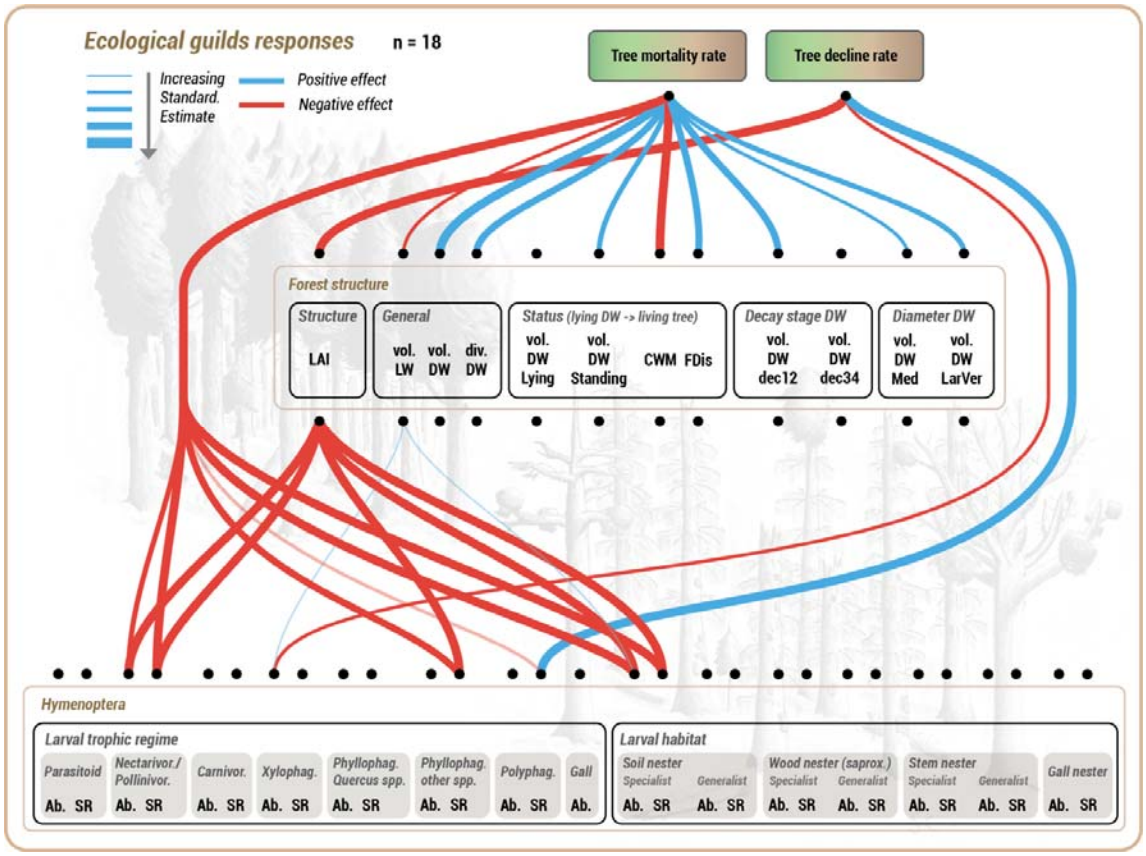

Figure 7. Results of the Structural Equation Modelling (SEM) for the effects of oak decline on Hymenoptera ecological guilds through changes in forest structure. Since we tested 14 predictors, we used 0.0036 as the p.value (0.05/14). See the caption for Figure 6 for complementary information.

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