

1 **Forest decline differentially affects trophic guilds of canopy-dwelling beetles**

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3 Aurélien Sallé¹, Guilhem Parmain², Benoît Nusillard², Xavier Pineau¹, Ravène Brousse¹,
4 Tiphane Fontaine-Guenel^{1,2}, Romain Ledet², Cécile Vincent-Barbaroux¹, Christophe Bouget²

5
6 ¹ Laboratoire de Biologie des Ligneux et des Grandes Cultures, INRAE, Université d'Orléans,
7 45067, Orléans, France

8 ² INRAE, UR EFNO, Domaine des Barres, Nogent-sur-Vernisson, France

9

10 * both authors contributed equally to this work

11

12 **Email addresses**

13 aurelien.salle@univ-orleans.fr

14 guilhem.parmain@inrae.fr

15 benoit.nusillard@irstea.fr

16 xavier.pineau@univ-orleans.fr

17 ravene.brousse@etu.univ-orleans.fr

18 tiphane.fontaine@etu.univ-orleans.fr

19 romain.ledet@etu.univ-orleans.fr

20 cecile.barbaroux@univ-orleans.fr

21 christophe.bouget2@inrae.fr

22

23 **Short title**

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25

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28

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32 Vincent-Barbaroux; Writing – original draft: A. Sallé & C. Bouget; Writing – review & editing: A.
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48

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50 The datasets generated during and/or analyzed during the current study are not publicly
51 available due to further analyses on the data but are available from the corresponding author on
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53

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55 The authors declare that they have no conflict of interest.

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69 **Forest decline differentially affects trophic guilds of canopy-dwelling beetles**

70

71 **Key message**

72 Decline can affect the structure, resources and microclimates of the forest canopy, and
73 potentially have cascading effects on canopy-dwelling species. Our survey shows that an oak
74 decline can promote saproxylic beetles, especially xylophagous ones, and generalist
75 phyllophagous weevils. However, it negatively affects specialist phyllophagous species and has
76 no effect on seminiphagous weevils.

77

78 **Keywords:** *Agrilus*, *Quercus*, saproxylic beetles, phyllophagous beetles, seminiphagous beetles

79

80 **Abstract**

81 **Context**

82 Decline in a context of climate change is expected to induce considerable changes in forest
83 structure, potentially affecting habitat opportunities and trophic resources for numerous species.
84 Nonetheless, the consequences of decline on forest biodiversity have rarely been studied.

85 **Aim**

86 We aimed to characterize the impact of oak decline on different guilds of canopy-dwelling
87 beetles.

88 **Methods**

89 Beetles were sampled for three consecutive years in oak stands exhibiting different levels of
90 decline. Several guilds were considered: (i) Buprestidae, (ii) other saproxylic beetles split into
91 wood-boring species and non-wood-boring species, (iii) seed-eating weevils, and (iv) specialist
92 and generalist leaf-eating weevils.

93 **Results**

94 Overall, decline had positive effects on the abundance and biomass of beetles, though
95 contrasting variations were observed at the species or guild levels. Xylophagous species,
96 especially the main oak-associated buprestids, and other saproxylic species benefitted from
97 decline conditions. However, at odds with the insect performance hypothesis, decline had a
98 positive effect on generalist phyllophagous species, a negative effect on specialist
99 phyllophagous species, and a null effect on seminiphagous species.

100 **Conclusion**

101 The increase in species richness for saproxylic and phyllophagous beetle communities suggests
102 that decline might promote forest biodiversity. Our results call for further studies to thoroughly
103 assess the functional outcomes of forest decline, and to suggest management strategies for
104 conservation biologists.

105

106 **Introduction**

107
108 Global change can dramatically affect the organization and functioning of forest ecosystems by
109 promoting the introduction and establishment of invasive species (Liebhold et al. 2017), by
110 intensifying land-use at the landscape level (Seibold et al. 2019), and through the direct and
111 indirect effects of climate change on forest health (Seidl et al. 2017). Climate change already
112 challenges the ability of European forests to adapt (Allen et al. 2010; Carnicer et al. 2011), and
113 unprecedented forest declines are expected in response to the predicted increase in frequency
114 and severity of droughts and heat waves (Allen et al. 2010; IPCC 2013).

115 Forest decline generally consists in a progressive loss of vigor of the trees, over several years,
116 in response to multiple, successive or concomitant driving factors (Manion 1981). These factors
117 include i) predisposing factors such as site conditions that constantly affect the stands, ii) inciting
118 factors such as defoliation or droughts that trigger declines, and iii) contributing factors such as
119 secondary pests and pathogens, which aggravate the deleterious effects of inciting factors,
120 ultimately killing trees (Sinclair 1967; Manion 1981; Thomas et al. 2002; Sallé et al. 2014). The
121 gradual loss of tree vigor progressively affects all forest compartments but the canopy is
122 certainly the first to exhibit conspicuous modifications as decline progresses. The crown of a
123 declining tree is characterized by an accumulation of dead branches, cavities and fruiting bodies
124 of saprotrophic or pathogenic fungi (Houston 1981; Ishii et al. 2004). Therefore, a forest decline
125 generates novel structures and favors the accumulation uncommon ones for healthy trees, and
126 consequently tends to increase the structural complexity of the canopy at stand, tree and branch
127 scales (Ishii et al. 2004). Crowns of declining trees also exhibit reduced foliage density, which in
128 turn can considerably alter microclimates within and beneath the canopy (Houston 1981; Ishii et
129 al. 2004). Such profound structural modifications affect habitat opportunities and trophic
130 resources, with likely marked cascading effects on canopy-dwelling communities.

131

132 The tree canopy and the soil are the two key compartments supporting forest biodiversity and
133 their contribution is tremendous (Stork and Grimbacher 2006). Compared to tropical forests,
134 temperate forests have less vertical stratification and a more marked seasonality with leaf fall, so
135 temperate forest canopies probably shelter a lower proportion of specific taxa (Ulyshen 2011).
136 Canopy functional biodiversity in temperate forests has therefore received relatively little
137 attention to date (Ulyshen 2011). However, the studies conducted in temperate forests (e.g.
138 Bouget et al. 2011; Vodka and Cizek 2013; Plewa et al. 2017) have shown a clear vertical
139 stratification of insect assemblages, just as in tropical forests, with 20 – 40% of all forest insect
140 species strictly associated with canopies (Bouget et al. 2011). In addition to these specialist
141 species, many Arthropods also rely on the canopy for a part of their life cycle, for maturation
142 feeding and mating on foliage, such as *Agrilus* spp. for instance (Ulyshen 2011; Sallé et al.
143 2014). However, canopies are still relatively unknown biotic frontiers. These crown ecosystems
144 harbor poorly understood, rarely described (both in terms of composition and abundance) insect
145 communities (Bouget et al. 2011). They potentially shelter an underestimated pool of rare or
146 patrimonial species (Plewa et al. 2017), but also native and invasive pests.

147
148 Canopy modifications in response to decline may change resource availability and microclimates
149 and may create novel colonization opportunities, thus modulating in different ways the
150 community dynamics of canopy-dwelling insects, depending on their functional guilds. Changes
151 in foliage quality during plant stress may influence the performance of leaf feeders, but the
152 magnitude and orientation of the herbivore response likely depends on both stress intensity and
153 the feeding strategy of the herbivore (Larsson 1989; Herms and Mattson 1992). In addition, the
154 decrease in the number of living branches in the canopy of declining trees may also negatively
155 affect leaf-, seed-, and flower-feeding species (Martel and Mauffette 1997). A survey of
156 Lepidopteran communities in declining maple stands indicated that exposed caterpillars became
157 more abundant while the density of semi-concealed or endophagous species decreased (Martel

158 and Mauffette 1997). This suggests that phyllophagous or seminiphagous insects with an
159 intimate relationship with their host-tree, like specialist species with an endophytic larval
160 development, may be negatively affected by the decrease in foliage quantity or quality and/or the
161 change in microclimate, while these modifications might promote generalist species (Martel and
162 Mauffette, 1997). Conversely, saproxylic beetles are likely to show a marked positive response
163 to forest decline, both in terms of abundance and species richness. Saproxylic beetles form a
164 functional guild associated with dead and decaying wood, related microhabitats, and other
165 saproxylic taxa (Stokland et al. 2012). This guild also includes xylophagous species developing
166 on weakened trees and acting as secondary pests, like the buprestids (Coleoptera:
167 Buprestidae), which are contributing agents during declines (Sallé et al., 2014; Tiberi et al.
168 2016). The weakened trees and the accumulation of dead wood and related microhabitats
169 typical of declining stands should promote the abundance and diversity of this functional guild.

170
171 Our investigation focused on oak forests, which have at least two relevant characteristics for our
172 study purpose. First, oak forests have regularly undergone periods of decline throughout Europe
173 during the last centuries (e.g. Delatour, 1983; Oszako, 2000; Thomas et al., 2002; Sonesson
174 and Drobyshev, 2010; Denman et al., 2014). Moreover, the frequency and intensity of declines
175 have recently increased, and extended canopy modifications have already been documented in
176 Mediterranean oak forests (Allen et al. 2010; Carnicer et al. 2011; Millar and Stephenson 2015).
177 Second, oak forests host a species-rich insect fauna (Southwood 1961). We sampled the
178 communities of leaf-dwelling weevils (Coleoptera: Curculionidae) and saproxylic beetles for
179 three consecutive years in oak stands exhibiting different levels of tree decline.

180 Firstly, we hypothesized that saproxylic beetles, especially xylophagous species, would be
181 favored by decline. Secondly, we expected to find contrasted responses to decline intensity for
182 leaf-feeding weevils, dependent on their relationship with the host plant. More specifically, we
183 hypothesized that weevils with endophytic larvae would be negatively affected by decline while

184 species feeding on foliage only during the adult stage would be favored. Finally, we
185 hypothesized that seminiphagous weevils would be negatively affected by the reduced amount
186 of acorns in declining stands. Consequently, our objectives were (i) to describe the canopy-
187 dwelling communities of buprestid beetles, other saproxylic species and weevils, and (ii) to
188 evaluate how the local intensity of forest decline was modifying the diversity of these
189 communities.

190

191 **Material and methods**

192

193 **Study area**

194 The study was conducted in the two adjacent state forests of Vierzon and Vouzeron, with a
195 surface area of 5,300 ha and 2,200 ha respectively, located in the center of France 200 km
196 south of Paris (47° 26' 89" N, 02° 10' 74" E). The Vierzon forest is dominated by oaks (mostly
197 *Quercus petraea* and *Quercus robur*), at 70%, and conifers (mostly *Pinus sylvestris* and *Pinus*
198 *nigra*), at 30%, in both pure and mixed stands. The Vouzeron forest is dominated by conifers
199 (mostly *Pinus sylvestris* and *Pinus nigra*), at 65%, in pure stands or mixed with *Q. robur* and *Q.*
200 *petraea*. The oaks, especially *Q. robur*, in the Vierzon forest have suffered from regular declines
201 (documented in 1920, 1940 and 1982 (Douzon 2006)). The last severe oak decline occurred
202 between 2000 and 2010, which was followed by a sanitation cutting of 100,000 m³ of oak over
203 1000 ha (Douzon, 2006). Several factors were implicated in these successive periods of decline.
204 The prominent predisposing factor was edaphic. In most areas the water table is shallow and
205 variable, and therefore inadequate for the development *Q. robur*, which was however extensively
206 planted in this forest (Douzon 2006; Marçais and Desprez-Loustau 2014). The prominent inciting
207 factors were severe droughts and defoliation caused by powdery mildew (Douzon, 2006;
208 Marçais and Desprez-Loustau 2014). Finally, the most frequently observed contributing biotic

209 agents were *Agrilus biguttatus* Fabricius and *Armillaria mellea* (Vahl ex Fr.) P. Kumm. (Douzon
210 2006).

211

212 **Site selection and characterization**

213 Overall, 14 stands dominated by mature oaks were monitored during our study in the two forests
214 (table 1). In 2016, 13 plots were set up in 11 stands (table 1). Plots were homogeneous areas
215 (approx. 2,000 m²) within stands in terms of tree composition and dendrometric parameters.
216 Most plots were located in different stands (table 1). They were located at a minimum of 100 m
217 from the others, but in most cases several kilometers from each other. In 2017 and 2018, 12
218 plots located in 11 stands were selected in the two forests (table 1). Some of the original plots
219 were changed in 2018 because the stands had been either cleared or harvested selectively
220 (table 1). We selected one tree at the center of each plot, on which we suspended one trap for
221 beetle collection (see below “Beetle sampling”).

222 The level of decline was evaluated yearly, during winter, at two embedded spatial scales. (i) At
223 the tree scale: individual decline status was assessed for all bearing-trap trees. (ii) At the plot
224 scale: decline status was assessed for trees surrounding the bearing-trap tree, which
225 encompassed only the five closest oak trees in 2016 and 2017, and all the oaks located within a
226 radius of 20 m around the bearing-trap tree in 2018. Decline level was evaluated following the
227 protocol designed by the French Forest Health Service (Département de la Santé des Forêts,
228 DSF) (Nageleisen 2005). In brief, crown transparency, the proportion of branches without
229 leaves, the proportion of dead branches and leaf distribution in the canopy were evaluated.
230 Based on these criteria, each tree was given a decline index ranging from 0 (no decline) to 5
231 (dead tree) (table 2). Trees with an index value equal to or below two were considered healthy.
232 Trees with an index value equal to or above three were considered in decline. For the plot scale,
233 the proportion of declining trees (with a decline index equal to or above three) was calculated,
234 following a routine DSF procedure (table 2).

235

236 **Beetle sampling**

237 **Optimization of the sampling protocol**

238 We used multi-funnel traps (Lindgren traps, Chemtica Internacional, San Jose, Costa Rica),
239 each with 12 fluon-coated funnels, to collect the insects. To optimize our protocol for sampling
240 canopy-dwelling beetles, we tested two trap heights and two trap colors. In 2016, we assessed
241 whether trap height significantly affected the composition or relative abundance of the captured
242 species. To do so, we suspended two green traps at different heights in the same tree, one
243 approximately 15 m from the ground and the other 10 m from the ground. Thirteen pairs of traps
244 were considered.

245 In 2017 and 2018, we also compared the trapping efficiency of green and purple multi-funnel
246 traps. Green multi-funnel traps have successfully captured a wide array of buprestid species in
247 North America and Europe (Petrice and Haack 2015; Rassati et al. 2019), but Brown et al.
248 (2017) showed that some European *Agrilus* species might be more attracted to purple than to
249 green. In ten trees, one green and one purple trap were both suspended roughly 15 m above the
250 ground.

251 **Routine sampling protocol**

252 For the sake of consistency, and because it was the best sampling design (see “Results), only
253 green multi-funnel traps, suspended at 15 m from the ground (i.e., among the lower branches of
254 the canopy) were considered to assess the effect of decline on canopy-dwelling beetles. One
255 trap was set up within each monitored plot. The collectors were filled with a 50% (v/v)
256 monopropylene glycol solution diluted with water, and a drop of detergent. No lure was added to
257 the traps. The traps were emptied every month and the captured species were recorded. In
258 2016, the traps were installed in June and collection continued until September. In 2017, the
259 traps were installed in April and collection continued until October. In 2018, the traps were
260 installed in April and collection continued until September.

261

262 **Beetle identification and ecological trait assignment**

263 Three beetle groups were considered for analysis: (i) oak-associated buprestid beetles, i.e.
264 xylophagous species specifically attracted by green Lindgren traps; (ii) other saproxylic beetles,
265 excluding “tourist” species associated to conifer tree species, split into two feeding guilds, i.e. the
266 xylophagous species guild (incl. xylophagous *sensu stricto* and saproxylophagous species) and
267 the non-xylophagous species guild (incl. saprophagous, zoophagous, mycetophagous species);
268 and (iii) oak-associated phytophagous weevils, which were split into two feeding guilds, i.e. the
269 leaf-eating (phylophagous, i.e. folivore) species guild and the seed- and fruit-eating
270 (seminiphagous, i.e. acorn borers) species guild. In the phylophagous guild, we considered
271 species whose adults feed on oak leaves (mainly leaf chewers) as generalist species, and
272 species whose both larvae and adults feed on oak leaves (larvae dwelling in foliar tissues) as
273 specialist species.

274 Certain saproxylic families were removed from the data set (Latridiidae, Leiodidae, Malachiidae,
275 Cantharidae, Corylophidae, Cryptophagidae, Ptiliidae, Staphylinidae), because they are often
276 difficult to identify at the species level and due to the lack of specialists able to check species
277 identifications. The French Frisbee database was used as the reference list of feeding guilds for
278 saproxylic beetle species from the 39 recorded beetle families (Bouget et al. 2019). Most of the
279 beetle specimens were identified by several of the authors (GP, BN, XP, RB, TFG and RL). The
280 remaining families were identified by specialists, as mentioned in the Acknowledgements. For
281 each guild, we computed number of species (richness), number of individuals (abundance) and
282 beetle biomass caught at the trap level and cumulated over all the sampling season per year.
283 Biomass, actually dry weight (in mg), was assessed through the following formula: Biomass =
284 $3.269 + L^{2.463}$, where “L” is the body length in millimeters (Ganihar 1997 in Seibold et al. 2019).
285 The abundance of several dominant species of oak-associated buprestids and phytophagous
286 weevils was also analyzed.

287

288 **Data analysis**

289 All analyses were performed in R, version 3.5.1 (R Core Team 2018). Trap color and trap height
290 effects on catches of buprestids, other saproxylic beetles and phytophagous weevils were
291 assessed with Wilcoxon signed-ranked tests. To analyze the effect of the decline level at tree
292 scale on cumulative number of detected species, we rarefied species richness to the same
293 sample size (interpolated rarefaction sampling without replacement; `specaccum` function, `vegan`
294 R-package). To rank the effect of decline level at tree or plot scale on variations in average
295 univariate metrics (mean values per trap of guild richness, species abundance, guild abundance,
296 guild biomass), we used the differences in the Akaike information criterion (AICc) scores to
297 compare the fit between the generalized linear mixed models including separately each of the
298 two explanatory variables and their fit with the null model. To assess the significance of the
299 estimates of the best decline features for each response variable, the error structure of the
300 generalized linear mixed-effects models was adjusted to better fit the data. To do so, `glmm` were
301 fitted for the negative binomial family, the Gaussian family, the log-normal family (i.e. log-
302 transformed response), and the Poisson family (functions `glmer.nb`, `glmer`, `lmer`, `lme4` R-
303 package). To account for repeated measures and configuration of sampling design, plot and
304 year were added as nested random effects on the intercept in mixed models. To rank the effect
305 of decline level at tree or tree-group scale on variations in species composition (including
306 singletons), we performed a Canonical Analysis of Principal coordinates (function `capscale`,
307 `vegan` R-package, CAP, Anderson and Willis 2003). Based on Bray-Curtis distance matrices, we
308 carried out inertia partitioning on all the explanatory environmental variables, as collinearity
309 among predictor variables is not a problem in CAP. We calculated total constrained inertia, the
310 total inertia explained by each variable, the latter's statistical significance (permutation tests –
311 100 runs) and the relative individual contribution of each variable to constrained inertia.

312 We used the IndVal method to identify beetle species indicating tree decline level (healthy vs.
313 declining) (Dufrêne and Legendre 1997, indicpecies R-package). This method calculates the
314 association value (IndVal index) between the species and a group of sites, based on between-
315 group variations in occurrence (fidelity) and abundance (specificity), and then tests the statistical
316 significance of this relationship with a permutation test. P-values were corrected for multiple
317 testing. Only species shown to be significant in the permutation test with an indicator value
318 above 25%, occurring in more than 10% of the samples and with more than 10 individuals
319 sampled were considered here.

320

321 **Results**

322 For all guilds, the number of individuals captured was higher in the upper traps (Fig. 1). For both
323 guilds of leaf-dwelling species (i.e. Agrilinae and phytophagous weevils), green traps were
324 markedly more attractive than purple traps, while no difference between traps was detected for
325 the other saproxylic species (Fig. 2).

326

327 Overall, for the assessment of decline effects on canopy-dwelling beetles, the compiled data set
328 of 27,627 individual specimens included 266 beetle species: 10,440 individuals and ten species
329 of oak-associated buprestid beetles; 8,280 individuals and 21 species of oak-associated
330 phytophagous weevils (4 seminiphagous, 10 specialist phyllophagous, 5 generalist
331 phyllophagous and 2 flower-eating (anthophagous) species); 3,008 individuals and 102 species
332 of non-xylophagous saproxylic beetles; and 5,899 individuals and 133 species of xylophagous
333 saproxylic beetles (table S1). This corresponds to 14,490 individuals and 223 beetle species
334 found in the 23 traps hanging from non- or slightly-declining trees, and 13,137 individuals and
335 194 species found in the 14 traps hanging from declining trees. On the whole, cumulative
336 species-richness estimates at a standardized sample size did not display any significant contrast

337 between decline levels at the tree scale, either for the whole beetle community, or for individual
338 guilds (Fig. S1).

339

340 We detected many significant effects of decline level on guild metrics (mean abundance,
341 biomass and richness per trap) and on species mean abundances (table 3). Most of these
342 effects were positive, except, at the plot scale, for (i) a negative effect of decline level on the
343 mean abundance of xylophagous beetles (table 3 and Fig. 3), and (ii) a negative effect of decline
344 level on the mean abundance of two specialist phyllophagous species, i.e. *Archarius*
345 *pyrrhoceras* Marsham and *Orchestes quercus* L. (table 3). We measured significant positive
346 effects of decline level at the tree scale on the species richness of xylophagous beetles (Fig. 3)
347 and on the biomass and abundance of buprestids (Fig. 4); and at plot scale, on the biomass of
348 non-xylophagous saproxylic beetles (Fig. 3), on species richness of buprestids (Fig. 4) and
349 phyllophagous weevils (Fig. 5), and on the abundance of generalist phyllophagous weevils (Fig.
350 5). Five of the six buprestid species tested responded positively in abundance to decline
351 intensity (at tree scale: *Agrilus angustulus* Illiger, *A. biguttatus*, *Agrilus laticornis* Illiger, *Agrilus*
352 *obscuricollis* Kiesenwetter, *Agrilus sulcicollis* Lacordaire; and at the plot scale: *Coraeus*
353 *undatus* Fabricius), as well as one of the two tested generalist phyllophagous weevil (*Phyllobius*
354 *pyri* L.) (table 3). Seminiphagous species were not significantly affected by decline level at any
355 scale, either at species or guild level (table 3, Fig. 5). Specialist phyllophagous weevils
356 responded to decline intensity at the species level but not at the guild level (table 3, Fig. 5).
357 When all the sampled species were pooled, we also observed significant positive effects of
358 decline at the tree scale on the biomass and abundance of all beetles (table 3, Fig. 6).

359 From CAP analyses, we estimated low but significant contributions of decline level to variations
360 in the community composition of most of the beetle groups, i.e. phytophagous weevils,
361 buprestids and xylophagous saproxylic, though not for the non-xylophagous saproxylic guild
362 (table 4). Significant effects on community composition were mainly related to decline level at

363 the plot scale, except for xylophagous saproxylic beetles, which were affected at the tree scale.

364 A larger portion of inertia was explained by sampling year.

365
366 The IndVal analysis detected 15 characteristic species in declining trees, and only one in healthy
367 trees (table 5). The group of species associated with declining trees consisted primarily of
368 xylophagous species, including four species of *Agrilus*, five other xylophagous beetle species,
369 and two saproxylophagous species.

370

371 **Discussion**

372

373 Oak decline affected the communities of the canopy-dwelling beetles considered in our study
374 differently depending on their feeding guild and/or host specialization. As predicted, the
375 abundance, biomass, and species richness of oak-associated buprestids increased with the
376 decline severity. The abundance of most major Agrilinae species followed a similar pattern.
377 Consequently, most species contributed to this overall increase. Agrilinae preferentially colonize
378 weakened hosts (e.g. Moraal and Hilszczanski 2000; Jennings et al. 2014; Petrice and Haack
379 2014; Poole et al. 2019). Their abundance is positively influenced by the availability of fresh
380 snags and coarse woody debris in the environment (Redilla and McCullough 2017), and
381 damaged trees (Brück-Dyckhoff et al. 2019); these features typically occur in declining stands.
382 Several of the species collected, namely *A. biguttatus*, *A. sulcicollis*, *A. angustulus*, and *C.*
383 *undatus*, can act as major contributing agents during oak declines (Sallé et al. 2014).
384 Consequently, they may also have exerted a positive feedback by further weakening their host
385 trees, thus contributing to the accumulation of favorable breeding material. Interestingly, three of
386 the four, *A. biguttatus*, *A. sulcicollis* and *A. angustulus*, were also good indicators of declining
387 trees, together with *Scolytus intricatus* Ratzeburg and *Gasterocercus depressirostris* Fabricius,
388 other contributing agents of oak decline (Saintonge and Nageleisen 2001; Sallé et al. 2014).

389 However, while the species richness of other xylophagous species also increased in declining
390 stands, their abundance slightly decreased. This might reflect increased competition among
391 xylophagous species in declining stands. However, the variation in abundance of these other
392 xylophagous beetles should be considered with caution since it was mostly driven by variations
393 in the abundance of *Anisandrus dispar* Fabricius. The abundance of this generalist ambrosia
394 beetle might have been loosely connected to oak decline level. The increased availability of
395 resources and habitats in declining stands, especially large woody debris, probably also
396 participated in the observed increase in the biomass of non-xylophagous saproxylic beetles,
397 since the size of saproxylic species tends to increase with the diameter of the available
398 deadwood resources (Brin et al. 2011).

399 Feeding guilds of phytophagous weevils responded differently to decline severity. The
400 abundance of generalist phyllophagous species, especially *P. pyri*, increased with decline
401 intensity, while the abundance of the two main specialist phyllophagous species, i.e. *O. quercus*
402 and *A. pyrrhoceras*, decreased. These variations support our hypotheses and are congruent with
403 previous observations by Martel and Mauffette (1997) for Lepidopteran communities colonizing
404 maple foliage. They are nonetheless inconsistent with predictions from the insect performance
405 hypothesis by Larsson (1989) concerning the response of folivores with various feeding habits to
406 tree stress. Several factors may have affected the abundance of phyllophagous weevils
407 differently. Environmental constraints can have contrasted effects on both biochemical and
408 morphological leaf traits (Günthardt-Goerg et al. 2013; Hu et al. 2013). Likewise, the greater
409 exposure of leaves in the opened canopies of declining oaks can alter their phytochemical
410 profile, and may have increased their content in phenolic compounds (Yamasaki and Kikuzawa
411 2003; Lämke and Unsicker 2018). Such modifications may in turn have different impacts on
412 phytophagous insects depending on their feeding guild and specialization (e.g. Gutbrodt et al.
413 2011; Forkner et al. 2014). In addition to modifying trophic resources or habitats, crown thinning
414 during a decline can also directly impact larval development by altering the thermal buffering

415 provided by the canopy (Martel and Mauffette 1997; Hardwick et al. 2015; De Frenne et al.
416 2019). Greater leaf exposure will affect leaf microclimate and may have detrimental effects on
417 endophytic larvae (e.g. Pincebourde et al. 2007), like those of *O. quercus* or *A. pyrrhoceras*.
418 Canopy thinning can also affect forest soil microclimates (De Frenne et al. 2013), allowing free-
419 living larvae like those of *P. pyri* to find optimal microclimatic conditions more easily. Finally,
420 greater leaf exposure may also lead to greater predation pressure on leaf-dwelling endophytic
421 larvae (e.g. Tschanz et al. 2005), which would further explain why specialist phyllophagous
422 weevils with endophytic larvae were negatively affected by oak decline. Overall, the negative
423 response of specialist phyllophagous species to decline may relate to a decrease in leaf
424 suitability (phytochemical profile and microclimatic conditions), an increase in predation pressure
425 or reduced food availability (fewer leaves) (Gely et al. 2019). Conversely, the positive response
426 of generalist phyllophagous species to decline severity could stem from a decrease in
427 interspecific competition with decreasing populations of specialist species (Kaplan and Denno
428 2007), and from improved conditions for larval development. For seminiphagous weevils, no
429 effect of decline was detected, suggesting either that acorn quantity or quality was not markedly
430 affected by oak decline or that the modifications were not significant enough to impact the
431 species considered.

432 We considered decline level at two spatial scales: the tree and the plot. Overall, we observed
433 significant responses mainly at the tree scale for xylophagous beetles, including oak-associated
434 buprestids, and mainly at the plot scale for phytophagous and non-xylophagous saproxylic
435 beetles. This might reflect differences among guilds in their dispersal capacity and host-selection
436 behavior. For instance, some xylophagous species might have emerged from the declining trees
437 carrying traps or might have been visually and/or chemically attracted by these declining trees,
438 since weakened hosts often attract secondary pests (e.g., Haack and Benjamin 1982). More
439 specifically host volatiles such as terpenes or ethanol emitted by weakened trees can be used

440 by these insects to discriminate suitable hosts (e.g., Montgomery and Vargo 1983; Sanchez-
441 Osorio et al. 2019).

442
443 For all the communities we monitored, further experiments would be necessary to identify the
444 main drivers of the variations observed. More specifically, the effect of decline on the abundance
445 of microhabitats and resources such as dead wood, cavities, opportunistic fungi, and acorns
446 should be quantified (Heitzman et al. 2007; Spetich 2007). Likewise, changes in microclimates
447 and predation pressure at the canopy and soil levels during a decline should be characterized. In
448 addition, in our study we were not able to take into account decline dynamics, since historical
449 data on decline onset, duration and intensity at the stand scale was lacking. We considered
450 stands exhibiting different decline levels, which may result from disturbances with different
451 frequency, severity and/or spatial and temporal extents at the stand scale. Past disturbance
452 regimes can modulate the current taxonomic, functional and phylogenetic composition forest
453 communities, notably the community of saproxylic beetles (Kozak et al. 2020). Therefore
454 integrating historical data in future studies would help to disentangle current decline effects from
455 past disturbance legacies.

456
457 Changes in species richness and abundance led to significant community modifications for both
458 xylophagous beetles and phytophagous weevils, which in turn contributed to a significant
459 modification of the overall beetle community. From a functional standpoint, this type of
460 modification may modulate important processes in forest ecosystems, since saproxylic insects
461 play a significant role in wood decomposition and the nitrogen cycle (Ulyshen 2015). In addition,
462 saproxylic and leaf-dwelling beetles can be important prey for insectivorous vertebrates (e.g.
463 Tillon et al. 2016; Koenig and Liebhold 2017), and changes in beetle community composition
464 may therefore have cascading effects on the food web (e.g. Koenig and Liebhold 2017). From a
465 conservation standpoint, the increase in species richness for the xylophagous and

466 phyllophagous beetle communities suggests that declining stands might enhance forest
467 biodiversity. Decline especially promoted saproxylic species. This community is particularly
468 sensitive to the intensification of management practices involving the extraction of weakened or
469 decaying wood material, and consequently includes several rare and protected species (Grove
470 2002; Seibold et al. 2015). The accumulation of suitable habitats and resources for this
471 community in declining stands may then counterbalance the adverse effects of intensive
472 management. The increase in abundance and/or biomass of xylophagous and phyllophagous
473 beetles also resulted in an overall increase in beetle abundance and biomass in the declining
474 stands. This also suggests that forest decline may mitigate the reduction in insect biomass
475 recently reported in European forests, in intensively managed landscapes (Seibold et al. 2019),
476 at least if the increase in resources and structural complexity persists over time (Winter et al.
477 2015). In this regard, increases in species richness, abundance and biomass of xylophagous
478 species at the stand scale, as in our study, might prove to be ephemeral (Winter et al. 2015).

479 In our forests, in the CAP sampling year explained a greater percentage of inertia than did
480 decline level for all guilds considered. This strong year effect could result from high inter-annual
481 variations in beetle abundance and/or occurrence, but may also incorporate multiple
482 methodological factors (i.e., (i) slight variations in sampling periods, (ii) changes in monitored
483 plots and (iii) modifications in the protocol of decline characterization at the plot level). Marked
484 variations in beetle abundance and biomass occurred on plots and at periods that were
485 consistently monitored throughout the three years of survey, and between years (i.e., 2016 and
486 2017) when the protocol of decline characterization was identical (data not shown). This rather
487 supports the hypothesis that the year effect mainly results from marked inter-annual variations in
488 beetle abundance and community composition. Such fluctuations in population and community
489 abundances are commonly observed in temperate forests (e.g. Stange et al. 2011). A longer
490 monitoring period on the same plots would be necessary to identify the factors contributing to the
491 between-year variations we observed.

492
493 Green Lindgren traps, placed at the canopy level, have proven to be effective in collecting leaf-
494 dwelling beetles. These traps were specifically designed to collect *Agrilus planipennis* Fairmaire
495 (Francese et al. 2011), but have also allowed researchers to collect North American and
496 European Agrilinae species (Petrice and Haack 2015; Rassati et al. 2019). During our survey, all
497 the Agrilinae species associated with oaks in France (i.e. *Agrilus* sp., *Coraebus* sp. and
498 *Meliboeus* sp.) were captured, except for *Agrilus grandiceps hemiphanes* Marseul, a rare
499 Mediterranean species, and *Coraebus florentinus* Herbst. The latter species had previously been
500 collected in the Vierzon forest, and typical shoot browning resulting from its larval activity has
501 already been reported there. The species might have been present but at too low population
502 density for detection, or it might not have been attracted by our traps. We also collected quite
503 diverse communities of phyllophagous and seminiphagous weevil species in our green Lindgren
504 traps, in large amounts for some species. These species were significantly more attracted to
505 green traps than to purple ones, which is congruent with the attraction to green substrates
506 reported for other phytophagous weevils (e.g. Cross et al. 1976; Gadi and Reddy 2014). Overall,
507 this suggests that green Lindgren traps are attractive to phyllobiont species in general, and
508 confirms the tool's utility when investigating canopy-dwelling beetles associated with foliage.

509
510 **Conclusion**
511 Our three-year survey in a declining forest allowed us to detect significant effects of decline on
512 different canopy-dwelling species and guilds, in spite of strong inter-annual variations and a
513 limited spatial extent, the survey being performed in two adjacent forests. Overall, decline had a
514 positive effect on the abundance and biomass of beetles, but contrasted variations were
515 observed at the species or guild levels, with positive effects for saproxylic and generalist
516 phyllophagous species, null effects for seminiphagous species and negative effects for specialist
517 phyllophagous species. These results call for studies conducted at larger spatial and temporal

518 scales to assess the functional outcomes of the unprecedented level of forest decline expected
519 to affect Europe, and to propose management strategies for conservation biologists.

520

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522

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707 Table 1: characteristics of the monitored oak stands

708

Stand ID	Latitude	Longitude	Mean \pm SE stand height (m)	Monitoring year	Composition	Mean \pm SE oak DBH (cm) ²	Oak density (n / ha) ³	Tree density (n / ha) ³	Total basal area (m ² / ha) ³
19	47.2579	2.1812	15 \pm 1	2018	Oak with a beech understorey	51.8 \pm 2.4	151	151	33
24	47.2681	2.1733	20 \pm 2	2016-2017	Pure oak	65.0 \pm 3.5	88	88	30
35-1	47.2980	2.1752	17 \pm 1	2016-2017-2018	Oak with scattered beech and Scots pine	54.2 \pm 3.4	111	207	47
35-2	47.2974	2.1743	17 \pm 1	2016-2017-2018	Oak with scattered beech and Scots pine	51.7 \pm 3.5	119	167	30
55	47.2567	2.1616	21 \pm 2	2016-2017-2018	Mixed stand of oak and beech	69.0 \pm 8.3	16	111	33
70	47.2886	2.1551	17 \pm 2	2016-2017-2018	Oak with scattered beech and Scots pine	47.1 \pm 5.0	64	119	21
71	47.2877	2.1536	15 \pm 1	2018	Oaks with scattered beech and Scots pine	39.7 \pm 3.7	119	223	26
81-1	47.2666	2.1967	23 \pm 2	2016	Oak with a hornbeam understorey	37.4 \pm 1.3	175	175	20
81-2	47.2672	2.1980	23 \pm 2	2016-2017-2018	Oak with a hornbeam understorey	37.4 \pm 1.3	175	175	20
133	47.2918	2.1434	18 \pm 2	2016-2017	Oak with scattered beech and Scots pine	75.0 \pm 2.6	56	80	28
161	47.2626	2.1243	22 \pm 1	2016-2017	Pure oak	64.6 \pm 5.6	80	88	31
179	47.2654	2.1189	19 \pm 2	2016-2017-2018	Pure oak	59.3 \pm 3.6	151	151	45
236	47.2675	2.0807	15 \pm 3	2016-2017-2018	Mixed stand of oak and beech	40.5 \pm 4.8	167	422	51
249	47.2656	2.0674	16 \pm 1	2018	Oak with scattered beech	48.2 \pm 1.3	199	223	38

290	47.26119	2.0328	16 ± 1	2016-2017-2018	Oak with scattered wild service trees	38.6 ± 1.7	183	207	24
299	47.2569	2.0257	21 ± 3	2016-2017-2018	Pure oak	47.8 ± 8.1	64	64	14

709 ¹Mean stand was measured on three trees, ²DBH was measured on all trees within a radius of 20 m around the tree carrying traps. ³Densities and total basal area were assessed
 710 through the inventory and measurement of all trees within a radius of 20 m around the tree carrying traps

711 Table 2: decline index of trees carrying traps and percentage of surrounding declining trees in
712 the monitored oak plots, for the three survey years
713

Stand ID	Decline index of trees with traps			Percentage of surrounding declining trees		
	2016	2017	2018	2016	2017	2018
19	NA	NA	3	NA	NA	89
24	4	3	NA	17	33	NA
35-1	2	1	1	17	0	19
35-2	0	1	1	17	33	14
55	3	3	3	83	67	100
70	3	3	3	83	71	100
71	NA	NA	3	NA	NA	87
81-1	1	1	1	17	17	14
81-2	2	NA	NA	0	NA	NA
133	3.5	2	NA	33	57	NA
161	2	2	NA	33	29	NA
179	2	4	2	17	57	61
236	3	3	3	33	33	45
249	NA	NA	3.5	NA	NA	60
290	2	2	2	33	14	43
299	3.5	2	2	50	57	50

714

715

716 Table 3: effect of decline on biomass, abundance and species richness for the different groups
717 and guilds of beetles, and on abundance for the main species collected in the canopy.

		Variable (mean value per trap)	Best ecological model	Delta[AICc] [°]	Effect of decline estimate	SE
Oak-associated buprestid beetles		biomass ⁽³⁾	Tree	-6	1.26 **	0.44
		abundance ⁽¹⁾	Tree	-5	1.38 **	0.48
		species richness ⁽⁴⁾	Plot	-2	0.14 *	0.06
		<i>Agrilus angustulus</i> ^{(3)°°}	Tree	-4	1.49 *	0.59
		<i>Agrilus biguttatus</i> ⁽¹⁾	Tree	-2	2.03 *	0.93
		<i>Agrilus hastulifer</i> ⁽¹⁾	Tree	0	1.84	1.05
		<i>Agrilus laticornis</i> ⁽¹⁾	Tree	-2	0.98 *	0.46
		<i>Agrilus obscuricollis</i> ⁽¹⁾	Tree	-2	1.87 *	0.93
		<i>Agrilus sulcicollis</i> ⁽¹⁾	Tree	-9	1.88 ***	0.51
		<i>Coraeus undatus</i> ⁽¹⁾	Plot	-7	0.94 ***	0.28
Saproxylic beetles (excl. buprestids)	Xylophagous	biomass ⁽³⁾	Tree	0	0.71	0.46
		abundance ⁽³⁾	Plot	-2	-0.39 *	0.16
		species richness ⁽¹⁾	Tree	-1	0.29 *	0.14
	Non-xylophagous	biomass ⁽³⁾	Plot	-3	0.31 **	0.10
		abundance ⁽¹⁾	Plot	+1	0.12	0.10
		species richness ⁽²⁾	Plot	0	3.41	1.84
All phytophagous	All phytophagous	biomass ⁽³⁾	Plot	0	0.19	0.12
		abundance ⁽³⁾	Tree	+2	0.10	0.10
		species richness ⁽²⁾	Plot	0	0.64	0.37
	All phyllophagous	biomass ⁽³⁾	Tree	-1	0.23	0.13
		abundance ⁽³⁾	Tree	+2	-0.10	0.26
		species richness ⁽³⁾	Plot	-3	0.10 *	0.04
Oak-associated weevils	Generalist phyllophagous	biomass ⁽³⁾	Plot	-1	0.59	0.32
		abundance ⁽³⁾	Plot	-5	0.77 **	0.23
		species richness ⁽³⁾	Tree	+5	0.04	0.12
		<i>Phyllobius pyri</i> ⁽¹⁾	Plot	-6	1.69 **	0.56
		<i>Polydrusus cervinus</i> ⁽¹⁾	Plot	+2	0.27	0.28
	Specialist phyllophagous	biomass ⁽³⁾	Tree	+2	-0.10	0.04
		abundance ⁽³⁾	Tree	+1	-0.12	0.10
		species richness ⁽⁴⁾	Plot	0	0.14	0.09
		<i>Archarius pyrrhoceras</i> ⁽¹⁾	Plot	-3	-0.79 *	0.37
		<i>Orchestes quercus</i> ⁽¹⁾	Plot	-1	-0.27 *	0.13
Seminiphagous	biomass ⁽³⁾	Tree	+1	-0.38	0.57	
	abundance ⁽¹⁾	Plot	+2	-0.14	0.21	
	species richness ⁽⁴⁾	Plot	+2	0.06	0.10	
	<i>Curculio glandium</i> ⁽¹⁾	Plot	+2	-0.15	0.22	
All beetles	biomass ⁽³⁾	Tree	-10	0.80 ***	0.22	
	abundance ⁽²⁾	Tree	-3	298.2 *	121.10	
	species richness ⁽²⁾	Tree	+1	3.70	2.33	

718 Generalized linear mixed-effects models fitted for the negative binomial family⁽¹⁾, the Gaussian family⁽²⁾, the log-
719 normal family⁽³⁾ (i.e. log-transformed response), the Poisson family⁽⁴⁾ with year as a random effect ; biomass = dry
720 weight (in mg); ° ΔAICc = AICc (best ecological model) – AICc (null model); °° the variable considered for species is
721 abundance. P<0.05: *; P<0.01: **; P<0.001: ***.

722

723 Table 4: Canonical Analysis of Principal coordinates, based on Bray-Curtis distance matrices,
 724 ranking the effect of the two spatial levels of decline (plot vs. tree) on variations in species
 725 composition.
 726

Group	Ecological variable with the best contribution to inertia	Inertia explained by the best ecological variable (and significance)	% inertia explained	Inertia explained by sampling year	% inertia explained by sampling year
Oak-associated buprestid beetles	Plot	0.60 *	5.9	2.19 ***	21.5
Xylophagous beetles (excl. buprestids)	Tree	0.58 *	6.7	4.70 ***	54.5
Non-xylophagous saproxylic beetles	Plot	0.13	1.3	3.14 ***	30.4
Oak-associated weevils	Plot	0.32 *	4.9	1.75 ***	26.2
All beetles	Plot	0.48 **	5.5	2.63 ***	30.5

727 P<0.001: ***.

728

729 Table 5: characteristic species for each tree-decline level, identified using the IndVal approach.
730 We retained only those species significant in the permutation test with an indicator value above
731 0.25, sampled in more than 10% of traps and with more than 10 individuals.
732

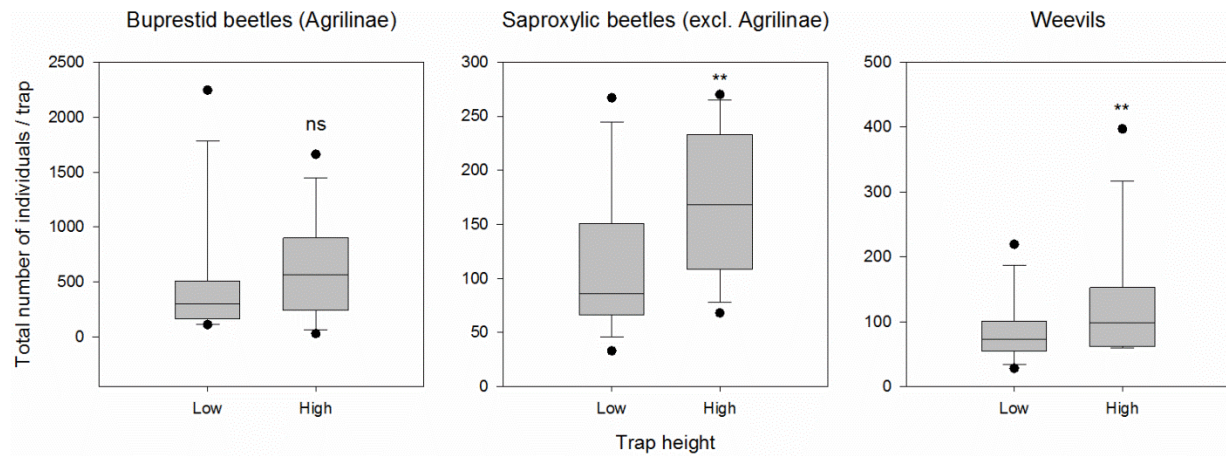
Group	Indicator species	Feeding guild	Indicator value	Frequency (%)
Declining trees	<i>Agrilus angustulus</i>	Xylophagous	0.891 *	86
	<i>Agrilus sulcicollis</i>	Xylophagous	0.889 **	81
	<i>Agrilus hastulifer</i>	Xylophagous	0.798 *	65
	<i>Agrilus biguttatus</i>	Xylophagous	0.794 **	51
	<i>Trichoferus pallidus</i>	Xylophagous	0.843 **	65
	<i>Rhagium sycophanta</i>	Xylophagous	0.573 *	16
	<i>Xylotrechus antilope</i>	Xylophagous	0.622 *	30
	<i>Scolytus intricatus</i>	Xylophagous	0.683 **	30
	<i>Gasterocercus depressirostris</i>	Xylophagous	0.517 *	14
	<i>Mordella brachyura</i>	Saproxylophagous	0.804 *	57
	<i>Cetonia aurata</i>	Saproxylophagous	0.699 **	35
	<i>Opilo mollis</i>	Zoophagous	0.787 *	62
	<i>Stenagostus rhombeus</i>	Zoophagous	0.733 *	59
	<i>Lygistopterus sanguineus</i>	Zoophagous	0.716 **	43
Healthy trees	<i>Calambus bipustulatus</i>	Zoophagous	0.693 **	35

733 P<0.05: *; P<0.01: **.

734

735 Figure 1: effect of trap height (10 m vs. 15 m above the ground) on the number of oak-
736 associated Agrilinae (i.e. *Agrilus* sp., *Coraebus* sp. and *Meliboeus* sp.), other saproxylic beetles,
737 and phytophagous weevils (i.e. phyllophagous and seminiphagous species) captured per trap.
738 $P < 0.01$:**.

739



740

741

742

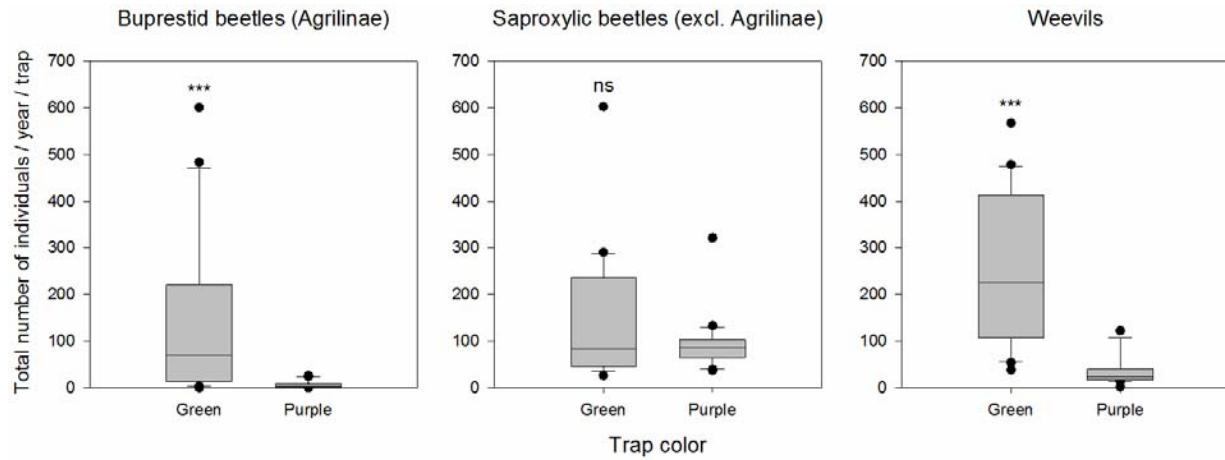
743 Figure 2

744 Effect of trap color (green vs. purple) on the number of oak-associated Agrilinae (i.e. *Agrilus* sp.,

745 *Coraebus* sp. and *Meliboeus* sp.), other saproxylic beetles, and phytophagous weevils (i.e.

746 phylophagous and seminiphagous species) captured per trap. P<0.01: **, P<0.001: ***.

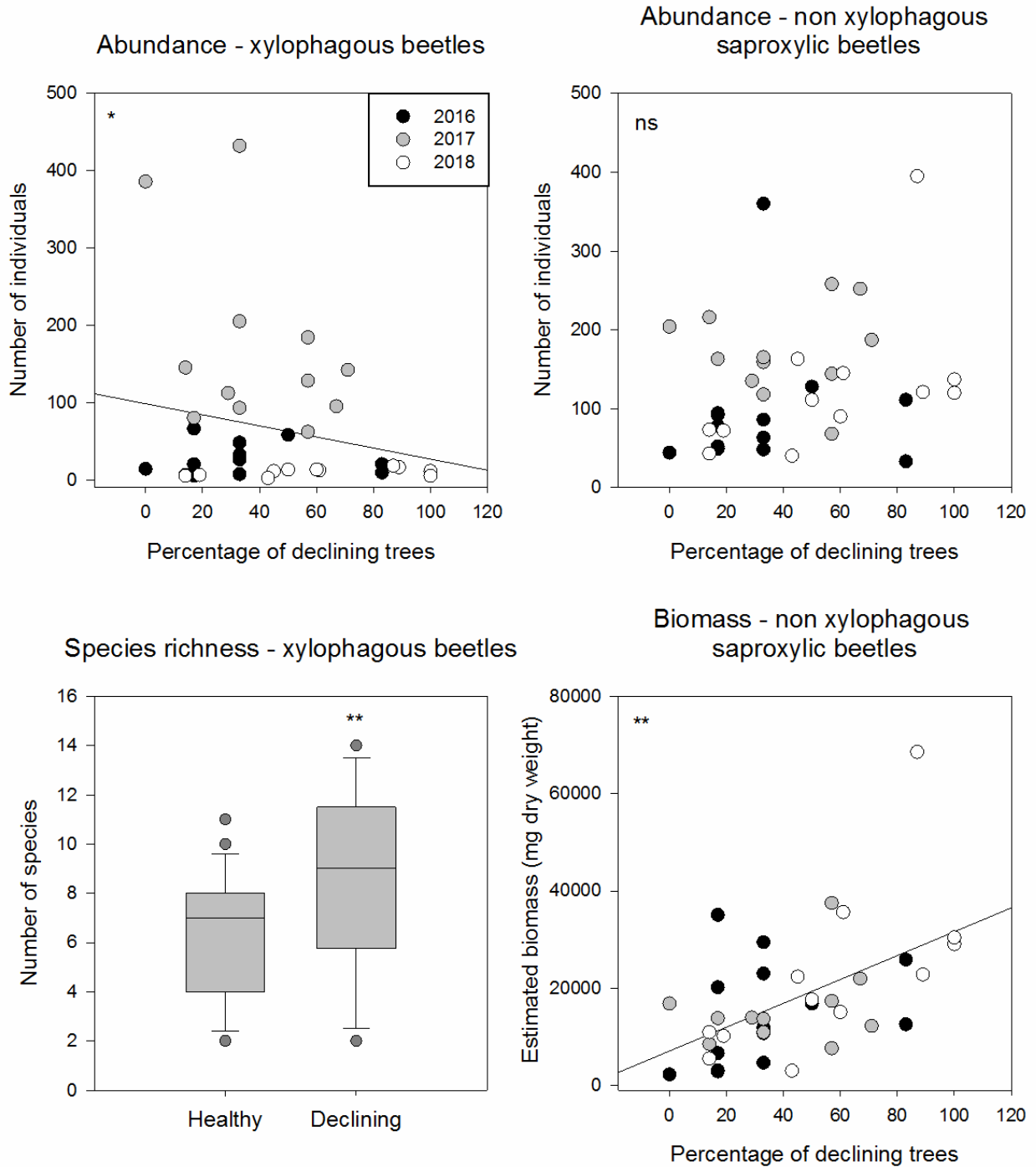
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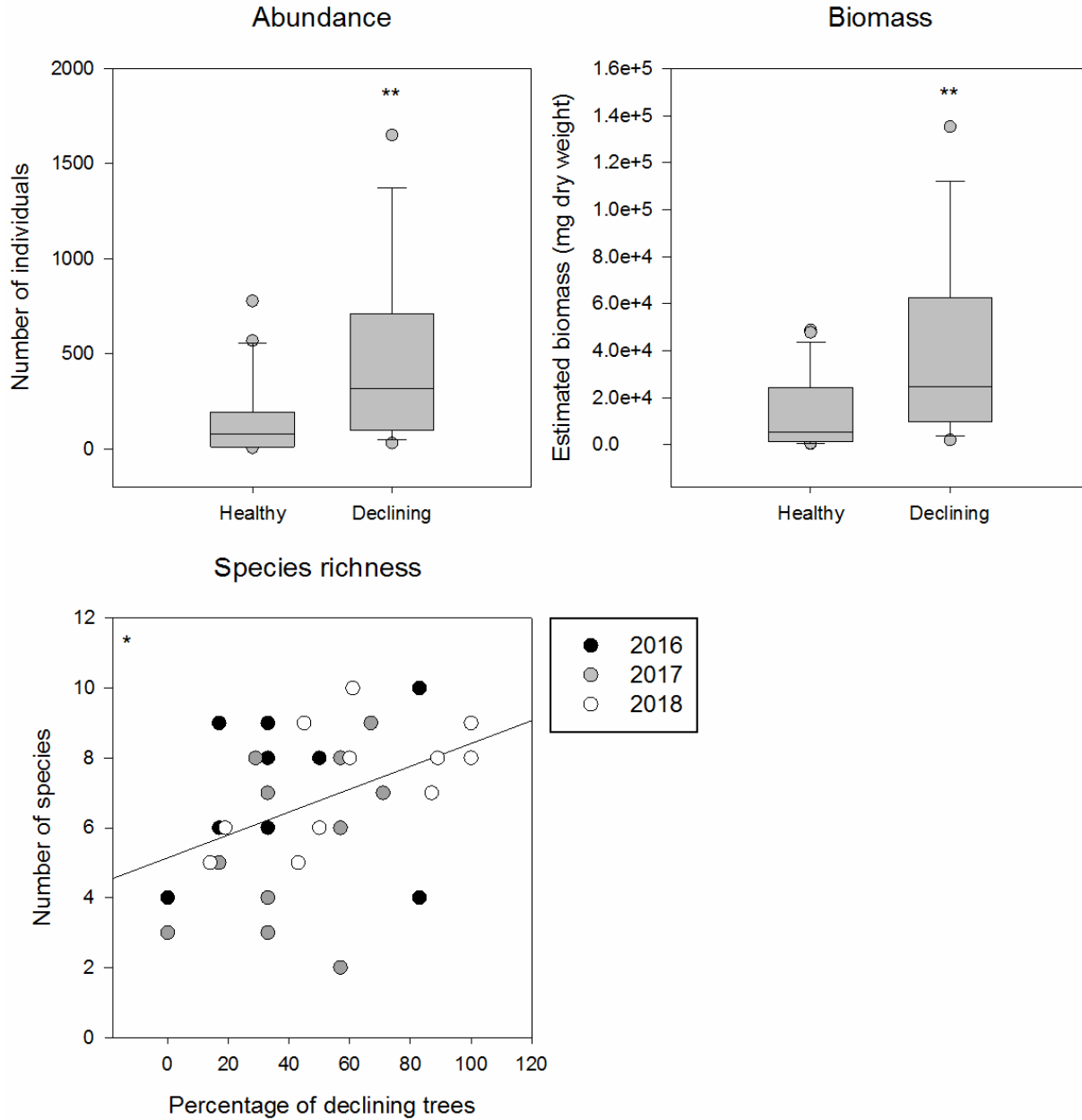
750 Figure 3: abundance of xylophagous and non-xylophagous saproxylic beetles, species richness
751 of xylophagous beetles, and biomass of non-xylophagous saproxylic beetles depending on
752 decline level at the tree scale (healthy vs. declining) or plot scale (percentage of declining trees).
753 See table 3 for statistical results; $P < 0.05$: *; $P < 0.01$: **.



754

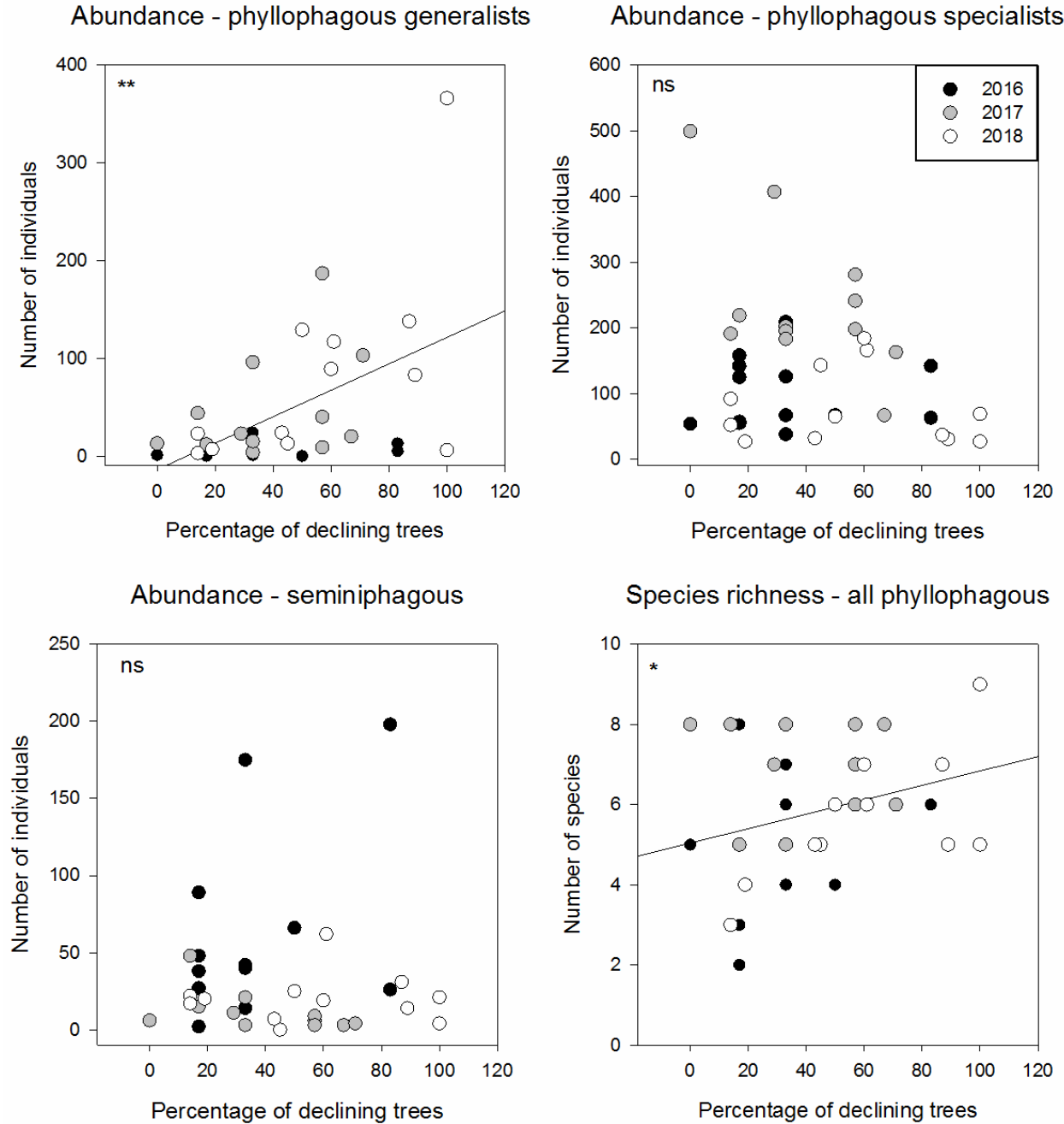
755 Figure 4: abundance, biomass and species richness of oak-associated buprestid beetles
756 depending on decline level at the tree scale (healthy vs. declining) or plot scale (percentage of
757 declining trees). See table 3 for statistical results; $P < 0.05$: *; $P < 0.01$: **.

758



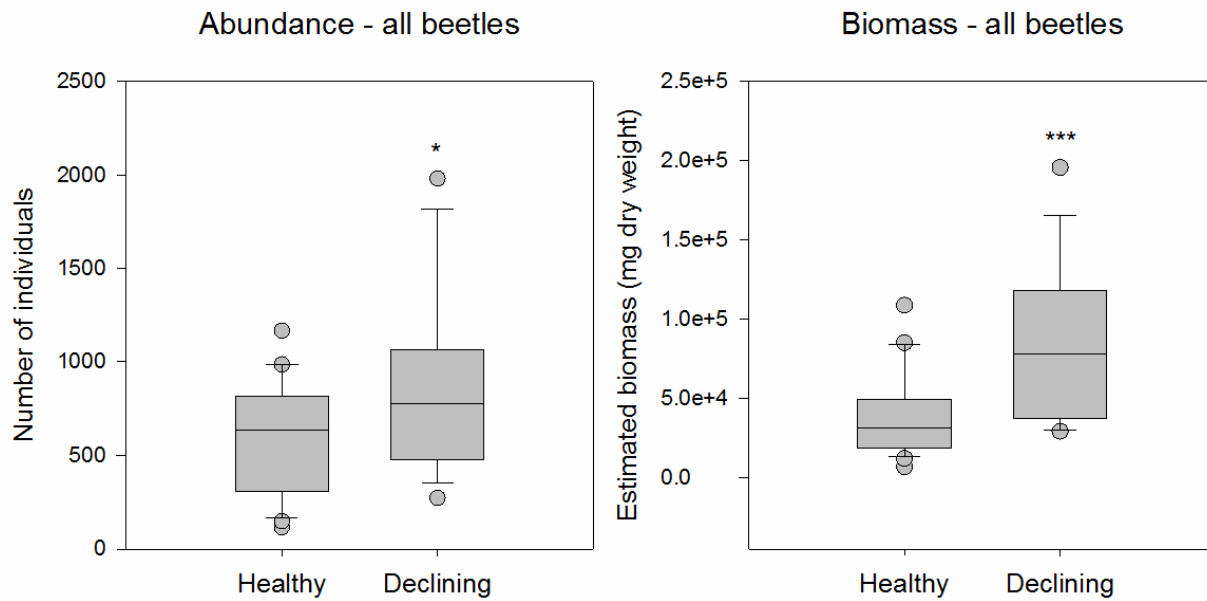
759

760 Figure 5: abundance of generalist phyllophagous, specialist phyllophagous and seminiphagous
761 weevils, and species richness of all phyllophagous weevils, depending on decline level at the
762 plot scale (percentage of declining trees). See table 3 for statistical results; $P < 0.05$: *; $P < 0.01$: **.
763



764
765

766 Figure 6: abundance and biomass of all the beetle species considered in the analyses,
767 depending on decline at the tree scale (healthy vs. declining). See table 3 for statistical results;
768 $P < 0.05$: *; $P < 0.01$: **.
769



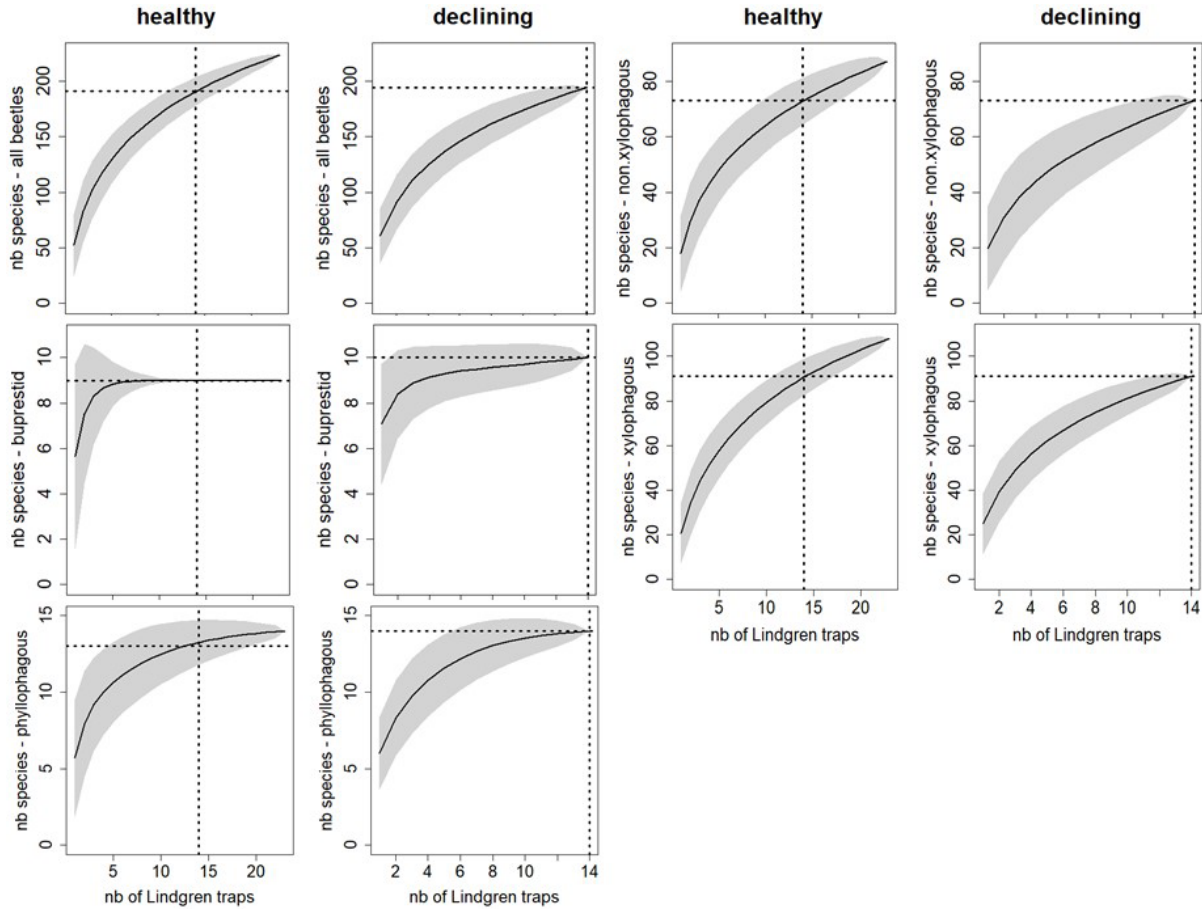
770
771

772 Figure S1

773 Cumulative interpolated rarefaction of species richness with sample size (sampling without
774 replacement) by dieback level at tree scale. Vertical dashed line = standard interpolated sample
775 size, horizontal dashed line = species richness estimate at the standardized sample size, and
776 grey area = standard deviation of species richness estimate.

777

778



779

780 Table S1: list of all the beetle species collected and used for the data analyses with their group,
781 their guild and their abundance

Group	Guild	Species	Family	Number of individuals
Oak-associated buprestid beetles (Agrillinae)	NA	<i>Agrilus angustulus</i>	BUPRESTIDAE	2089
	NA	<i>Agrilus biguttatus</i>	BUPRESTIDAE	282
	NA	<i>Agrilus curtulus</i>	BUPRESTIDAE	1
	NA	<i>Agrilus graminis</i>	BUPRESTIDAE	65
	NA	<i>Agrilus hastulifer</i>	BUPRESTIDAE	1603
	NA	<i>Agrilus laticornis</i>	BUPRESTIDAE	4029
	NA	<i>Agrilus obscuricollis</i>	BUPRESTIDAE	1433
	NA	<i>Agrilus sulcicollis</i>	BUPRESTIDAE	664
	NA	<i>Coraeus undatus</i>	BUPRESTIDAE	198
	NA	<i>Meliboeus fulgidicollis</i>	BUPRESTIDAE	76
Oak-associated phytophagous weevils	anthophagous	<i>Coeliodes ilicis</i>	CURCULIONIDAE	4
	anthophagous	<i>Coeliodes transversealbofasciatus</i>	CURCULIONIDAE	2
	seminiphagous	<i>Curculio elephas</i>	CURCULIONIDAE	67
	seminiphagous	<i>Curculio glandium</i>	CURCULIONIDAE	926
	seminiphagous	<i>Curculio pellitus</i>	CURCULIONIDAE	41
	seminiphagous	<i>Curculio venosus</i>	CURCULIONIDAE	111
	generalist phyllophagous	<i>Brachyderes incanus</i>	CURCULIONIDAE	74
	generalist phyllophagous	<i>Phyllobius pyri</i>	CURCULIONIDAE	1277
	generalist phyllophagous	<i>Polydrusus cervinus</i>	CURCULIONIDAE	260
	generalist phyllophagous	<i>Polydrusus marginatus</i>	CURCULIONIDAE	4
	generalist phyllophagous	<i>Strophosoma capitatum</i>	CURCULIONIDAE	15
	specialist phyllophagous	<i>Archarius pyrrhoceras</i>	CURCULIONIDAE	425
	specialist phyllophagous	<i>Attelabus nitens</i>	CURCULIONIDAE	7
	specialist phyllophagous	<i>Curculio villosus</i>	CURCULIONIDAE	6
	specialist phyllophagous	<i>Lasiorhynchites coeruleocephalus</i>	CURCULIONIDAE	29
	specialist phyllophagous	<i>Neocoenorhinidius interpunctatus</i>	CURCULIONIDAE	109
	specialist phyllophagous	<i>Neocoenorhinus minutus</i>	CURCULIONIDAE	10
	specialist phyllophagous	<i>Orchestes avellanae</i>	CURCULIONIDAE	120
	specialist phyllophagous	<i>Orchestes irroratus</i>	CURCULIONIDAE	10
	specialist phyllophagous	<i>Orchestes pilosus</i>	CURCULIONIDAE	13
specialist phyllophagous	<i>Orchestes quercus</i>	CURCULIONIDAE	4770	
Saproxylous beetles associated with deciduous trees	non-xylophagous	<i>Anthribus nebulosus</i>	ANTHRIBIDAE	16
	non-xylophagous	<i>Teredus cylindricus</i>	BOTHRIDERIDAE	1
	non-xylophagous	<i>Dromius agilis</i>	CARABIDAE	7
	non-xylophagous	<i>Dromius quadrimaculatus</i>	CARABIDAE	14
	non-xylophagous	<i>Cerylon ferrugineum</i>	CERYLONIDAE	1
	non-xylophagous	<i>Cerylon histeroides</i>	CERYLONIDAE	1
	non-xylophagous	<i>Cis pygmaeus</i>	CIIDAE	1
	non-xylophagous	<i>Cis villosulus</i>	CIIDAE	2
	non-xylophagous	<i>Ennearthron cornutum</i>	CIIDAE	1
	non-xylophagous	<i>Orthocis lucasi</i>	CIIDAE	2
	non-xylophagous	<i>Clambus armadillo</i>	CLAMBIDAE	1
	non-xylophagous	<i>Clerus mutillarius</i>	CLERIDAE	9
	non-xylophagous	<i>Opilo mollis</i>	CLERIDAE	59
	non-xylophagous	<i>Tilloidea unifasciata</i>	CLERIDAE	8
	non-xylophagous	<i>Tillus elongatus</i>	CLERIDAE	3

782

783 Table S1 cont.

784

Group	Guild	Species	Family	Number of individuals
Saproxylic beetles (excl. Agrilinae) associated with deciduous trees	non-xylophagous	<i>Aplocnemus impressus</i>	DASYTIDAE	11
	non-xylophagous	<i>Aplocnemus nigricornis</i>	DASYTIDAE	4
	non-xylophagous	<i>Dasytes aeratus</i>	DASYTIDAE	159
	non-xylophagous	<i>Dasytes caeruleus</i>	DASYTIDAE	180
	non-xylophagous	<i>Dasytes niger</i>	DASYTIDAE	2
	non-xylophagous	<i>Dasytes nigrocyaneus</i>	DASYTIDAE	26
	non-xylophagous	<i>Dasytes pauperculus</i>	DASYTIDAE	116
	non-xylophagous	<i>Dasytes plumbeus</i>	DASYTIDAE	8
	non-xylophagous	<i>Dasytes subaeneus</i>	DASYTIDAE	1
	non-xylophagous	<i>Dasytes virens</i>	DASYTIDAE	1
	non-xylophagous	<i>Psilothrix viridicoerulea</i>	DASYTIDAE	1
	non-xylophagous	<i>Trichoceble floralis</i>	DASYTIDAE	3
	non-xylophagous	<i>Attagenus brunneus</i>	DERMESTIDAE	1
	non-xylophagous	<i>Attagenus pelio</i>	DERMESTIDAE	1
	non-xylophagous	<i>Ctesias serra</i>	DERMESTIDAE	34
	non-xylophagous	<i>Dermestes lardarius</i>	DERMESTIDAE	4
	non-xylophagous	<i>Dermestes murinus</i>	DERMESTIDAE	8
	non-xylophagous	<i>Dermestes undulatus</i>	DERMESTIDAE	69
	non-xylophagous	<i>Globicornis fasciata</i>	DERMESTIDAE	8
	non-xylophagous	<i>Globicornis nigripes</i>	DERMESTIDAE	3
	non-xylophagous	<i>Megatoma undata</i>	DERMESTIDAE	11
	non-xylophagous	<i>Ampedus balteatus</i>	ELATERIDAE	4
	non-xylophagous	<i>Ampedus elongatulus</i>	ELATERIDAE	30
	non-xylophagous	<i>Ampedus nigerrimus</i>	ELATERIDAE	197
	non-xylophagous	<i>Ampedus pomorum</i>	ELATERIDAE	50
	non-xylophagous	<i>Ampedus quercicola</i>	ELATERIDAE	13
	non-xylophagous	<i>Ampedus rufipennis</i>	ELATERIDAE	8
	non-xylophagous	<i>Ampedus sanguinolentus</i>	ELATERIDAE	59
	non-xylophagous	<i>Brachygonus megerlei</i>	ELATERIDAE	26
	non-xylophagous	<i>Calambus bipustulatus</i>	ELATERIDAE	20
	non-xylophagous	<i>Cardiophorus ruficollis</i>	ELATERIDAE	2
	non-xylophagous	<i>Denticollis linearis</i>	ELATERIDAE	1
	non-xylophagous	<i>Elater ferrugineus</i>	ELATERIDAE	1
	non-xylophagous	<i>Hemicrepidius hirtus</i>	ELATERIDAE	17
	non-xylophagous	<i>Melanotus villosus</i>	ELATERIDAE	29
non-xylophagous	<i>Podeonius acuticornis</i>	ELATERIDAE	2	
non-xylophagous	<i>Stenagostus rhombeus</i>	ELATERIDAE	37	
non-xylophagous	<i>Symbiotes gibberosus</i>	ENDOMYCHIDAE	2	
non-xylophagous	<i>Dacne bipustulata</i>	EROTYLIDAE	43	
non-xylophagous	<i>Triplax lepida</i>	EROTYLIDAE	65	
non-xylophagous	<i>Triplax russica</i>	EROTYLIDAE	14	
non-xylophagous	<i>Tritoma bipustulata</i>	EROTYLIDAE	2	
non-xylophagous	<i>Gnathoncus nidorum</i>	HISTERIDAE	2	
non-xylophagous	<i>Laemophloeus monilis</i>	LAEMOPHLOEIDAE	2	
non-xylophagous	<i>Placonotus testaceus</i>	LAEMOPHLOEIDAE	1	
non-xylophagous	<i>Lygistopterus sanguineus</i>	LYCIDAE	28	
non-xylophagous	<i>Abdera biflexuosa</i>	MELANDRYIDAE	10	
non-xylophagous	<i>Monotoma picipes</i>	MONOTOMIDAE	1	

785

786

787 Table S1 cont.
788

Group	Guild	Species	Family	Number of individuals	
Saproxyllic beetles (excl. Agrilinae) associated with deciduous trees	non-xylophagous	<i>Rhizophagus bipustulatus</i>	MONOTOMIDAE	3	
	non-xylophagous	<i>Rhizophagus dispar</i>	MONOTOMIDAE	1	
	non-xylophagous	<i>Rhizophagus ferrugineus</i>	MONOTOMIDAE	2	
	non-xylophagous	<i>Berginus tamarisci</i>	MYCETOPHAGIDAE	100	
	non-xylophagous	<i>Eulagius filicornis</i>	MYCETOPHAGIDAE	84	
	non-xylophagous	<i>Litargus balteatus</i>	MYCETOPHAGIDAE	1	
	non-xylophagous	<i>Litargus connexus</i>	MYCETOPHAGIDAE	72	
	non-xylophagous	<i>Mycetophagus piceus</i>	MYCETOPHAGIDAE	2	
	non-xylophagous	<i>Mycetophagus populi</i>	MYCETOPHAGIDAE	1	
	non-xylophagous	<i>Cryptarcha strigata</i>	NITIDULIDAE	157	
	non-xylophagous	<i>Cryptarcha undata</i>	NITIDULIDAE	149	
	non-xylophagous	<i>Cychramus luteus</i>	NITIDULIDAE	1	
	non-xylophagous	<i>Epuraea sp</i>	NITIDULIDAE	1	
	non-xylophagous	<i>Soronia grisea</i>	NITIDULIDAE	295	
	non-xylophagous	<i>Dorcatoma androgyna</i>	PTINIDAE	1	
	non-xylophagous	<i>Dorcatoma chrysomelina</i>	PTINIDAE	3	
	non-xylophagous	<i>Dorcatoma flavicornis</i>	PTINIDAE	1	
	non-xylophagous	<i>Dorcatoma robusta</i>	PTINIDAE	1	
	non-xylophagous	<i>Dorcatoma substriata</i>	PTINIDAE	2	
	non-xylophagous	<i>Pyrochroa coccinea</i>	PYROCHROIDAE	58	
	non-xylophagous	<i>Salpingus planirostris</i>	SALPINGIDAE	4	
	non-xylophagous	<i>Salpingus ruficollis</i>	SALPINGIDAE	1	
	non-xylophagous	<i>Uleiota planatus</i>	SILVANIDAE	1	
	non-xylophagous	<i>Nemozoma elongatum</i>	TROGOSSITIDAE	1	
	non-xylophagous	<i>Tenebroides fuscus</i>	TROGOSSITIDAE	3	
	non-xylophagous	<i>Colobicus hirtus</i>	ZOPHERIDAE	4	
	non-xylophagous	<i>Colydium elongatum</i>	ZOPHERIDAE	2	
	non-xylophagous	<i>Endophloeus markovichianus</i>	ZOPHERIDAE	3	
	xylophagous		<i>Euglenes pygmaeus</i>	ADERIDAE	1
	xylophagous		<i>Dissoleucas niveirostris</i>	ANTHRIBIDAE	1
xylophagous		<i>Phaeochrotes pudens</i>	ANTHRIBIDAE	3	
xylophagous		<i>Platystomos albinus</i>	ANTHRIBIDAE	38	
xylophagous		<i>Pseudeuparius sepicola</i>	ANTHRIBIDAE	6	
xylophagous		<i>Rhaphitropis oxyacanthae</i>	ANTHRIBIDAE	1	
xylophagous		<i>Tropideres albirostris</i>	ANTHRIBIDAE	41	
xylophagous		<i>Lyctinae</i>	BOSTRICHIDAE	1	
xylophagous		<i>Xylopertha retusa</i>	BOSTRICHIDAE	1	
xylophagous		<i>Anthaxia salicis</i>	BUPRESTIDAE	1	
xylophagous		<i>Chrysobothris affinis</i>	BUPRESTIDAE	1	
xylophagous		<i>Alosterna tabacicolor</i>	CERAMBYCIDAE	1	
xylophagous		<i>Anaesthetis testacea</i>	CERAMBYCIDAE	2	
xylophagous		<i>Anoplodera sexguttata</i>	CERAMBYCIDAE	6	
xylophagous		<i>Callimus angulatus</i>	CERAMBYCIDAE	1	
xylophagous		<i>Cerambyx cerdo</i>	CERAMBYCIDAE	1	
xylophagous		<i>Cerambyx scopolii</i>	CERAMBYCIDAE	8	
xylophagous		<i>Chlorophorus figuratus</i>	CERAMBYCIDAE	3	
xylophagous		<i>Clytus arietis</i>	CERAMBYCIDAE	9	
xylophagous		<i>Clytus tropicus</i>	CERAMBYCIDAE	4	
xylophagous		<i>Cortodera humeralis</i>	CERAMBYCIDAE	8	
xylophagous		<i>Dinoptera collaris</i>	CERAMBYCIDAE	1	

789 Table S1 cont.
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Group	Guild	Species	Family	Number of individuals
Saproxylic beetles (excl. Agrilinae) associated with deciduous trees	xylophagous	<i>Exocentrus adspersus</i>	CERAMBYCIDAE	3
	xylophagous	<i>Grammoptera abdominalis</i>	CERAMBYCIDAE	5
	xylophagous	<i>Grammoptera ruficornis</i>	CERAMBYCIDAE	9
	xylophagous	<i>Grammoptera ustulata</i>	CERAMBYCIDAE	7
	xylophagous	<i>Leiopus femoratus</i>	CERAMBYCIDAE	1
	xylophagous	<i>Leiopus linnei</i>	CERAMBYCIDAE	5
	xylophagous	<i>Leiopus nebulosus</i>	CERAMBYCIDAE	6
	xylophagous	<i>Mesosa curculionoides</i>	CERAMBYCIDAE	1
	xylophagous	<i>Mesosa nebulosa</i>	CERAMBYCIDAE	27
	xylophagous	<i>Pedostrangalia revestita</i>	CERAMBYCIDAE	1
	xylophagous	<i>Phymatodes testaceus</i>	CERAMBYCIDAE	11
	xylophagous	<i>Plagionotus detritus</i>	CERAMBYCIDAE	8
	xylophagous	<i>Poecilium alni</i>	CERAMBYCIDAE	1
	xylophagous	<i>Poecilium rufipes</i>	CERAMBYCIDAE	22
	xylophagous	<i>Pogonocherus ovatus</i>	CERAMBYCIDAE	2
	xylophagous	<i>Pseudosphegesthes cinerea</i>	CERAMBYCIDAE	4
	xylophagous	<i>Rhagium sycophanta</i>	CERAMBYCIDAE	16
	xylophagous	<i>Rutpela maculata</i>	CERAMBYCIDAE	1
	xylophagous	<i>Tetrops praeustus</i>	CERAMBYCIDAE	2
	xylophagous	<i>Trichoferus pallidus</i>	CERAMBYCIDAE	95
	xylophagous	<i>Xylotrechus antilope</i>	CERAMBYCIDAE	66
	xylophagous	<i>Anisandrus dispar</i>	CURCULIONIDAE	1600
	xylophagous	<i>Cydorhipidion bodoanum</i>	CURCULIONIDAE	24
	xylophagous	<i>Ernoporicus fagi</i>	CURCULIONIDAE	1
	xylophagous	<i>Gasterocercus depressirostris</i>	CURCULIONIDAE	10
	xylophagous	<i>Hylastinus obscurus</i>	CURCULIONIDAE	6
	xylophagous	<i>Hylesinus varius</i>	CURCULIONIDAE	1
	xylophagous	<i>Magdalis flavicornis</i>	CURCULIONIDAE	46
	xylophagous	<i>Platypus cylindrus</i>	CURCULIONIDAE	4
	xylophagous	<i>Pteleobius kraatzii</i>	CURCULIONIDAE	1
	xylophagous	<i>Scolytus intricatus</i>	CURCULIONIDAE	52
	xylophagous	<i>Scolytus multistriatus</i>	CURCULIONIDAE	2
	xylophagous	<i>Scolytus pygmaeus</i>	CURCULIONIDAE	1
	xylophagous	<i>Scolytus rugulosus</i>	CURCULIONIDAE	9
	xylophagous	<i>Scolytus scolytus</i>	CURCULIONIDAE	1
	xylophagous	<i>Taphrorychus bicolor</i>	CURCULIONIDAE	23
	xylophagous	<i>Taphrorychus villifrons</i>	CURCULIONIDAE	2
	xylophagous	<i>Trypodendron signatum</i>	CURCULIONIDAE	2
	xylophagous	<i>Xyleborinus saxesenii</i>	CURCULIONIDAE	291
	xylophagous	<i>Xyleborus dryographus</i>	CURCULIONIDAE	4
xylophagous	<i>Xyleborus monographus</i>	CURCULIONIDAE	122	
xylophagous	<i>Xylosandrus germanus</i>	CURCULIONIDAE	1	
xylophagous	<i>Dromaeolus barnabita</i>	EUCNEMIDAE	46	
xylophagous	<i>Eucnemis capucina</i>	EUCNEMIDAE	4	
xylophagous	<i>Hylis olexai</i>	EUCNEMIDAE	2	
xylophagous	<i>Hylis simonae</i>	EUCNEMIDAE	7	
xylophagous	<i>Isorhipis melasoides</i>	EUCNEMIDAE	1	
xylophagous	<i>Melasis buprestoides</i>	EUCNEMIDAE	12	
xylophagous	<i>Microrhagus pygmaeus</i>	EUCNEMIDAE	2	
xylophagous	<i>Microrhagus pyrenaeus</i>	EUCNEMIDAE	2	
xylophagous	<i>Dorcus parallelipedus</i>	LUCANIDAE	2	

791 Table S1 cont.
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Group	Guild	Species	Family	Number of individuals
Saproxyllic beetles (excl. Agrilinae) associated with deciduous trees	xylophagous	<i>Platycerus caraboides</i>	LUCANIDAE	50
	xylophagous	<i>Lymexylon navale</i>	LYMEXYLIDAE	1
	xylophagous	<i>Anisoxya fuscula</i>	MELANDRYIDAE	1
	xylophagous	<i>Conopalpus brevicollis</i>	MELANDRYIDAE	4
	xylophagous	<i>Conopalpus testaceus</i>	MELANDRYIDAE	6
	xylophagous	<i>Melandrya barbata</i>	MELANDRYIDAE	2
	xylophagous	<i>Phloiotrya tenuis</i>	MELANDRYIDAE	7
	xylophagous	<i>Mordella brachyura</i>	MORDELLIDAE	207
	xylophagous	<i>Mordella leucaspis</i>	MORDELLIDAE	1
	xylophagous	<i>Mordellistena humeralis</i>	MORDELLIDAE	4
	xylophagous	<i>Mordellistena neuwaldeggiana</i>	MORDELLIDAE	25
	xylophagous	<i>Mordellistena variegata</i>	MORDELLIDAE	11
	xylophagous	<i>Tolida artemisiae</i>	MORDELLIDAE	2
	xylophagous	<i>Tomoxia bucephala</i>	MORDELLIDAE	44
	xylophagous	<i>Ischnomera caerulea</i>	OEDEMERIDAE	223
	xylophagous	<i>Nacerdes carniolica</i>	OEDEMERIDAE	54
	xylophagous	<i>Oedemera flavipes</i>	OEDEMERIDAE	1
	xylophagous	<i>Gastrallus immarginatus</i>	PTINIDAE	7
	xylophagous	<i>Gastrallus laevigatus</i>	PTINIDAE	38
	xylophagous	<i>Gastrallus vavrai</i>	PTINIDAE	1
	xylophagous	<i>Hadrobregmus denticollis</i>	PTINIDAE	1
	xylophagous	<i>Hemicoelus costatus</i>	PTINIDAE	4
	xylophagous	<i>Hemicoelus fulvicornis</i>	PTINIDAE	3
	xylophagous	<i>Hyperisus plumbeum</i>	PTINIDAE	6
	xylophagous	<i>Mesocoelopus niger</i>	PTINIDAE	11
	xylophagous	<i>Oligomerus brunneus</i>	PTINIDAE	7
	xylophagous	<i>Ptilinus pectinicornis</i>	PTINIDAE	1
	xylophagous	<i>Ptinomorphus imperialis</i>	PTINIDAE	51
	xylophagous	<i>Xyletinus pectinatus</i>	PTINIDAE	2
	xylophagous	<i>Cetonia aurata</i>	SCARABAEIDAE	37
	xylophagous	<i>Cetonischema speciosissima</i>	SCARABAEIDAE	22
	xylophagous	<i>Gnorimus nobilis</i>	SCARABAEIDAE	1
	xylophagous	<i>Liocola marmorata</i>	SCARABAEIDAE	1
	xylophagous	<i>Potosia fieberi</i>	SCARABAEIDAE	14
	xylophagous	<i>Valgus hemipterus</i>	SCARABAEIDAE	2
	xylophagous	<i>Anaspis fasciata</i>	SCRAPTIIDAE	35
	xylophagous	<i>Anaspis flava</i>	SCRAPTIIDAE	29
	xylophagous	<i>Anaspis frontalis</i>	SCRAPTIIDAE	277
	xylophagous	<i>Anaspis lurida</i>	SCRAPTIIDAE	100
	xylophagous	<i>Anaspis maculata</i>	SCRAPTIIDAE	134
	xylophagous	<i>Anaspis pulicaria</i>	SCRAPTIIDAE	11
	xylophagous	<i>Anaspis regimbarti</i>	SCRAPTIIDAE	66
	xylophagous	<i>Scraptia testacea</i>	SCRAPTIIDAE	4
	xylophagous	<i>Allecula morio</i>	TENEBRIONIDAE	1
	xylophagous	<i>Gonodera luperus</i>	TENEBRIONIDAE	4
xylophagous	<i>Mycetochara maura</i>	TENEBRIONIDAE	10	
xylophagous	<i>Nalassus laevioctostriatus</i>	TENEBRIONIDAE	2	
xylophagous	<i>Platydema violacea</i>	TENEBRIONIDAE	2	
xylophagous	<i>Prionychus ater</i>	TENEBRIONIDAE	1	
xylophagous	<i>Prionychus fairmairii</i>	TENEBRIONIDAE	29	

