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1 **Growth and mortality of the oak processionary moth, *Thaumetopoea processionea* L., on two oak**
2 **species: direct and trait-mediated effects of host and neighbour species identity**

3

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12 **Abstract:**

13 The presence of heterospecific neighbours can affect damage caused by pest insects on focal plants.
14 However, how plant neighbours influence herbivore performance is poorly understood. We tested the
15 independent and interactive effects of tree species identity and tree neighbour type (conspecific vs.
16 heterospecific) on the performance of a major oak pest, the oak processionary moth larvae (OPM,
17 *Thaumetopoea processionea*) fed on *Quercus robur* and *Q. petraea*. We performed a factorial
18 greenhouse experiment in which we grew two oak saplings per pot, either from the same species or
19 from both species. We quantified growth and mortality of OPM larvae, leaf phenolic compounds, C:N
20 ratio and bud phenology. OPM larvae performed significantly better on *Q. petraea* than on *Q. robur*,
21 regardless of plant neighbour type. Phenolic compounds and C:N, but not phenology, differed between
22 oak species and neighbour species identity. Only bud phenology had a significant effect on OPM
23 performance, which was better when young larvae had access to recently unfolded leaves, regardless
24 of oak species and neighbour identity. Although oak neighbour identity altered the expression of leaf
25 traits, this effect had no measurable consequences on OPM performance. However, further studies
26 should consider the effect of oak species neighbour on OPM preferences for either *Q. robur* or
27 *Q. petraea*, in pure and mixed stands, before translating current results into recommendations for
28 forest management.

29

30 **Key words:** Associational effects; Herbivory; Indirect trait-mediated effects; Leaf traits; Plant-insect
31 interaction; *Quercus*

32

33 **Author Contribution:**

34 TD and BC conceived the study and acquired the data. TD performed experiment and analysed the
35 data. EV, TD and XM performed the chemical analyses. TD and BC drafted the first version of the
36 manuscript and all authors wrote the final version of the manuscript.

37 TD, BC conceived and designed research. TD performed experiment and analysed data. EV, TD, XM
38 performed the chemical analyses. TD, BC wrote the manuscript. All authors read and approved the
39 manuscript.

40 AM and DB conceived and designed research. AM and BB conducted experiments. GR contributed
41 new reagents or analytical tools. AM, BB and GR analysed data. AM wrote the manuscript. All
42 authors read and approved the manuscript.

43 **Introduction**

44 Plants are embedded in heterogeneous environments where the identity, density and diversity of
45 neighbouring plants can strongly influence their interactions with insect herbivores. Associational
46 resistance theory predicts that plants are less prone to damage by insect herbivores when surrounded
47 by heterospecific neighbours (Barbosa et al. 2009). Associational resistance provided by neighbours is
48 generally attributed to reduced herbivore accessibility to host plants, or to physical or chemical
49 disruption of host searching behaviour of insect herbivores foraging for food or egg laying sites
50 (Zhang and Schlyter 2004; Bruce et al. 2005; Barbosa et al. 2009; Jactel et al. 2011; Bruce and Pickett
51 2011; Castagneyrol et al. 2013, 2014; Verschut et al. 2016). Accordingly, most studies investigating
52 associational resistance have addressed plant colonization by herbivores or documented damage in
53 various neighbourhood contexts (reviewed by Moreira et al. 2016). However, plant neighbourhood
54 might also influence performance (e.g. growth rate, survival) of insect herbivores once established on
55 the host plant (e.g. Castagneyrol et al. 2018).

56 Herbivore performance is mainly driven by host plant traits, and particularly by those determining its
57 nutritional quality. For instance, nitrogen is an important limiting factor for phytophagous insects
58 (Mattson 1980), and low nitrogen content (or high C:N ratio) has been commonly associated with low
59 nutritional plant quality and reduced herbivore performance (Mattson 1980; White 1984). In addition,
60 secondary metabolites (e.g. phenolic compounds) are commonly considered as effective plant defences
61 against many leaf-feeding herbivores in several tree species (Feeny 1976; Lill and Marquis 2001;
62 Forkner et al. 2004). These compounds are often toxic (Salminen and Karonen 2011; Mithöfer and
63 Boland 2012) and some have been shown to reduce digestibility in herbivores, hence potentially
64 reducing herbivore damage (Feeny 1970; Roslin and Salminen 2008; Abdala-Roberts et al. 2016;
65 Moreira et al. 2018b). For instance, condensed and hydrolysable tannins and flavonoids can reduce
66 plant digestibility by binding digestive enzymes and altering herbivores' digestive tissues through the
67 production of reactive oxygen species (Barbehenn et al. 2009; Barbehenn and Constabel 2011;
68 Falcone Ferreyra et al. 2012). Similarly, lignins act as toxic compounds and contribute to increased
69 tissue (leaf or shoot) toughness (Bidlack et al. 1992; Bonawitz and Chapple 2010), a common physical
70 defensive trait (Clissold et al. 2009; Pearse 2011; Caldwell et al. 2016)

71 There is increasing evidence that the identity and diversity of neighbouring plants can indirectly affect
72 herbivore performance on focal plants by modifying plant nutritional and defensive traits. These
73 indirect, trait mediated effects of plant neighbourhood can result from several mechanisms such as
74 competition for resources (e.g. light, water, nutrients), emission of volatile organic compounds by
75 neighbouring plants or plant-soil feedbacks (Arimura et al. 2001; Turlings and Ton 2006; Agrawal et
76 al. 2006; Barbosa et al. 2009; Ballaré 2014; Kos et al. 2015a, c, b; Castagneyrol et al. 2017). For
77 instance, plants growing under the shade of their neighbours tend to be more favourable for herbivores
78 since the allocation of resources to plant defences, such as phenolic compounds and terpenes, is

79 markedly lower (Dudt and Shure 1994; Ballaré 2014). Moreover, the emission of volatile organic
80 compounds by neighbouring plants after a herbivore attack might induce the expression of defensive
81 traits in focal undamaged plants (Arimura et al. 2001; Turlings and Ton 2006; Barbosa et al. 2009;
82 Scala et al. 2013), Despite these evidences, how neighbour-mediated changes in plant traits influence
83 herbivore performance remains poorly studied and this has precluded a better understanding of the
84 mechanisms underlying associational resistance to insect herbivores.

85 In the present study, we tested for independent and interactive effects of plant species identity and
86 plant neighbourhood type (conspecific vs. heterospecific) on insect herbivore performance, leaf
87 nutritional and defensive traits and plant phenology of two oak species (pedunculate oak *Quercus*
88 *robur* L and sessile oak *Q. petraea* Liebl.). To this end, we performed a factorial greenhouse
89 experiment in which we grew pedunculate and sessile oak saplings in pots with either conspecific or
90 heterospecific neighbours and quantified growth and mortality of oak processionary moth (OPM,
91 *Thaumetopoea processionea* L., Lepidoptera) larvae, leaf chemical (phenolic compounds) and
92 nutritional (leaf C:N ratio) traits and plant phenology (bud developmental stage). Overall, this study
93 builds towards a better understanding of the effects of plant neighbourhood composition on insect
94 herbivory, plant defensive traits and the mechanisms underpinning such effects.

95

96 **Materials and methods**

97 *Natural history* – The oak processionary moth (OPM), *Thaumetopoea processionea* L., is a pest
98 responsible for major defoliations on deciduous oaks in western and central Europe and part of the
99 Middle East (Groenen and Meurisse 2012). The OPM is considered an oligophagous herbivore species
100 feeding mainly on *Quercus* and occasionally on other Fagaceae (e.g. beech) or Betulaceae (e.g.
101 hornbeam) species (Stigter et al. 1997). Its life cycle is synchronized with their host trees (Wagenhoff
102 et al. 2013); larvae emerge at the time of host budburst and feed on flushing leaves in spring and early
103 summer. OPM caterpillars are gregarious, with sometimes thousands of individuals concentrating on a
104 single tree. From the fourth to the sixth instar, OPM larvae produce urticating setae which are
105 responsible for severe allergic reactions in both humans and animals (Maier et al. 2003). Managing to
106 increase oak forest resistance to OPM attacks is therefore of crucial importance, in terms of both forest
107 and public health.

108 *Study design* – We established a greenhouse experiment at INRA forest station in Cestas
109 (Southwestern France, GPS: 44°44'10.32" N, 0°46' 26.21" W), with potted trees. In January 2017, we
110 planted 100 two-year-old oak saplings in 5L pots. In total, we prepared 25 pots with two *Q. petraea*
111 individuals, 25 pots with two *Q. robur* individuals, and 50 pots with one individual of each species.
112 Saplings of the two oak species were similar in size. We kept pots in a greenhouse with ambient
113 temperature, humidity and light and watered as needed for one year before the start of the experiment.

114 In December 2017, we collected OPM egg masses in mature oak forests in North-Eastern France. In
115 April 2018, before oak budburst, we installed one egg mass (about 100 eggs) on one oak tree per pot.
116 We established two ‘focal species’ treatments (*Q. petraea* vs. *Q. robur*) crossed with two ‘neighbour
117 species’ treatments (conspecific vs heterospecific) resulting in the four following experimental
118 treatments with 25 replicates each: (i) one egg mass on one *Q. robur* in a pot with *Q. petraea* kept
119 intact; (ii) one egg mass on one *Q. robur* in a pot with *Q. robur* kept intact; (iii) one egg mass on one
120 *Q. petraea* in a pot with *Q. petraea* kept intact; (iv) one egg mass on one *Q. petraea* in a pot with *Q.*
121 *robur* kept intact. We used 30 × 15 cm nylon bags with a mesh size of 0.05 × 0.05 cm to prevent the
122 movement of larvae from treated saplings to their intact neighbours. In case of food shortage, larvae
123 and bags were moved to another neighbouring branch of the same sapling.

124 *Oak and OPM phenology* – We checked egg masses every day from 4 to 30 April 2018 and noted
125 OPM developmental stage (unhatched eggs, L1, L2, L3), in order to estimate proportion of each larval
126 instar at the end of our experiment. Within OPM colonies, individual development is synchronized
127 because hatching and moulting are synchronous among larvae from the same egg mass. We recorded
128 the developmental stage of the terminal bud of each oak at the time OPM eggs hatched, using a seven-
129 level ordinal scale from 0 to 6 (0 = dormant bud, 1 = bud swollen, 2 = bud open, 3 = beginning of leaf
130 expansion, 4 = one leaf free, 5 = internodes are elongating, 6 = fully expanded leaves) (Ducousso et al.
131 1996; Derory et al. 2010).

132 *OPM larval growth and mortality* – When the first colonies reached the third larval instar (i.e., 26 days
133 after installing egg masses on trees 53 colonies out of 100 had reached the third larval instar), we
134 removed larvae from trees to avoid any risk of urtications (starting at fourth instar). We counted the
135 number of living larvae and the initial larval density (i.e. number of empty eggs from which larvae
136 emerged) in order to estimate mortality rate (i.e., (Number of hatched eggs – Number of living larvae)/
137 Number of days after hatching, day⁻¹). We kept living larvae for 24 hours without food and then
138 weighed them to the closest 10 µg (Balances NewClassic MS semi-micro), giving weight at day *j* (w_j).
139 In a preliminary trial, we weighted 30 samples of 10 neonate larvae (L1) and found that the average
140 weight (\pm se) of a neonate was 0.225 ± 0.004 mg. Because of the small variability in neonate weight
141 and because this value was much lower than the mean of w_j (5.24 ± 0.50 mg), we considered the
142 neonate weight negligible and thus defined larvae growth rate as $GR = w_j /$ Number of days after
143 hatching, mg.day⁻¹.

144 *Leaf chemical traits* – We measured leaf C:N and phenolic content on 5-10 fully expanded intact
145 leaves collected on focal oak trees with larvae. Because larvae emerged before oak budburst, we were
146 able to collect leaves only at the end of the experiment. We were therefore not able to estimate leaf
147 traits before larvae started to feed and potentially induced systemic defences. We considered that
148 phenolic content measured on intact leaves represented constitutive defences before attacks occur
149 (Abdala-Roberts et al. 2016), but we acknowledge that the amount of phenolics may partly reflect

150 systemic induction of oak defences after attacks began. We dried leaves for 48h at 45°C directly after
151 leaf collection and ground dried material to fine powder before further chemical analyses.

152 First, we extracted phenolic compounds using 20 mg of dry plant tissue with 1 ml of 70% methanol in
153 an ultrasonic bath for 20 min, followed by centrifugation (Moreira et al. 2014b). We diluted
154 methanolic extracts (1:4 vol:vol) with an extraction solvent and transferred them to chromatographic
155 vials to perform chromatographic analyses. We carried out chromatographic analyses with an Ultra-
156 High-Performance Liquid-Chromatograph (UHPLC Nexera LC-30AD; Shimadzu Corporation, Kyoto,
157 Japan) equipped with a Nexera SIL-30AC injector and one SPD-M20A UV/VIS photodiode array
158 detector. The UHPLC column was a Kinetex™ 2.6 µm C18 82–102 Å, LC Column 100 × 4.6 mm,
159 protected with a C18 guard cartridge. The flow rate was 0.4 ml min⁻¹ and the oven temperature was set
160 to 25 °C. The mobile phase consisted of two solvents: water-formic acid (0.05%) (A) and acetonitrile-
161 formic acid (0.05%) (B), starting with 5% B and using a gradient to obtain 30% B at 4 min, 60% B at
162 10 min, 80% B at 13 min and 100% B at 15min. The injection volume was 3 µl. We recorded
163 chromatograms at 330 nm and processed data with the LabSolutions software (Shimadzu). We
164 identified four groups of phenolic compounds: flavonoids, ellagitannins and gallic acid derivatives
165 (“hydrolysable tannins” hereafter), proanthocyanidins (“condensed tannins” hereafter)
166 and hydroxycinnamic acid precursors to lignins (“lignins” hereafter). We quantified flavonoids as
167 rutin equivalents, condensed tannins as catechin equivalents, hydrolysable tannins as gallic acid
168 equivalents and lignins as ferulic acid equivalents. We achieved the quantification of these phenolic
169 compounds by external calibration using calibration curves based on chemical equivalent at 0.25, 0.5,
170 1 and 2 µg ml⁻¹. Second, we quantified leaf C:N ratio with a gas chromatography in an automatic
171 elemental analyser (FlashEA 1112; Thermo Fisher Scientific Inc.) using 0.006 g of dried leaf powder.

172 *Statistical analysis – Effect of focal and neighbour tree species identity on OPM performance and leaf*
173 *traits* – We tested the effect of focal oak species identity (*Focal*: *Q. petraea* vs. *Q. robur*), neighbour
174 species identity (*Neighbour*: Conspecific vs. Heterospecific) and their interaction (all fixed factors) on
175 OPM mortality (day⁻¹, square-root transformed) and growth rates (mg day⁻¹, log-transformed), as well
176 as on leaf chemical and nutritional traits and plant phenology. We used initial larval density as
177 covariate in models predicting OPM mortality and growth rate. We used Linear Model with Gaussian
178 error distribution and identity link, except for bud developmental stage (scored as an ordinal variable)
179 where we used an Ordinal Logistic Regression. For the growth rate, we performed the tests only for
180 plants with larvae still alive at the end of the experiment (i.e. n = 86 plants).

181 *Leaf traits associated with effects of focal and neighbour tree species identity on OPM performance* –
182 Based on previous analyses, if focal or neighbour tree identities had significant effects on herbivore
183 performance (growth and mortality), we ran the model again (with the same main fixed effects and
184 their interaction), while additionally including leaf traits as covariates potentially associated with
185 effects on leaf herbivory (“mechanistic model”; Abdala-Roberts et al. 2016; Moreira et al. 2017).

186 Rather than including all plant traits as covariates in the herbivore performance models and to reduce
187 issues arising from collinearity among predictors, we only retained traits which were significantly
188 associated with herbivore performance. For this, we ran a separate multiple regression including only
189 leaf traits (concentration of the four phenolic groups, bud development stage and C:N ratio) as
190 predictors of herbivore performance (two models, one for mortality and one for growth). We
191 computed variance inflation factors (VIFs) and verified that correlations among traits (in particular
192 among the concentration of the four types of phenolic compounds) did not inflate coefficient
193 parameter standard error estimates. All VIFs were < 5 . However, because there is no clear threshold
194 above which collinearity should be seen as a serious issue (O'Brien 2007), we also ran separate models
195 with the concentration of only one type of phenolic compound at a time. The results were unchanged
196 so we retained the complete model in the final analysis. Then we ran a second set of models including
197 the above selected traits as co-variates in models testing the effect of *Focal* and *Neighbour* species
198 identity on OPM performance. We used sequential decomposition of variance to test the effect of each
199 predictor. We fitted leaf traits before the effect of *Focal* and *Neighbour* species identity. With this
200 approach, if leaf traits mediate effects of focal species or neighbourhood on herbivore performance in
201 these mechanistic models, then the significant main effects in the prior models (without covariates)
202 should turn non-significant after including the covariates.

203 All analyses and figures were performed in R v3.5.1 (R Core Team 2018) with the following
204 packages: *tidyr*, *doBy* and *FSA* (Højsgaard and Halekoh 2018; Wickham and Henry 2018; Ogle et al.
205 2019) for data analysis, *multcomp*, *car* and *MASS* (Venables and Ripley 2002; Hothorn et al. 2008;
206 Fox and Weisberg 2011) for statistical analysis, *ggplot2*, *ggpubr* and *cowplot* (Wickham 2016; Wilke
207 2017; Kassambara 2019) for plots.

208 **Results**

209 *Effect of focal and neighbour tree species identity on OPM performance, leaf traits and plant* 210 *phenology*

211 OPM performance significantly differed between focal oak species (Table 1). In particular, OPM
212 larval mortality was on average twice higher and OPM growth rate was on average twice lower on
213 *Q. robur* than on *Q. petraea* (Fig. 1A, 1B), indicating that *Q. petraea* is a more suitable host for this
214 herbivore species. We did not find any significant effects of neighbour tree species identity nor *Focal*
215 \times *Neighbour* interaction on OPM larval mortality or growth rate (Fig 1, Table 1).

216 Some leaf traits significantly differed among focal oak species (Table 1). In particular, concentrations
217 of hydrolysable tannins and flavonoids were on average 1.7-fold higher and lower (respectively) in *Q.*
218 *petraea* than in *Q. robur* (Fig. 2). We did not find significant effects of neighbour tree species identity
219 on leaf traits (Table 1). However, the *Focal* \times *Neighbour* interaction significantly affected leaf
220 flavonoid concentration and C:N (Table 1). Specifically, the concentration of flavonoids was on

221 average 1.5 times higher in *Q. robur* in presence of heterospecific neighbours, whereas the C:N ratio
222 was on average 1.2 time higher in *Q. petraea* in presence of conspecific neighbours (Fig 3). Phenology
223 was not significantly affected by focal or neighbour species (Table 1).

224 *Leaf traits associated with effects of focal and neighbour tree species identity on OPM performance*

225 Bud phenology, but not C:N nor concentrations of any type of phenolic compounds, had a significant
226 effect on OPM growth and mortality rate (Table S1). OPM larvae performed better (lower mortality
227 and better growth) when neonate had access to open buds with expanding leaves (Fig. 3 AB).

228 The significant effect of focal oak species identity on OPM performance (growth and mortality)
229 remained significant after including bud phenology as covariate (Table 2), indicating that phenology
230 did not determine all the observed differences in herbivore performance between the two oak species.

231 **Discussion**

232 *Effects of oak species identity on OPM performance and leaf traits*

233 Our results showed tree species-specific differences in OPM performance. In particular, OPM grew
234 faster and suffered lower mortality rates when feeding on *Q. petraea* in comparison with *Q. robur*.
235 Noteworthy, although our study was not designed to survey OPM development time, a greater
236 proportion of *Q. petraea* than *Q. robur* seemed to have OPM larvae that had reached the third instar at
237 the end of our experiment (26 days) (Fig 4). These findings are consistent with two previous studies
238 from our group. In a field experiment with mature oak trees, (Damestoy et al. under review) found that
239 *Q. petraea* was consistently more attractive to OPM moths (i.e. more captures of moths in *Q. petraea*
240 stands by pheromone trapping) and more defoliated than *Q. robur* (Damestoy et al. under review).
241 Similarly, in a greenhouse experiment with one-year-old oak saplings Moreira et al. (2018a) found that
242 leaf damage by gypsy moth larvae (*Lymantria dispar*) was significantly greater on *Q. petraea* than on
243 *Q. robur*.

244 We also found species-specific differences in oak leaf traits. Contents of hydrolysable tannins were
245 higher in *Q. petraea* whereas flavonoids were higher in *Q. robur*. These two oak species have
246 previously been reported to differ in leaf and wood chemistry (Thomas and Schafellner 1999; Guchu
247 et al. 2006; Hu et al. 2013). For instance, several studies have shown that the wood of *Q. petraea* is
248 characterised by lower amounts of ellagitannins compared to *Q. robur* (Mosedale and Savill 1996;
249 Feuillat et al. 1997; Mosedale et al. 1998; Prida et al. 2006, 2007). Together, these results suggest that
250 intra-specific variability in herbivore performance were independent of plant defences.

251

252 *Leaf traits associated with effects of focal tree species identity on OPM performance*

253 Our results showed that only leaf phenology had a significant effect on OPM performance.
254 Specifically, OPM larvae performed better when neonate had access to open buds with expanding

255 leaves. The need for synchrony between herbivore and plant phenology is well documented in the
256 literature (van Asch and Visser 2007; Forkner et al. 2008; Wagenhoff and Veit 2011; Meurisse et al.
257 2012; Wagenhoff et al. 2013). In oaks, leaf quality for lepidopteran larvae decreases sharply after
258 budburst. Larvae emerging before leaf flush starve because of a lack of food while larvae emerging too
259 late after budburst have to cope with harder, less nutritious and more defended leaves (Feeny 1968,
260 1970; Tikkanen and Julkunen-Tiitto 2003; Forkner et al. 2004; van Asch and Visser 2007; Van Asch et
261 al. 2010). Several studies showed that OPM neonates are able to survive for a period of up to 2-3
262 weeks without food (Wagenhoff and Veit 2011; Meurisse et al. 2012; Wagenhoff et al. 2013), making
263 less stringent the need for synchrony. In our study, most of the trees had already opening buds when
264 OPM larvae emerged such that only few of them were exposed to a brief starvation period. However,
265 we conducted this experiment in a greenhouse and larvae were bagged in only one branch. Larvae
266 were therefore subjected to competition for the available resource (i.e. opening buds and young
267 leaves). Food may have been particularly limiting for those larvae that emerged on late-flushing oaks,
268 which could explain why OPM larvae performed better on oaks whose leaves were more developed at
269 the time of egg hatching.

270 Although bud phenology and herbivore performance were significantly correlated, we found that the
271 effect of focal species identity on OPM performance remained significant after bud phenology was
272 accounted for as a covariate in statistical models. This result indicates that differences in herbivore
273 performance between the two studied oak species depend on other factors than plant phenology. For
274 instance, both oak species might markedly differ in chemical (e.g. volatiles) or physical (e.g. leaf
275 toughness, trichomes) defensive traits (Clissold et al. 2009; Carmona et al. 2011; Caldwell et al. 2016),
276 which could in turn drive herbivore response.

277 Contrary to our predictions, neither the concentration of phenolic compounds nor C:N ratio had
278 significant effects on OPM performance. These results contradict the common view that phenolic
279 compounds act as chemical anti-herbivore defences (Feeny 1976; Lill and Marquis 2001; Forkner et
280 al. 2004). It is possible that their negative effect on OPM performance were balanced by a
281 compensatory feeding (Lazarevic et al. 2002; Barbehenn et al. 2009; Damestoy et al. 2019). Moreover,
282 most herbivores are generally N-limited (Mattson 1980), resulting in negative relationship between
283 herbivore performance and C:N ratio in consumed plant tissues (Mattson 1980; White 1984). In our
284 study, C:N ratio was negatively correlated with the concentration of phenolic compounds such that
285 their adverse effect on OPM larvae could have been compensated by the positive effect of nitrogen
286 relative abundance. It is also important to note that because of methodological constraints, we
287 measured chemical traits at the end of the experiment. As a consequence, our measured leaf traits
288 might not perfectly represent the nutritional quality and defences of leaves OPM larvae had access to.

289 *Effects of oak neighbour species identity on OPM performance and leaf traits*

290 Oak neighbour species identity had no significant effects on OPM performance. However, it is
291 important to note these non-significant results should be interpreted with caution for several reasons.
292 First, our experiment was conducted on the short term so we cannot extrapolate our findings to neither
293 OPM complete development time and adult mass or fecundity nor population dynamics. Second, we
294 randomly allocated OPM egg-masses to the different treatments. Yet, in the wild, OPM performances
295 on a particular tree primarily depend on host selection by gravid females foraging for oviposition sites,
296 which may be influenced by neighbours (Damestoy et al. under review; Gripenberg et al. 2010). For
297 instance, studies conducted on the pine processionary moth showed that the presence of non-host trees
298 in mixed stands could protect the host trees from pest attacks. In this model, non-host trees were found
299 to disrupt host detection by the pine processionary moth by interfering with the visual and chemical
300 cues emitted by the host tree (Jactel et al. 2011; Dulaurent et al. 2012; Castagneyrol et al. 2013, 2014).
301 Third, because we kept the neighbouring saplings intact, it is possible that the rate of VOCs emission,
302 usually induced by leaf damage (Arimura et al. 2001; Turlings and Ton 2006; Barbosa et al. 2009;
303 Scala et al. 2013), was too low to induce noticeable change in leaf traits of the focal oak sapling. A
304 better understanding of the effect of oak neighbours on OPM would therefore require the integration of
305 the effects of neighbours on both host selection behaviour and their subsequent consequences for the
306 fitness of OPM offspring.

307 Our results also showed that oak neighbour species identity did not significantly affect leaf traits.
308 These results contradict previous findings showing changes in leaf traits (physical, nutritional or
309 chemical defence traits) in mixtures e.g., in oak (Nickmans et al. 2015; Castagneyrol et al. 2017), birch
310 (Castagneyrol et al. 2018a; Muiruri et al. 2019), mahogany (Moreira et al. 2014a), common ragwort
311 (Kos et al. 2015c; Kostenko et al. 2017) or velvet grass (Walter et al. 2012). In forests, neighbour-
312 induced changes in leaf traits can be mediated by changes in the abiotic conditions (e.g. light) around
313 focal trees (Castagneyrol et al. 2017, 2018a; Muiruri et al. 2019). Here, our oak saplings had the same
314 age and similar size such that they were unlikely affected by the shade of their neighbours. Neighbour-
315 mediated effects on leaf traits can be also mediated by the emission of volatile organic compounds by
316 neighbouring trees (Arimura et al. 2001; Turlings and Ton 2006; Barbosa et al. 2009). However, we
317 conducted the experiment in a greenhouse with only few decimetres between adjacent pots, such that
318 volatiles emitted by every oak may have blended within the greenhouse. Finally, neighbour-mediated
319 effects on leaf traits can be also mediated by belowground processes. For example, plants have well
320 documented effects on soil microbes which can in turn influence the growth and defences of their
321 neighbours through plant-soil feedbacks (Pineda et al. 2010; Van der Putten et al. 2013; Kos et al.
322 2015c, b; Correia et al. 2018). Moreover, there is evidence that microbes in the rhizosphere of a plant
323 can influence herbivory on another plant through changes in its leaf chemical content (Badri et al.
324 2013). In the condition of our experiment these belowground processes could explain the significant
325 effect of *Focal* × *Neighbour* species identity interaction. In particular, *Q. robur* saplings increased

326 their investment in flavonoids and *Q. petraea* had lower C:N when they were associated with
327 heterospecific neighbours. Although this research area is too recent as yet to allow further speculation
328 on the mechanisms that drove species-specific differences in oak leaf traits in the presence of
329 conspecific *vs.* heterospecific neighbours, this would represent a fascinating area for further
330 investigations.

331 *Conclusion*

332 Overall, our study showed that OPM larvae performed better on *Q. petraea* than *Q. robur* saplings,
333 suggesting that *Q. petraea* trees are more susceptible to OPM defoliation. These findings have
334 implications for forest management as they indicate that the pedunculate oak should be preferred over
335 the sessile oak to promote oak forest resistance to OPM. However, we need more insight into host
336 preference mechanisms and particularly how OPM females use volatile organic compounds to
337 differentiate and choose between the two oak species.

338 We found that synchronization between leaf and larval development is key factor for OPM
339 performances. Because changes in temperature might differentially affect bud burst and egg hatching
340 phenologies more controlled experiments, *e.g.* in climatic chambers, are needed to predict the effects
341 of climate change on OPM performances and associated defoliation damage.

342 We could not find clear impact of neighbour identity on OPM performance. However, we used sibling
343 species as models to test diversity effects. We therefore suggest matching oaks with more distant
344 species, such as other non-host deciduous trees or conifers, to identify associative resistance processes
345 as a means of managing OPM.

346

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572

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577

578 **Legends figures and table**

579 **Fig 1AB** Effect of focal (symbols) and neighbour (colour) tree species identity on OPM mortality (A)
580 and growth rates (B). Small symbols represent raw data. Large symbols and vertical error bars
581 represent raw means \pm SE. Letters above dots represent outputs of post-hoc tests. Different letters
582 indicate statistically significant differences between treatments

583 **Table 1** Summary statistics of models testing the effects of Focal and Neighbour species identities and
584 their interaction on OPM larval performances (mortality and growth rate), leaf traits and leaf
585 phenology. Linear models were used to test the effects of Focal and Neighbour species identity on
586 OPM growth and mortality and all leaf traits. For Bud phenology we used Ordinal logistic regression.
587 Significant coefficients ($P < 0.05$) are in bold

588 **Fig 2** Effect of focal (symbols) and neighbour (colour) tree species identity on the leaf traits of the
589 focal trees. Small symbols represent raw data. Large symbols and vertical error bars represent raw
590 means \pm SE. Letters above dots represent outputs of post-hoc tests. Different letters indicate
591 statistically significant differences between treatments

592 **Fig 3AB** Effect of bud developmental stage (measured with a seven-levels ordinal scale from 0 [closed
593 apical bud] to 6 [fully expanded leaves]) at the time OPM hatched on OPM growth rate (A) and
594 mortality (B). Symbols and vertical error bars represent raw means \pm SE, black squares are for
595 *Q. robur* and white triangles for *Q. petraea*. Letters above dots represent outputs post-hoc tests.
596 Different letters indicate statistically significant differences between bud developmental stages

597 **Table 2** Summary statistics of mechanistic models testing the effects of Focal and Neighbour species
598 identities and their interaction on OPM performance (mortality and growth rate). For both models, we
599 included bud phenology as a covariate to test if the effect of focal species identity on herbivore
600 performance was determined by this factor. We also include initial larval density as covariate.
601 Significant coefficients ($P < 0.05$) are in bold

602 **Fig 4** *Proportion of plant with each of larval instar in each treatment at the end of the experiment. L1*
603 *= light grey, L2 = mid grey, L3 = dark grey.*

604

605 **Table 1**

Response Variables	Predictors					
	Focal species		Neighbour species		F × N	
	F _{numdf, dendif}	P-value	F _{numdf, dendif}	P-value	F _{numdf, dendif}	P-value
OPM mortality	17.46 _{1, 91}	< 0.001	17.83 _{1, 90}	0.214	0.08 _{1, 89}	0.776
OPM growth	8.99 _{1, 84}	0.004	2.79 _{1, 82}	0.099	0.34 _{1, 81}	0.563
Flavonoids	16.16 _{1, 90}	< 0.001	1.36 _{1, 90}	0.245	5.41 _{1, 90}	0.022
Lignins	0.78 _{1, 91}	0.379	2.03 _{1, 92}	0.157	2.67 _{1, 90}	0.105
Condensed tannins	1.29 _{1, 92}	0.258	0.00 _{1, 91}	0.962	1.48 _{1, 90}	0.227
Hydrolysable tannins	14.57 _{1, 92}	< 0.001	0.95 _{1, 91}	0.331	0.76 _{1, 90}	0.387
C:N	2.32 _{1, 90}	0.131	0.94 _{1, 90}	0.334	8.86 _{1, 90}	0.004
	LR Chisq (Df)	P-value	LR Chisq (Df)	P-value	LR Chi-sq (Df)	P-value
Bud phenology	2.40 (1)	0.122	1.07 (1)	0.300	0.44 (6)	0.508

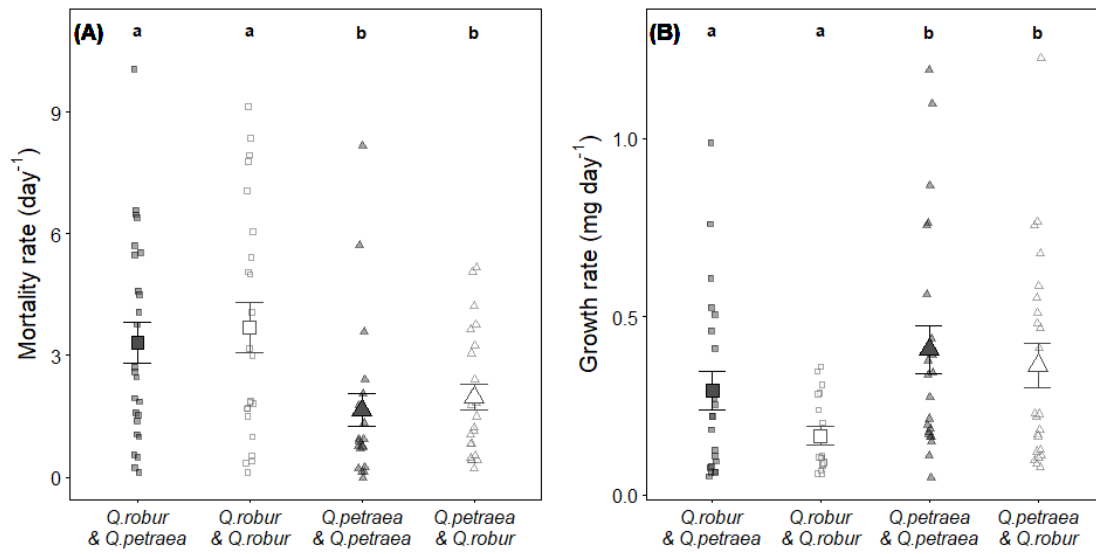
606

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608 **Table 2**

Predictors	OPM mortality		OPM growth	
	F _{numdf, dendif}	P-value	F _{numdf, dendif}	P-value
Focal	9.47 _{1, 85}	0.002	9.54 _{1, 77}	0.003
Neighbour	2.34 _{1, 84}	0.130	3.63 _{1, 76}	0.061
Focal × Neighbour	1.47 _{1, 83}	0.229	0.24 _{1, 75}	0.629
Bud phenology	6.28 _{6, 85}	< 0.001	4.28 _{6, 77}	< 0.001
Initial density	24.97 _{1, 85}	< 0.001	4.40 _{1, 77}	0.039

609

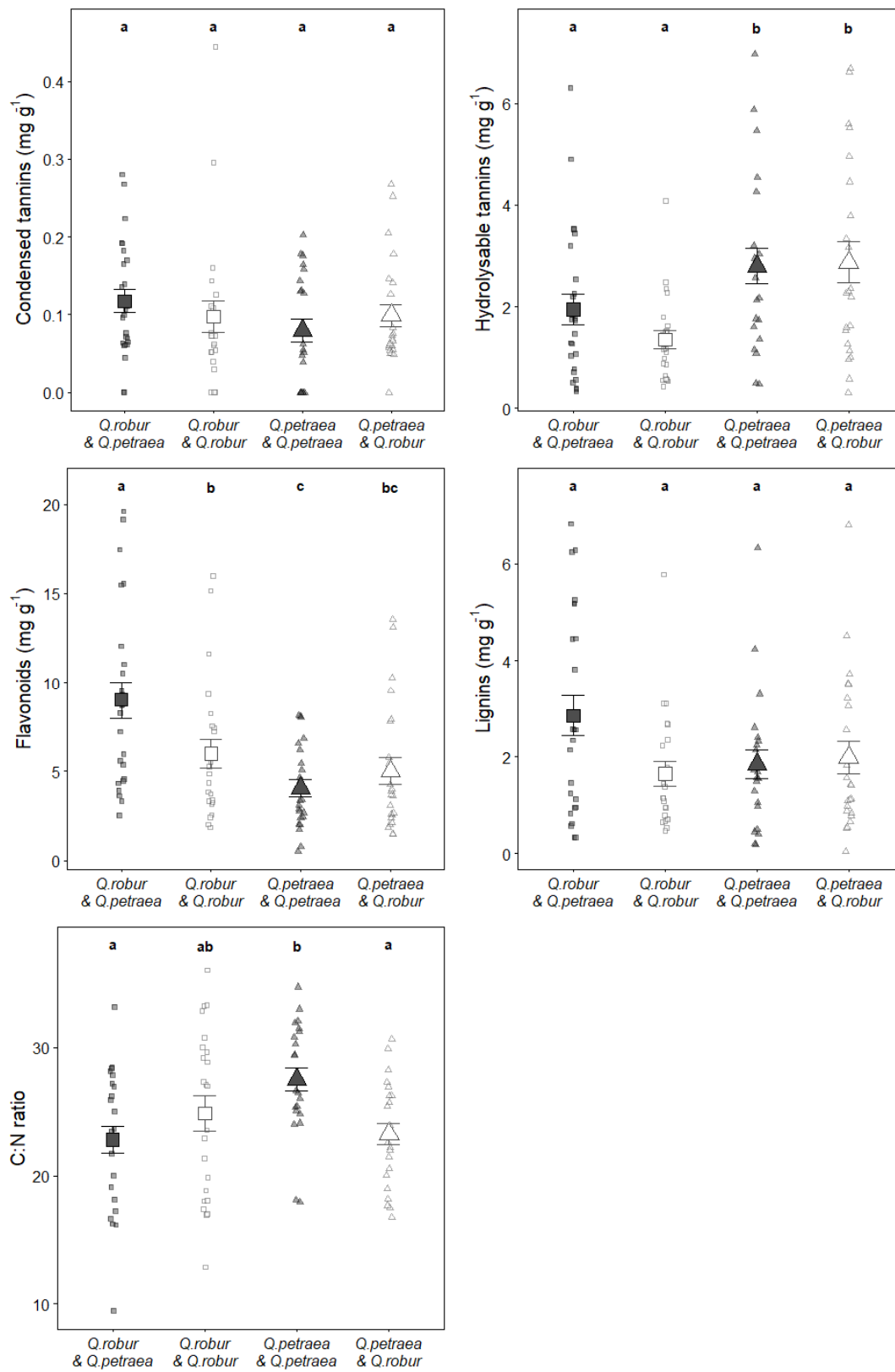


1

2 **Figure 1AB**

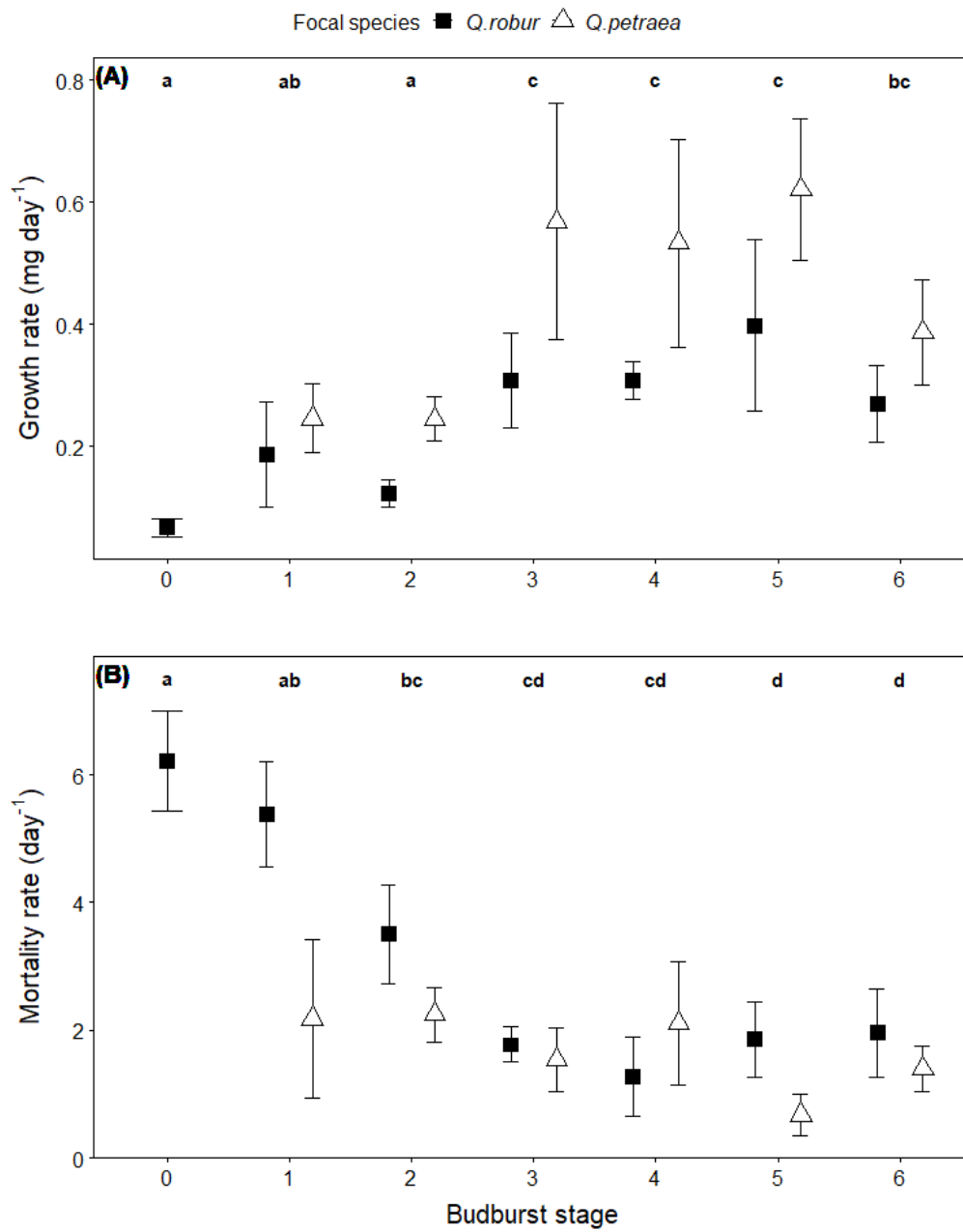
3

4



5

6 **Figure 2**



7

8 **Figure 3AB**

9

10

OPM larval instars

L1 → L2 → L3

Q. petraea > 65% larvae reached L3 instar



Q. robur > 34% larvae still in L1 instar



11 0 25 50 75 100 %

12 **Figure 4**

13

14