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1 **Changes in host basal area explain associational resistance of mixed forests to** 2 **primary pests**

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8 **Abstract**

9 Tree species diversity generally has positive effects on forest primary productivity and resistance to
10 natural perturbations, but diversity-function relationships can vary with site conditions. Recently,
11 studies in forest diversity experiments have shown that tree diversity and local climate, in particular
12 drought intensity, interactively affect insect herbivory. On the other hand, many studies focused on
13 the response of forests to drought in terms of tree growth but without analysing the concomitant
14 effects on susceptibility to pests. It is of particular interest to understand the combined effects of
15 drought and tree diversity on the growth of the host tree, since host resource concentration is a
16 determining factor of a pest's host choice.

17 We used a tree diversity experiment where tree species diversity and drought conditions were both
18 manipulated to evaluate their interactive effects on the susceptibility of maritime pine (*Pinus*
19 *pinaster* Ait.) forests to two primary pests (i.e. infesting healthy trees): the pine stem borer (PSB)
20 *Dioryctria sylvestrella*, and the pine processionary moth (PPM; a leaf chewer), *Thaumetopoea*
21 *pityocampa*. Using structural equation models, we investigated the direct and indirect effects (i.e.
22 mediated by host resources) of the presence of birch and drought on the total number of attacks of
23 PPM and PSB, in the same plots and in the same year.

24 We showed that pine-birch plots were more resistant to both PPM and PSB attacks than pine
25 monocultures. Furthermore, we found that this associational resistance pattern was due to direct
26 effects of birch trees on attacks, possibly related to disrupting non-host volatiles (NHVs), but also to
27 indirect, resource-mediated effects whereby the presence of birch trees reduced the amount of host
28 pine resources available to the pests. Drought conditions modulated birch mediated effects on
29 resistance of maritime pine forests only for PSB attacks. Overall, our work improves our
30 understanding of tree diversity-herbivory relationships and helps explain how climate might
31 modulate such relationships.

32

33 **Keywords**

34 *Betula pendula*, biodiversity, *Dioryctria sylvestrella*, host concentration, non-host volatiles, *Pinus*
35 *pinaster*, *Thaumetopoea pityocampa*, tree growth

36 **Introduction**

37 A consensus is arising about the relevance of tree species diversity for forest ecosystem functioning
38 (Pretzsch et al., 2017). Observational and experimental evidence are accumulating on positive effects
39 of forest compositional diversity on primary productivity (e.g. Zhang et al., 2012; Liang et al., 2016)
40 and resistance to natural perturbations (Jactel et al., 2017). In particular, it has been shown that
41 insect herbivore damage is often less severe on a tree species grown in a mixed stand than in a
42 monoculture, a phenomenon known as associational resistance (Jactel et al. 2021). However,
43 another general finding is that relationships between tree diversity and ecosystem functioning show
44 wide variations at the regional or continental scale, being largely dependent on site conditions
45 (Ratcliffe et al., 2017). For example, Jactel et al. (2018) and Steckel et al. (2019) showed that
46overyielding in mixed species forests decreases with dryer conditions. This is important because the
47 frequency and severity of droughts are expected to increase under the current climate change (IPCC,
48 2014; Lehner et al., 2017) with consequences for the long-term stability of mixed forest productivity
49 (Jucker et al., 2014; Morin et al. 2018). Much less is known on how local climatic conditions modulate
50 the effect of tree species diversity on forest resistance to insect herbivores. Only recently, studies in
51 forest diversity experiments have shown that local climate, in particular drought intensity, affected
52 diversity–herbivory relationships in tree stands (Castagneyrol et al., 2018; Jactel et al., 2019; Field et
53 al., 2020; Poeydebat et al., 2020). Conversely, a number of recent studies have investigated the
54 effect of tree species mixing on forest resistance to drought, showing positive, neutral and negative
55 effects depending on forest biomes (Grossiord et al. 2014) and forest species (Forrester et al. 2016).
56 However, these studies mostly focused on the response of forests to drought in terms of tree growth
57 but without analysing the concomitant effects on susceptibility to pests.

58 One main mechanism to explain associational resistance to insect herbivory in mixed forests is that
59 the presence of heterospecific neighbours around a tree of a focal species leads to a lower
60 probability of host tree finding by insect herbivores (Jactel et al. 2021) due i) to lower host

61 abundance or frequency (resource concentration hypothesis, Root 1973) or ii) to the disrupting effect
62 resulting from the visual or olfactory cues emitted by non-host trees (host apparency hypothesis,
63 Castagneyrol et al. 2013). The positive effects of species mixing on tree growth (Jactel et al. 2018)
64 may affect both mechanisms, as larger host trees provide more food resources but may also release
65 more attractive signals. However, there is a general trade-off between growth and differentiation
66 (Herms and Mattson 1992), so that any effect of tree diversity on growth may alter the ability of
67 trees to produce secondary metabolites (Moreira et al., 2014; Muiruri et al., 2019).

68 Drought, by causing stomatal closure, and reduced photosynthesis and carbon fixation, can affect
69 host tree growth and secondary metabolism as well (Koricheva et al., 1998; Peñuelas & Staudt,
70 2010), and thus may interact with species diversity effects on resistance to herbivory (Castagneyrol
71 et al., 2018a; b). Similarly, drought conditions can also affect the growth of heterospecific neighbours
72 and the amount of non-host volatiles (NHVs) they release, thus modulating their role in preventing
73 insect pests from finding their host trees. There is growing evidence that drought conditions and
74 heterospecific neighbours jointly determine the visual and olfactory apparency of host trees, as well
75 as their suitability and nutritional quality to herbivores (Castagneyrol et al., 2018; Muiruri et al.,
76 2020).

77

78 In this study, we used a tree diversity experiment where tree species richness and drought conditions
79 were both manipulated to evaluate their interactive effects on the susceptibility of maritime pine
80 (*Pinus pinaster* Ait.) forests to two moths that are both primary pests (i.e. infesting healthy trees): the
81 pine processionary moth (*Thaumetopoea pityocampa* Denis & Schiffermüller) with larvae feeding on
82 the needles and the pine stem borer (*Dioryctria sylvestrella* Ratz.) with larvae feeding on the trunk
83 phloem. Although several studies have demonstrated that processionary moth infestations are
84 significantly lower in mixed stands than in pure stands of maritime pine, particularly in the presence
85 of the non-host species *Betula pendula* (Castagneyrol et al., 2013; Damien et al., 2016; Castagneyrol

86 et al., 2020), none have yet investigated whether this associational resistance pattern would change
87 with drought conditions. The pine stem borer preferentially attacks fast-growing trees with more
88 bark cracks that release attractive chemicals (terpenes) in greater quantity (Jactel et al. 1996, 2019).
89 In a previous study, we found that the number of stem borer attacks per plot decreased with the
90 presence of birch, but only in non-water stressed plots, suggesting an interaction between drought
91 and tree species diversity (Jactel et al. 2019).

92 However, we did not specifically evaluate the respective direct and indirect effects of the presence of
93 birch on associational resistance, i.e. via a direct repellence effect of non-host volatiles (NHVs) or
94 indirectly via a reduction of pine growth due to competition with fast-growing birch neighbours,
95 particularly under water stress conditions. In this study, we particularly focused on the plot scale
96 because it better allowed us to test the resource concentration hypothesis to explain associational
97 resistance in mixed forests (here of pine and birch). Patrolling insects may already come into contact
98 with specific host tree cues, i.e. visual or olfactory signals, outside the forest stand (Hambäck et al.,
99 2010). Once in a suitable habitat, the “resource concentration hypothesis” (Hambäck and Englund,
100 2005) predicts that insect specialists are less likely to emigrate from habitat patches where host
101 plants are more abundant (Hambäck et al., 2000; Underwood et al., 2014), which is the case in pure,
102 high density stands. In mixed forests, resource abundance would instead decrease in relative (due to
103 the presence of non-host trees) and absolute (depending on host tree density and host tree size)
104 terms, making them less susceptible to pest attack.

105 Here, using structural equation models, we aimed at disentangling the direct and indirect
106 associational effects of the presence of birch and moderate drought on the number of processionary
107 moth and stem borer attacks on maritime pines, in the same plots and in the same year. By direct
108 effects we mean the effects of the presence of birch trees that disturb the insects' recognition of the
109 favourable habitat (plot) by their olfactory or visual signals. By indirect effects we mean the effects of
110 the proximity of birches on the growth of maritime pine and therefore the quantity of substrate

111 favourable to insect feeding (at the plot level), as well as the amount of visual and olfactory host
112 cues. As this amount of substrate also depends on the density of host trees per plot, we also took
113 this explicitly into account in our models.

114 **Materials & Methods**

115 Model species

116 The maritime pine (*Pinus pinaster*) is a coniferous species that originates from the western
117 Mediterranean basin (Abad Viñas et al., 2016). Naturally, it grows in warm temperate regions with an
118 oceanic influence, mainly in humid and sub-humid areas, with a preference for poor siliceous soils
119 with a coarse texture (sandy soils, dunes and other poor substrates). Maritime pine is a fast-growing
120 species that cannot tolerate shade but exhibits good tolerance to drought (embolism resistance Ψ_{50}
121 ≈ -3.6 MPa, Corcuera et al., 2011).

122 The silver birch (*Betula pendula*) is a deciduous tree native to most of Europe (Beck et al., 2016) that
123 tolerates a wide range of climatic and edaphic conditions, but shows lower tolerance to drought than
124 *P. pinaster* ($\Psi_{50} \approx -2.3$ MPa, Cochard et al., 2005). It is a pioneer, fast-growing species, with low
125 tolerance to shading.

126 The pine processionary moth (PPM) *Thaumetopoea pityocampa* (Notodontidae) and the pine stem
127 borer (PSB) *Dioryctria sylvestrella* (Pyralidae) are two lepidopteran pests of pines. Both are
128 oligophagous pests that can attack several species of pines (e.g. *Pinus pinaster*, *Pinus nigra*, *Pinus*
129 *sylvestris*). They can attack and develop successfully on healthy trees and are therefore considered
130 primary pests (Jactel et al., 1996; Régolini et al., 2014). PPM is the main defoliator of pine species
131 around the Mediterranean Basin (Roques et al., 2015).

132 In both species, adults emerge in early summer. After mating, females choose a host pine on which
133 to lay their eggs. PPM females deposit their eggs on the needles of the selected host. Larvae develop
134 throughout autumn and winter and feed on needles causing low to extreme defoliation, leading to

135 more or less severe growth loss the next two years (Jacquet et al., 2013; Sangüesa-Barreda et al.,
136 2014). In winter when temperature is low, larvae weave dense silk nests (white and easily detectable
137 from the ground, see Fig. 1a) to protect themselves from the frost. At the end of winter, caterpillars
138 move down from the tree crown to the ground in procession and bury themselves in the soil where
139 they pupate until next summer.



140 **Figure 1.** Pine processionary moth (*Thaumetopoea pityocampa*) nest in the crown of a maritime pine during
141 winter (a) and the entry point of a pine stem borer (*Dioryctria sylvestrella*) gallery with a typical resin-and-frass
142 exudate (b).
143

144 PSB females are attracted by volatile terpenic compounds of the resin and preferentially choose
145 vigorous host pines with more bark cracks and a stronger resin smell (Jactel et al., 1996, Kleinheintz
146 et al. 1999). Eggs are laid individually in bark cracks of the trunk during the summer. Young larvae
147 tunnel through the bark into the phloem where they feed until autumn. They overwinter in their
148 gallery and resume boring activity in early spring until the pupal stage in late spring. The horizontal,
149 subcortical larval galleries break resin ducts, inducing resin flow mixed with frass, through the entry
150 hole (see Fig. 1b). Yellow to pinkish coagulated resin on a tree trunk indicate a recent PSB attack.
151 Larval galleries interrupt the flow of sap, resulting in deformation of the trunk and an increased risk
152 of breakage in the event of windstorm (Baronio & Butturini, 1988).

153 Experimental design (ORPHEE)

154 The ORPHEE tree diversity experiment (<https://sites.google.com/view/orpheexperiment/home>) is
155 located in Southwest of France (44°44'24.9"N; 00°47'48.1"W) and consists of a 25600 trees
156 plantation covering 12 hectares. It was planted in 2008 on a sandy soil. At ORPHEE location, mean
157 annual temperature is 13.6 °C and mean annual cumulated rainfall is 893 mm (1979-2013 average
158 climate from the CHELSA database; <https://chelsa-climate.org/>; Karger et al., 2017).

159 The experimental set up consists of 8 replicated blocks, of which half have been irrigated since 2015.
160 Each of the four irrigated blocks is sprinkled at night with 42m³ of water (block area of 1.28 ha), daily
161 from May to October, which significantly reduces tree water stress as compared to non-irrigated
162 blocks (Castagneyrol et al. 2017; Maxwell et al., 2020). In view of the ombrothermic data (Maxwell et
163 al., 2020 Fig. S1) and the absence of severe drought-induced damage to pines and birches (in 2016,
164 the mean \pm sd predawn leaf water potential of maritime pines in non-irrigated blocks was $-1.54 \pm$
165 0.43 MPa), drought conditions in non-irrigated blocks were considered moderate.

166 The ORPHEE experiment involves 5 tree species: maritime pine (*Pinus pinaster*), silver birch (*Betula*
167 *pendula*), pedunculate oak (*Quercus robur*), Pyrenean oak (*Quercus pyrenaica*) and green oak
168 (*Quercus ilex*). Each block of the experiment consists of 32 randomly distributed plots corresponding
169 to all the possible combinations of one to five tree species: each species monoculture and each 2- to
170 5-species mixture, the 5-species mixture being duplicated. Each plot contains 100 trees planted in 10
171 rows of 10 trees spaced 2m apart. Mixed plots were planted following a substitutive design with a
172 regular alternate pattern.

173 At the time of sampling (8 years after ORPHEE plantation), oaks were still very small (less than 1m
174 tall) compared to pines and birches (about 5.5m tall) (Damien et al., 2016). They were considered to
175 belong to the understorey vegetation of the plots, with very limited impact on tree (pine and birch)
176 growth. Therefore, mixtures of pines and oaks were considered pine monocultures, and mixtures of
177 pines, birches and oaks were considered pine-birch mixtures, both with different pine densities

178 depending on the number of oak species in the plot (see Supporting Information Table S1). In each
179 block, we selected all the plots with maritime pine, except the true pine monoculture and the 5-
180 species mixtures, to have both pine monocultures and pine-birch mixtures at the three levels of pine
181 density considered, i.e. 50, 33 and 25 pines per plot (Damien et al. 2016). In total, we surveyed 14
182 plots per block, representing 112 plots in total, half of which were irrigated (4 irrigated blocks and 4
183 non-irrigated blocks). We removed 8 plots where data from more than 30% of the trees were missing
184 for either pest species, resulting in a total of 104 plots for the analyses of both pest species.

185 We measured the circumference at breast height (CBH) of each pine in the central part (i.e. 36 inner
186 trees) of all plots, and computed the basal area (BA) in cm² of each pine as follows:

$$187 \quad BA = \frac{CBH^2}{4\pi}$$

188 We computed a proxy of the total pine basal area of the plot as the sum of the basal area of all pines
189 in the inner part of the plot, where CBH was measured. Because the plots of the ORPHEE experiment
190 were planted in a regular pattern, the density of pines in the inner portion of the plot was the same
191 as that of the entire plot. We did the same for *B. pendula* in plots where it was present (see
192 Supporting Information Table S2 for details per plot type). Since all trees are of the same age in the
193 ORPHEE experiment, we believe it was reasonable to consider total basal area per plot to be a good
194 proxy of the concentration of pine resources in a plot.

195 We assessed the total number of PPM and PSB attacks (*i.e.* nests and resin-and-frass exudates,
196 respectively) in each plot, considering all the pines present for PPM and pines of the inner part of
197 plots for PSB (as for BA). We counted the total number of PPM nests in pine crowns in January 2017,
198 when the nests corresponding to summer 2016 egg laying were detectable (*i.e.* white silk tents). In
199 late summer 2016, we counted the total number of fresh (from the current year) PSB attacks on tree
200 trunks.

201

202

203 Statistical analysis

204 We used structural equation models (SEM; Grace, 2006) to investigate the direct (association with
205 birch) and indirect (i.e. mediated by the concentration of host resources, here basal area) effects of
206 tree diversity, climate (drought) and their interaction on the number of PPM and PSB attacks in pine
207 plots, while accounting for pine density (i.e. number of host trees).

208 We built one SEM per pest species at the plot level, each composed of two linear mixed-effect
209 models (M1 and M2) in which we added the block and the irrigation treatment as nested random
210 intercept effects, to account for the non-independence of the plots due to the experimental design
211 (Zuur et al., 2009). Because the application of traditional SEM is restricted to normally distributed
212 data, we used the piecewise SEM approach (Shipley, 2009; Lefcheck et al., 2016), which generalises
213 the method to a larger range of distribution families and to mixed effect models. The SEMs were
214 written as follow in R syntax:

215 M = psem

216 (M1 = glmer (Total number of attacks per plot ~ (Birch presence + Pine density) * Irrigation + Total
217 pine basal area + (1|Block:Irrigation), data, family="poisson"),

218 M2 = lmer (Total pine basal area ~ (Birch presence + Pine density) * Irrigation + (1|Block:Irrigation),
219 data))

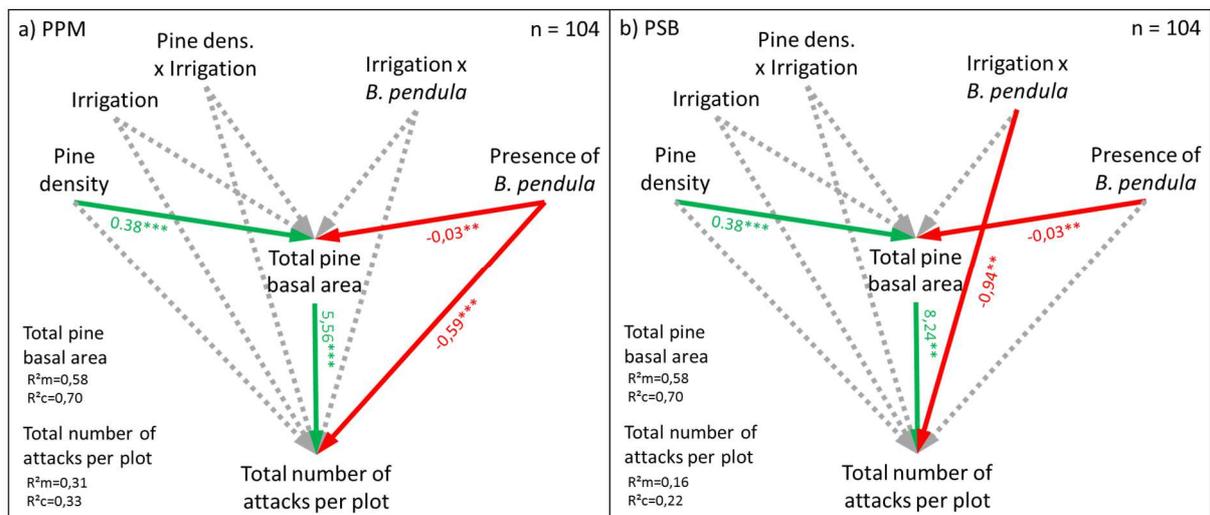
220 We identified the significant relationships and computed an unstandardized coefficient for each
221 path. Unstandardized coefficients are expressed in the same unit as the response variable and are
222 therefore useful to interpret the magnitude of the effects. In our case, they also allowed comparison
223 of the PPM and PSB models. We also computed the marginal R^2 (R^2_m , i.e. the variance explained by
224 fixed effects) and the conditional R^2 (R^2_c , i.e. the variance explained by both fixed and random
225 effects) as indicators of the goodness-of-fit of each sub-model (Nakagawa and Schielzeth, 2013).

226 All analyses were run using R (R Core Development Team, 2013) and the lmer4 (Bates et al., 2015)
 227 and piecewiseSEM (v2.1.0, Lefcheck et al., 2016) packages.

228 **Results**

229 The total number of attacks per plot varied from 0 to 12 for PPM and from 0 to 7 for PSB. On
 230 average, there were more PPM than PSB attacks per plot: 3.50 ± 2.73 nests vs 1.54 ± 1.59 resin-and-
 231 frass exudates per plot, respectively (see Supporting Information Table S2 for detail per plot type).

232



233

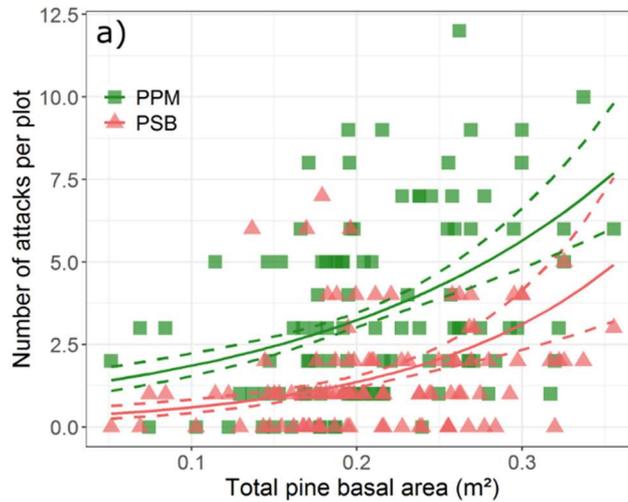
234 **Figure 2.** Structural equation models (SEM) for a) the pine processionary moth (PPM) and b) the pine stem borer
 235 (PSB) at the plot level. Grey dashed arrows represent non-significant paths. Red and green arrows represent
 236 significant paths, respectively associated with a negative or a positive coefficient. The path coefficients
 237 correspond to unstandardized coefficients interpretable in the unit of the variables. Stars indicate the
 238 significance level as follow: “****” when p-value is ≤ 0.001 , “***” when p-value is between 0.001 and 0.01, and
 239 “**” when p-value is between 0.01 and 0.05. Details are provided in Table S3.

240

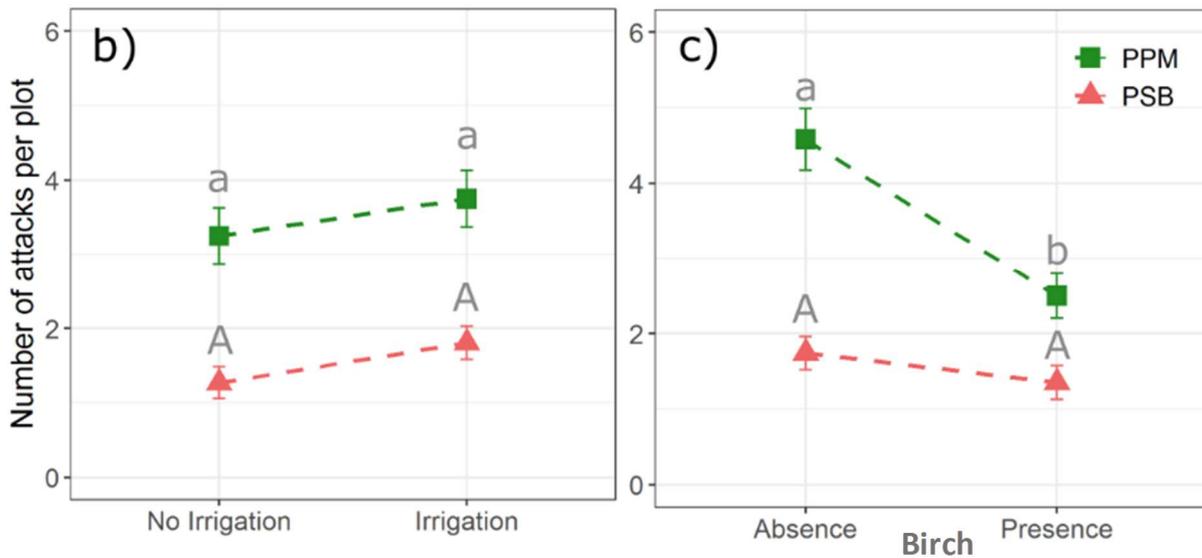
241 Logically, total pine basal area per plot increased with increasing pine density (Fig. 2). Total pine basal
 242 area per plot was not affected by the irrigation treatment (Supporting Information Fig. S1a and Table
 243 S3), but it significantly decreased with the presence of birch trees in the plot after pine density was
 244 accounted for (i.e. not due to dilution; Fig. 2; Supporting Information Fig. S1b and Table S3). The

245 effect of pine density on the total number of both PPM and PSB attacks was entirely mediated by the
 246 total pine basal area.

247



248



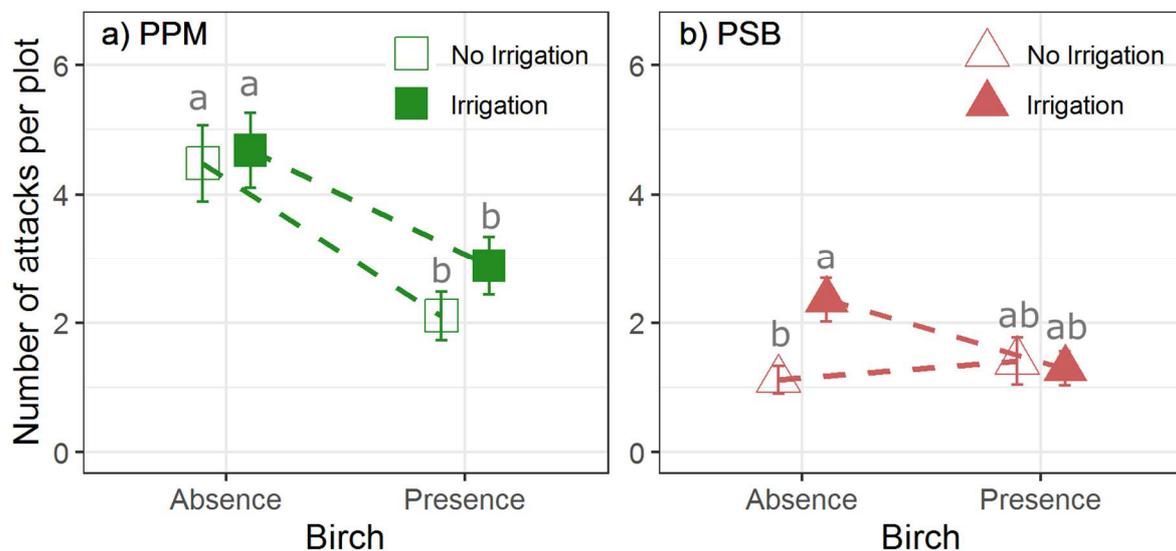
249

250 **Figure 3.** Effects of total pine basal area per plot (a), irrigation (b) and birch presence (c) on pine processionary
 251 moth (PPM) and pine stem borer (PSB) total number of attacks per plot. On panel a, solid lines represent model
 252 predictions and dashed lines the standard deviation around these predictions. On panels b and c, dots and error
 253 bars represent raw means and corresponding standard errors, respectively, and letters indicate whether
 254 subgroup means differ significantly (different letters) or not (same letter).

255

256 Both the total number of PPM and PSB attacks per plot significantly increased with total pine basal
257 area per plot (Figs. 2 and 3a; Supporting Information Table S3).

258 The total number of PPM attacks per plot did not significantly vary with irrigation (Figs. 2a and 3b;
259 Supporting Information Table S3). The presence of birch had both direct and indirect (through
260 reduced total pine basal area) negative effects on the total number of PPM attacks per plot (Fig. 2a).
261 On average, there were half as many PPM attacks when birch trees were present in the plot (Fig. 3c).
262 This associational resistance to PPM was observed in both irrigated and non-irrigated conditions (Fig.
263 4a).



264
265 **Figure 4.** Combined effects of irrigation and birch presence on (a) pine processionary moth (PPM) and (b) pine
266 stem borer (PSB) total number of attacks per plot. Dots and error bars represent raw means and corresponding
267 standard errors, respectively, and letters indicate whether subgroup means differ significantly (different letters)
268 or not (same letter).

269
270 There was an interactive effect of irrigation and the presence of birch on the total number of PSB
271 attacks, whereby the presence of birch reduced the total number of PSB attacks per plot in irrigated
272 conditions only (Figs. 2b and 4b; Supporting Information Table S3). On average, there were half as

273 many PSB attacks when birch trees were present in irrigated plots (Fig. 4b). The presence of birch
274 also had an indirect, negative effect on the total number of PSB attacks, through the reduction of
275 total pine basal area (Fig. 2b).

276 Overall, irrigation, total pine basal area, pine density and the presence of birch explained 31% and
277 16% of the variance of the total number of PPM and PSB attacks, respectively.

278 **Discussion**

279 With this study, we showed that pine-birch mixtures are more resistant to both PPM and PSB attacks
280 than pine monocultures, a case of associational resistance to several pests (i.e. when attacks
281 decrease with increasing tree species diversity). Furthermore, we found that associational resistance
282 was due not only to direct effects of birch trees, possibly related to repellent or disrupting non-host
283 volatiles (NHVs), but also to indirect, growth-mediated effects whereby the presence of birch trees
284 reduced host pine resources for the pests. The influence of drought was limited to an interference
285 with the direct effect of birch on the number of PSB attacks.

286

287 Primary pests responded to the concentration of host resource

288 In line with resource concentration hypothesis (Root 1973), the total number of attacks per plot of
289 the two pests increased with total pine basal area. The effect of pine density per plot on the total
290 number of attacks was mediated by the effect on total pine basal area, suggesting that the resource
291 concentration effect is due more to the total amount of resources than the total number of
292 individual trees (Hambäck and Englund, 2005). Total pine basal area is an indicator of the food
293 resources available to both pests, being directly correlated to the volume of tree trunks where PSB
294 larvae can develop, but also allometrically and positively related to the biomass of needles (Shaiek et
295 al., 2011) that PPM larvae feed on. Pine basal area is also a proxy for the visual and olfactory
296 apparency of host pines to the pests. Because all trees were of the same age in our experiment, it is

297 reasonable to consider that pine basal area was also positively correlated with pine growth rate (i.e.
298 vigour), which can be considered a predictor of bark cracking and thus terpene emission, an olfactory
299 cue used by PSB to choose their host tree (Jactel et al. 1996). Similarly, the attraction of female PPM
300 was probably enhanced by the volume of crowns, through increased visual apparency and higher
301 release of host odours (Jactel et al. 2015).

302 Resource-mediated associational resistance in pine-birch forests

303 We found that the presence of birch resulted in lower PPM and PSB attacks on pines, i.e. a case of
304 associational resistance, which is consistent with predictions for oligophagous insect herbivores in
305 mixtures of broadleaved and conifer trees (e.g. Castagneyrol et al. 2014; Jactel et al. 2021). For both
306 pests, this was partly explained by an indirect effect of birch on attacks whereby the presence of
307 birch trees in the plot induced a reduction of pine basal area, likely making the pine resources less
308 abundant and attractive to the two primary pests. By focusing on the plot scale (total number of
309 attacks per plot and total basal area per plot) we could clearly demonstrate that a reduction of
310 feeding substrate in mixed species forests can lead to reduced infestation by primary pests, providing
311 support to the resource concentration hypothesis. This associational resistance effect was not due to
312 increased dilution of host tree resources within mixed stands (Hambäck et al. 2014) because there
313 was no direct effect of the number of individual trees (pine density) on total number of attacks. It
314 was due to the fact that the non-host trees reduced the growth of neighbouring host trees, probably
315 mainly through competition for light as both pine and birch are light demanding species and not
316 through competition for water since the presence of birch resulted in lower pine basal area in both
317 irrigated and non-irrigated blocks.

318 We found no significant effect of irrigation on total pine basal area. More precisely, there was a
319 tendency for pines to grow bigger in irrigated plots; however, this was not significant at the time of
320 sampling. It is likely that the benefit of irrigation in terms of water stress reduction (Maxwell et al.,

321 2020 Fig. S1) was not sufficient after only two growing seasons to be significant in terms of tree
322 growth, and perhaps tree nutritional quality.

323 Growth-mediated effects of birch on pest attacks occurred independently of drought conditions and
324 there was no direct effect of irrigation on the level of pest infestation. The responses of forest insects
325 to drought seem to differ between feeding guilds and drought intensity, which can be explained by
326 the main physiological mechanisms of tree resistance (Jactel et al., 2012; Gely et al., 2020). Under
327 moderate water stress, leaf chewers (e.g. PPM) would increase their damage because of higher
328 quality of leaf tissues, in particular higher nitrogen content (Gely et al., 2020). On the contrary, the
329 damage of bark-and phloem feeders (e.g. PSB) would be negatively affected by moderate drought
330 because reduced vegetative growth would induce reallocation of carbohydrates to secondary
331 metabolism, leading to a decrease in the quality of wood tissues and a strengthening of induced
332 defence reactions involving terpenes and phenols (Jactel et al. 2012). Since we did not analyse the
333 chemical composition of pine needle and phloem, we could not determine whether the effect of
334 heterospecific neighbours on pine growth was accompanied by a reduction in host suitability, i.e.
335 through increased allocation of resources to chemical defences against herbivores, following the
336 growth-defence trade-off (Herms and Mattson, 1992). However, in our study, the change in nutrient
337 quality of trees induced by their heterospecific neighbours (e.g., nitrogen or carbohydrate
338 concentration) that might have affected PPM or PSB attacks was probably not strong enough or was
339 largely offset by the unlimited availability of needles and stems.

340

341 Direct associational effects of birch

342 We also found that the presence of birch directly reduced the number of both primary pests' attacks,
343 which confirms previous results (Jactel et al., 2011, 2019; Castagneyrol et al., 2019). This "protective"
344 effect was possibly due to the emission of non-host volatile compounds by birch trees, and in
345 particular methyl salicylate (MeSa) that was shown to repel PPM females (Jactel et al. 2011) and has

346 been since found to be repellent against the pine weevil *Hylobius abietis* (Azeem et al. 2015) and the
347 shot hole borer *Euwallacea fornicatus* (Byers et al. 2021).

348 However, this associational resistance effect likely related to NHVs released by birch trees did not
349 operate on PSB attacks in drought conditions (Fig.4). Birch basal area was marginally and non-
350 significantly higher in irrigated plots than in non-irrigated plots (see Supporting Information Table S4
351 and Fig. S2), maybe leading to slightly higher release of NHVs in irrigated blocks.

352 Conclusion and Perspectives

353 In this study, using structural equation modelling, we show that associational resistance of pine-birch
354 forests to two pine primary pests was explained by both direct and indirect, growth-mediated effects
355 of birch. Our findings also confirmed that associational effects could be modulated by drought
356 conditions. In fact, the predicted increase in drought frequency and intensity could reduce the
357 resistance of pine-birch mixed forests to PSB attacks, but not to PPM attacks. Future studies should
358 investigate the effect of drought on tree growth and tree diversity-herbivory relationship on a longer
359 term basis, to verify whether the growth-mediated associational effects of birch can be really
360 modulated by drought.

361 We detected a negative effect of heterospecific neighbours on host tree growth, and a tendency for
362 host tree growth to decrease in drought conditions, but we could not determine whether this was
363 accompanied by an increase in chemical defences according to the growth-differentiation balance
364 hypothesis. The next step is to analyse the combined effects of heterospecific neighbours and
365 drought on tree traits involved in associational resistance to primary pests, focusing on host and non-
366 host VOCs release and resource nutritional quality.

367 Finally, birch improved pine resistance to primary pests, but this was partly due to pine growth
368 limitation that may not be desirable from a forester point of view. Future studies, should assess the
369 benefit of birch-induced pest resistance against the negative effect of the presence of birch on pine
370 biomass production to determine the true benefit of diversification.

371 We hope this work will encourage researchers to further disentangle the mechanisms behind
372 associational resistance, which should help build toward a more general predictive framework of tree
373 diversity-herbivory relationships.

374 **Credit authorship contribution statement**

375 **Charlotte Poeydebat**: Methodology, Formal analysis, Visualization, Writing – Original draft. **Bastien**
376 **Castagneyrol**: Methodology, Writing – Review and editing. **Inge Van Halder**: Investigation, Writing –
377 Review and editing. **Hervé Jactel**: Supervision, Investigation, Methodology, Writing – Original draft.

378

379 **Declaration of Competing Interest**

380 The authors declare that they have no known competing financial interests or personal relationships
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382

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394

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