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Journal                      Journal of Pest Science

DOI                              The final authenticated version is available online at  
<https://doi.org/10.1007/s10340-019-01148-y>

CITATION                      Castagneyrol, B., Kozlov, M.V., Poeydebat, C. *et al.* Associational resistance to a pest insect fades with time. *J Pest Sci* **93**, 427–437 (2020). <https://doi.org/10.1007/s10340-019-01148-y>

1 **Associational resistance to a pest insect**  
2 **fades with time**

3  
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12

13 **Key Message:**

- 14 • Our knowledge on mixed forest resistance to herbivores is largely based on short-term studies.
- 15 • We monitored pines for attacks by a pest defoliator for six consecutive years in a large scale tree  
16 diversity experiment.
- 17 • Birch triggered associational resistance to the pine processionary moth, but this resistance faded  
18 over time.
- 19 • The resistance of planted forests to herbivores can be improved by carefully choosing both forest  
20 composition and the timing of species planting.

21  
22 **Abstract**

23 Tree diversity is one of the drivers of forest resistance to herbivores. Most of current understanding  
24 of diversity-resistance relationship comes primarily from short-term studies. Knowing whether tree  
25 diversity effects on herbivores is maintained over time is important for perennial ecosystems like  
26 forests. We addressed the temporal dynamics of the diversity-resistance relationship by conducting a  
27 six-year survey of pine attacks by the pine processionary moth *Thaumetopoea pityocampa* (PPM) in  
28 a tree diversity experiment where we could disentangle tree composition vs. host density effects.  
29 During the first years after planting the trees, PPM attacks on maritime pine *Pinus pinaster* were  
30 reduced in presence of birch *Betula pendula*, a fast-growing non-host tree (*i.e.*, associational  
31 resistance). This effect maintained but faded with time as pines eventually grew taller than  
32 neighbouring birches. The number of repeated attacks of individual pine trees also decreased in mixed  
33 pine – birch stands. Pine density had a positive effect on stand colonisation by PPM, and a negative  
34 effect on the proportion of attacked trees. Pines were less likely to be repeatedly attacked as pine  
35 density increased, attacks being spread over a larger number of host trees. Collectively, these results  
36 unravel the independent contribution of tree species composition and host density to tree resistance  
37 to herbivores. Both processes had directional changes with time. These results indicate that the  
38 resistance of planted forests to herbivores can be improved by carefully choosing the composition of  
39 mixed forests and the timing of species planting.

40  
41 **Keywords:** associational effects, forest, ORPHEE experiment, plant-insect interactions,  
42 *Thaumetopoea pityocampa*

43  
44 **Authors' contributions:** BC & HJ designed the study. BC, HJ, MT and CP collected the data. BC  
45 analysed the data, with advices from MT, MK and CP. BC wrote the first draft. MK, HJ and all authors  
46 contributed critically to the final version.

# 47 Introduction

48 Tree diversity has well documented, albeit variable, effects on insect herbivores. Several  
49 observational and experimental studies demonstrated that the presence of heterospecific neighbours  
50 of a tree reduces its risk to be attacked by herbivores, which is known as associational resistance  
51 (Barbosa et al. 2009; Moreira et al. 2016). Associational resistance is a common phenomenon in  
52 naturally grown and planted forests (Barbosa et al. 2009; Castagneyrol et al. 2014b; Guyot et al. 2016)  
53 although the opposite, associational susceptibility, was also reported (Schuldt et al. 2010; Wein et al.  
54 2016; Castagneyrol et al. 2018). Despite decades of research on associational effects in forest  
55 ecosystems, predicting their direction and strength remains elusive. Three sources of variation can  
56 explain discrepancies among studies. First, associational effects may depend more on the composition  
57 of tree species assemblages controlling for forest vertical and horizontal heterogeneity than on tree  
58 species richness *per se* (van Schroyen et al. 2018). Second, different herbivores may  
59 have contrasting responses to tree diversity, with associational resistance being more common, albeit  
60 not always, in specialist herbivore species (Castagneyrol et al. 2014b). Third, tree diversity effects on  
61 herbivores may vary with herbivore population density and differ between endemic *vs.* outbreak  
62 periods (Fernandez-Conradi et al. 2017; Bognounou et al. 2017; Merwin et al. 2017). Forest structure,  
63 herbivore population density and community composition also change over time, which may  
64 therefore alter the direction and strength of associational effects. Yet, these aspects remain almost  
65 unexplored, as most studies were short term (but see Bognounou et al. 2017). Understanding the  
66 dynamics of associational effects is therefore of crucial importance for perennial systems such as  
67 forests, especially at early stages of their development.

68 Resource density and frequency are major drivers of associational effects (Verschut et al. 2016). The  
69 resource concentration hypothesis predicts that herbivores – in particular specialist herbivore species  
70 – are more likely to be attracted and to aggregate in patches with high resource concentration. Yet,  
71 for such specialist herbivore species, resource density (*i.e.* number of host individuals) and frequency  
72 (*i.e.* relative abundance of hosts) often correlate negatively with plant diversity. The resource  
73 concentration hypothesis therefore predicts lower herbivore aggregation on host plants surrounded  
74 by a greater diversity of non-host plants (Root 1973; Hambäck and Englund 2005; Kim and  
75 Underwood 2014; Damien et al. 2016). This hypothesis has been well explored by the literature, but  
76 the opposite pattern whereby herbivores aggregate on the fewer number of available plants was also  
77 reported (the resource dilution hypothesis, Otway et al. 2005; Damien et al. 2016). The resource  
78 concentration and resource dilution hypotheses conflict in what should be the consequences of host  
79 plant density and frequency on per capita herbivore load. On the one hand, specialist herbivores may  
80 be less attracted by patches where their host plants are diluted among non-host plants. This would  
81 result in a lower per capita herbivore load (resource concentration hypothesis). On the other hand,  
82 albeit less abundant, herbivores may concentrate on the fewer available host plants, thus increasing  
83 per capita herbivore load (resource dilution hypothesis). For the same reasons, in perennial systems,  
84 the probability that the same host plants are repeatedly attacked every year by herbivores may be  
85 higher in patches where host availability is reduced. Disentangling how the absolute and relative  
86 abundance of host- and non-host plants contribute to herbivore aggregation among and within patches  
87 therefore emerges as a major challenge in theory for associational effects.

88 Associational effects depend on the identity of neighbours a focal plant has. Herbivores rely on a  
89 mixture of host and non-host cues to identify and orientate towards host plants while avoiding non-

90 host plants. Non-host plants surrounding a focal plant can reduce its physical and chemical apparency  
91 to herbivores (i.e., the probability of being found by herbivores, Feeny 1976; Strauss et al. 2015) by  
92 emitting repellent cues or hiding host's attractive cues (Zhang and Schlyter 2004; Jactel et al. 2011;  
93 Castagneyrol et al. 2013). For instance, a focal plant being visually hidden by taller neighbours has  
94 proved to be less damaged by herbivores than physically more apparent focal plants (Miller et al.  
95 2007; Dulaurent et al. 2012, Castagneyrol et al. 2013; Damien et al. 2016). Another possibility is that  
96 a small focal plants would emit fewer attractive volatile cues than non-attractive or even repellent  
97 volatile cues emitted by taller heterospecific neighbours, thus reducing its 'chemical apparency'  
98 through higher semiochemical diversity of mixed forests (Zhang and Schlyter 2004; Schiebe et al.  
99 2011). However, isolating the effect of heterospecific neighbours on the physical vs. chemical  
100 apparency of a focal plant is a difficult task as both are confounded.

101 Different species in a mixture may have different growth rate such that the physical and chemical  
102 apparency of a given plant may change with time as a function of its growth rate and that of its  
103 neighbours. For instance, Damien *et al.* (2016) reported that the initial protection against a specialist  
104 herbivore, which was provided to pines by taller neighbouring birches, tended to decrease with time  
105 as pine eventually grew taller than birches. Temporal changes in the relative size of plants in a  
106 community may further alter competitive and facilitative interactions among plant species, thus  
107 altering patterns of resource allocation to growth vs. defences and ultimately plant-herbivore  
108 interactions (Hakes and Cronin 2012; Kostenko and Bezemer 2013). Although not well documented,  
109 both mechanisms are likely to contribute to shifts in the strength and direction of associational effects  
110 with time. Yet predicting these effects is not trivial, as tree shape and growth rate of plant species in  
111 mixtures also depend on diversity-mediated processes (Jucker et al. 2015).

112 Recent studies suggested that the strength and direction of associational effects could be partly  
113 determined by the density of herbivore population (Fernandez-Conradi et al. 2017; Merwin et al.  
114 2017). Yet, several herbivore species have eruptive or cyclic population dynamics (Haynes et al. 2014;  
115 Li et al. 2015), so that strength and, potentially, even the direction of associational effects may change  
116 with herbivore population density. For instance in a recent study, Bognounou et al. (2017) showed  
117 that while damage caused by the spruce budworm to its preferred host species (balsam fir) increased  
118 with host concentration and decreased with the abundance of a less preferred host species (black  
119 spruce) at low pest densities, damage was independent of the relative densities of preferred and less-  
120 preferred host species during an outbreak period. Yet, overall herbivore pressure can hardly be  
121 controlled in large-scale studies, but controlling statistically for temporal changes in herbivore density  
122 may contribute to a better understanding of processes generating associational effects.

123 We addressed the temporal dynamics of associational effects by using the pine processionary moth  
124 *Thaumetopoea pityocampa* (PPM) and its principal host, the maritime pine *Pinus pinaster*, as model  
125 species. PPM is an oligophagous insect, feeding mainly on pine species (*Pinus sp.*) and is a major  
126 pine defoliator in southern Europe and northern Africa (Battisti et al. 2015). PPM has a cyclic  
127 population dynamics with a seven-year period (Li et al. 2015). Gravid females flying outside pine  
128 stands rely on attractive physical and volatile cues released by pines to select and orientate their flight  
129 towards host trees, and are deterred by physical and chemical cues emitted by non-host trees, in  
130 particular by broadleaved species (Battisti et al. 2015; Jactel et al. 2015). In a previous study using  
131 the same tree diversity experiment associating maritime pine with four different broadleaved species,  
132 we showed that pines were less prone to PPM infestation when associated with birch (Castagneyrol  
133 et al. 2014c). A likely mechanism was the reduction of pine apparency by the neighbouring fast

134 growing birch trees (Damien et al. 2016). The objective of the present study was to assess the temporal  
135 dynamics of tree diversity effects on pine infestation by the PPM during the first years after the forest  
136 establishment, while controlling statistically for fluctuation in PPM population density. We first  
137 hypothesised that associational resistance conveyed by birch decreases with time, as pines grew taller  
138 than neighbouring birches. We further asked whether the same individual pines were more often  
139 attacked over time in plots where pines were more diluted by broadleaved species. We addressed  
140 these questions by quantifying PPM attacks on pines in a long-term tree diversity experiment in South  
141 West France in which we could disentangle the effects of tree species composition vs. pine density  
142 (Damien et al. 2016). By doing so, we hoped to provide new insights into our understanding of the  
143 mechanisms driving plant-herbivore interactions.

## 144 **Materials and methods**

### 145 **Experimental design**

146 The ORPHEE experiment (<https://sites.google.com/view/orpheeexperiment/home>) is located 40 km  
147 south of Bordeaux (SW France). It was established in 2008 on a 12ha clear cut of maritime pine  
148 stands. In total, 25,600 trees belonging to five native species were planted (European birch *Betula*  
149 *pendula*; Pedunculate oak *Quercus robur*; Pyrenean oak *Q. pyrenaica*; Holm oak *Q. ilex*; and  
150 Maritime pine *Pinus pinaster*). Eight blocks were established with 32 plots in every block  
151 corresponding to the 31 possible combinations of 1–5 species, with an additional replicate of the  
152 combination of the five species. In particular, 17 species combinations contained pines, either alone,  
153 or in association with one, two, three or all of the four other broadleaved species. Plots were separated  
154 by a distance of 3 m and were randomly distributed within blocks. Each plot consisted of 10 rows of  
155 10 trees planted 2 m apart, resulting in 100 trees per plot. Plot area was 400 m<sup>2</sup>. Tree species mixtures  
156 were established according to a substitutive design, keeping overall number of trees equal across  
157 plots. Within plots, individual trees from different species were planted in a regular alternate pattern,  
158 such that a tree from a given species had at least one neighbour from each of the other species within  
159 a 3 m radius (Castagneyrol et al. 2013).

### 160 **PPM infestation**

161 During winter, PPM larvae feed at night on pine needles and spend daytime in white silky nests that  
162 are visible from the ground (Battisti et al. 2015). The number of winter nests is a common proxy for  
163 PPM infestation level (Hóðar et al. 2002; Régolini et al. 2014). We counted the number of winter  
164 nests per tree on every pine of the ORPHEE experiment, every winter from 2013 to 2018, which  
165 corresponds to oviposition events that occurred in previous summers (i.e., from 2012 to 2017). We  
166 considered dead and broken trees for which there was no assessable crown as missing values. PPM  
167 nest count was carried out from the ground by a team of two people carefully looking at the crown of  
168 individual pines from two opposite sides. Two persons realized field observation every year (BC, HJ)  
169 but received help from a varying number of people.

### 170 **Pine density and apparency**

171 We measured tree height from the ground to the highest living bud on every plot from 2008. From  
172 2008 to 2015, we measured the height of the 36 innermost trees per plot. In 2015-2018, we kept  
173 measuring the height of every living oak among these 36 innermost trees per plot, but restricted height  
174 measurements of pine and birch to seven individuals of each species, which were haphazardly chosen  
175 among these 36 innermost trees.

176 Previous studies on the same experiment have shown that birch and pines grew much faster than oaks  
177 (Damien et al. 2016; Castagneyrol et al. 2018), which were below the lowest living branches of most  
178 pines already by the year 2014 (B. Castagneyrol, personal observations) and partially confounded  
179 with the dense and bushy understorey vegetation. We therefore considered the mixtures of pines and  
180 oaks, with no birch, as low density pine monocultures, forming a gradient of pine density, from 100%  
181 in pine monocultures to 25% in plots with pine mixed with three oak species. We used this gradient  
182 to test independently the effects of pine density and the pure associational effects provided by the  
183 presence of birch, while controlling for pine density (see Fig. 1 in Damien et al. 2016). Overall pine  
184 mortality was very low (4.5% dead pines among 1858 surveyed in 2017), so that the number of pines  
185 per plot remained almost the same as it was when we planted the experiment.

186 We defined pine apparency ( $A$ ) as follows:  $A = \frac{1}{S} \times \sum_i^{S-1} (H_p - H_i)$ , where  $H_p$  and  $H_i$  were species-  
187 specific mean height of pine and associated species  $i$ , respectively, and  $S$  the number of species  
188 planted in the plot (i.e., 1 to 5). We characterised mean pine apparency by averaging tree height at the  
189 species level, within plots, because the sample size varied among years and among species. Although  
190 they were initially smaller than pines, we retained oaks in the calculation of pine apparency as some  
191 individuals were  $> 2\text{m}$  height from 2016 on. Pine apparency therefore quantifies how much a pine  
192 was on average taller (positive values) or smaller (negative values) than its neighbours. It must be  
193 noticed that the design of the ORPHEE experiment does not allow disentangling the effect of pine  
194 neighbours on pine visual vs. chemical apparency as taller neighbours may alter PPM host searching  
195 behaviour through both the physical disruption of pine physical cues and the emission of non-host  
196 volatiles diluting pine volatiles or acting as repellents.

## 197 Resource availability to PPM

198 In 2013 and 2014, we additionally measured pine diameter at breast height (dbh) on the same seven  
199 trees that were measured for height. From 2015 on, we measured the dbh of every living pine within  
200 the 36 innermost trees per plot. In order to quantify the amount of resource available to PPM, we used  
201 allometric equations to estimate needle biomass at the plot level. Allometric equation was obtained  
202 from Shaiek et al. (2011): Needle biomass =  $1.916 \times dbh^{2.07} \times Age^{-0.67}$ , where  $dbh$  and  $Age$  are mean  
203 pine diameter at breast height (cm) and pine age (years), respectively. Then, we multiplied the  
204 obtained value by the number of living pines per plot to estimate plot-specific needle biomass, which  
205 served as a proxy for resource concentration (i.e., resource available to PPM at the plot scale).

## 206 Statistical analyses

207 All analyses were done using the *R* language programming with the *R studio* interface. We used the  
208 following packages for data analysis: *lmerTest*, *MuMIn*, *multcomp* (Kuznetsova et al. 2015; Bartoń  
209 2016; Hothorn et al. 2016).

## 210 Temporal changes in the effects of pine density 211 and presence of birch on PPM infestations

212 We analysed two response variables: (i) PPM density, which was the total number of nests per plot  
213 and (ii) PPM attack rate, which was the proportion of trees with at least one PPM nest. PPM density  
214 informed on plot colonization by PPM, while PPM attack rate represented how many host trees were  
215 damaged once the plot has been colonized (Damien et al. 2016).

216 We tested the effect of pine age (*Age*, continuous variable), presence of birch (*Birch*, present/absent),  
217 pine density (i.e., number of pines per plot, continuous variable) and all two- and three-ways  
218 interactions on PPM density and attack rate as fixed effects in Generalized Linear Mixed-effects  
219 Models (GLMM). We used *Block*, *Plot* (nested within block) and *Year* (as a factor, crossed with *Block*  
220 and *Plot* factors) as random factors. The random *Block* factor accounted for heterogeneity among  
221 blocks and non-independence of different plots of the same pine density within blocks (20–50 pines  
222 per plot). The individual-level random *Plot* factor accounted for repeated measurements at the plot  
223 level. The random effect of *Year* accounted for differences in overall PPM population density among  
224 years. All continuous predictors were standardised across years by subtracting the mean and dividing  
225 by the standard error to allow direct comparison among model coefficient parameter estimates. We  
226 used Poisson and binomial GLMM with *log*- and *logit*-links to analyse PPM density and attack rate,  
227 respectively.

228 For each response variable, we applied model simplification by sequentially removing non-significant  
229 terms, starting with the least significant highest order interaction. We did not simplify the random  
230 part of the model as it was imposed by the experimental design. We tested the significance of  
231 predictors with *F*-tests and Kenward-Roger's approximation for degrees of freedom. We calculated  
232 marginal ( $R_m^2$ ) and conditional ( $R_c^2$ )  $R^2$  to estimate the variance explained by fixed effects and fixed  
233 plus random effects, respectively.

## 234 Number of repeated attacks

235 In order to test the effect of birch and pine density on the repeated attacks of individual pine trees, we  
236 calculated how many times each individual pine was attacked (i.e. presence of at least one nest) during  
237 six observation years. Trees that died during the survey were excluded from this analysis. We then  
238 analysed the number of repeated attacks (ranging from zero to six) at the level of individual trees  
239 using GLMM with Poisson error family and log-link function. Fixed effects were presence of birch,  
240 pine density and their interaction. Random factors were *Block* and *Plot*, nested within *Block*.  
241 Significance of fixed effects was tested using log-likelihood  $\chi^2$  tests. We analysed the number of  
242 repeated attacks instead of the probability of repeated attack (i.e., number of repeated attacks divided  
243 by the number of years) because of better model residual distribution.

## 244 Temporal changes in pine apparency and resource availability

245 Changes in tree diversity effects on PPM density or attack rate may have been caused by differential  
246 dynamics of pine apparency and resource concentration in presence or absence of birch. Yet, because  
247 pine apparency and resource availability were calculated from tree dimensions, they both varied with  
248 time. Having included these variables together with pine age in statistical models would have caused  
249 serious collinearity issues. At the contrary, pine density and presence or absence of birch were  
250 imposed by the original design and did not vary with time (see above). We therefore used pine density  
251 and presence/absence of birch to model PPM attacks (see above) and analysed the dynamics of pine



252   apparency and resource availability in mixed plots in separate models, but using the same modelling  
253   approach as for PPM attacks.

## 254   **Results**

### 255   PPM population density

256   During the six-year survey, we counted a total of 5,591 PPM nests on 4,585 pine trees (the same tree  
257   could have been attacked more than once). Pines attacked by the PPM had on average 1.21 PPM  
258   nests. Over the time of the survey, only 21 trees had four nests or more in a given year. PPM  
259   population density peaked in 2015 (which corresponds to the middle of the survey period) and in  
260   2018 (Fig. 1). There was therefore no risk that fluctuation in PPM population density was confounded  
261   with tree growth dynamics.

### 262   Dynamics of pine density and birch effects on PPM

#### 263   PPM density

264   Overall, PPM nest density (*i.e.*, the number of PPM nests per plot) was reduced in plots associating  
265   pine with birch and tended to increase with increasing pine density (Table 1, Fig. 2). However, both  
266   the effect of pine density and presence of birch on PPM density varied with time, as indicated by the  
267   significant *Age* × *Birch* and *Age* × *Density* interactions (where ‘*Birch*’ is presence/absence of birch,  
268   Table 1). The coefficient parameter estimate ( $\pm$  SE) of the *Age* × *Birch* interaction was positive ( $0.16$   
269    $\pm 0.03$ ), indicating that the negative effect of birch on PPM density ( $-0.57 \pm 0.08$ ) decreased in  
270   magnitude with time. This result thus indicates that associational resistance conveyed by birch faded  
271   with time (Fig. S1). Likewise, the coefficient parameter estimate of the *Age* × *Density* interaction was  
272   negative ( $-0.10 \pm 0.02$ ), indicating that the positive effect of pine density on PPM density  
273   ( $0.08 \pm 0.04$ ) weakened with time and eventually nullified (Fig. 2). There was no significant  
274   interaction between pine density and presence of birch (Table 1).

#### 275   PPM attack rate

276   Overall, PPM attack rate (*i.e.*, the proportion of pines with at least one PPM nest) was reduced in  
277   plots associating pine with birch and decreased with pine density (Table 1, Fig. 2). However, both the  
278   effect of pine density and presence of birch on PPM attack rate varied with time, as indicated by the  
279   significant *Age* × *Birch* and *Age* × *Density* interactions (Table 1). The coefficient parameter estimate  
280   of the *Age* × *Birch* interaction was positive ( $0.15 \pm 0.04$ ), indicating that the negative effect of birch  
281   on PPM attack rate ( $-0.63 \pm 0.10$ ) decreased in magnitude with time, which corresponds to a fading  
282   protective effect of birch with time (Fig. S1). At the contrary, the coefficient parameter estimate of  
283   the *Age* × *Density* interaction was negative ( $-0.12 \pm 0.02$ ), indicating that the (negative,  $-0.29 \pm 0.05$ )  
284   effect of pine density on PPM attack rate strengthened and became even more negative with time  
285   (Fig. 2).

### 286   Number of repeated attacks

287   A total of 2,118 pines (44%) were attacked at least once during six years of survey. Conversely, 56%  
288   of pines were never attacked. Only 46 individual pines (1%) were attacked every year (*i.e.*, 6 attack  
289   records in the present survey). The number of repeated attacks was lower in presence of birch ( $\chi^2 =$

290 29.98,  $P < 0.001$ , Fig. 3) and decreased with pine density ( $\chi^2 = 57.89$ ,  $P < 0.001$ , Fig. 3). This means  
291 that individual pines were more likely to be repeatedly attacked every year in low density plots and  
292 in the absence of birch. There was a significant interaction between the presence of birch and pine  
293 density ( $\chi^2 = 3.88$ ,  $P = 0.049$ ) with a negative model coefficient parameter estimate ( $-0.28 \pm 0.14$ )  
294 indicating that the effect of birch increased in magnitude with increasing pine density (Fig. 3).

## 295 Temporal dynamics of pine apparency and resource avail- 296 ability

297 At the end of the 2016 growing season, birches were on average ( $\pm$  SE)  $6.48 \pm 0.04$  m ( $n = 1139$ ),  
298 pines were on average ( $\pm$  SE)  $7.80 \pm 0.03$  m ( $n = 1139$ ), and oaks (regardless of the species) were on  
299 average  $1.54 \pm 1.51$  m tall ( $n = 3348$ ). The consequence of species-specific differences in growth  
300 dynamics is that in presence of birch, pine apparency – that is how much pines were apparent and  
301 easily perceived by herbivores – changed drastically with time (Fig. 4A), but in a different manner  
302 depending on initial pine density and on the presence of birch as indicated by the significant  $Age \times$   
303  $Density \times Birch$  interaction (Table 1). In particular, pine apparency was on average lower in presence  
304 of birch, and the effect of birch was more pronounced in denser plots (Fig. 4A). Comparisons among  
305 slopes of the regression of pine apparency against time (Table S1) indicated that pine apparency  
306 increased faster in absence of birch than in presence of birch (Fig. 4A), and faster in plots with lower  
307 density.

308 The amount of resource available to PPM (estimated pine needle biomass at the plot scale) increased  
309 with time, but in a different manner depending on initial pine density (Table 1) and on the presence  
310 of birch (Table 1). Resource increased significantly faster in plots with initial density of 50 pines per  
311 plots than in plots with initial density of 25 pines per plot (Table S1), and in plots with initial density  
312 of 33 pines per plots than in plots with initial density of 25 pines per plot (Table S1). However,  
313 resource dynamics was not significantly different in plots with initial density of 50 vs. 33 pines per  
314 plot (Table S1). Because the  $Age \times Density \times Birch$  interaction was not significant ( $\chi^2 = 0.16$ ,  $P =$   
315  $0.922$ ), the difference in the slope of resource amount over time between plots with vs. without birch  
316 was the same, regardless of pine initial density (Table S1). Likewise, differences in slopes among the  
317 three initial pine density levels were the same, regardless of the presence or absence of birch.

## 318 Discussion

319 In this study, the experimental design and modelling approach allowed the distinction between two  
320 mechanisms driving tree diversity effects on herbivores, namely resource density and host apparency,  
321 while accounting for fluctuation in herbivore population density. More importantly, we were able to  
322 analyse the temporal dynamics of such effects at the time of intensive growth of young forest. In  
323 particular, we found that associational resistance against PPM conveyed by birch (a non-host species  
324 for PPM) faded with time due to contrasting growth rates between PPM host and non-host tree  
325 species. We also found that host density had opposite effects on the recruitment of PPM and on their  
326 distribution among individual host trees. In particular, we found that pine stand colonisation by PPM  
327 increased with pine density, but that this effect decreased and eventually nullified with time,  
328 suggesting that factors other than host density drove variability in pine stand colonisation as stands  
329 aged. At the opposite, PPM attack probability of individual pine trees decreased as pine density  
330 increased, and this effect strengthened with time. Our study therefore highlights the mechanisms  
331 driving insect herbivory on trees in mixed forests during the first decade after tree plantation.

## 332 Birch protected pines against PPM attacks, 333 but this effect faded with time

334 Pine attacks by PPM were reduced in presence of birch. Both PPM density (*i.e.*, the total number of  
335 PPM nests at the plot level) and PPM attack rate (*i.e.*, the proportion of pines attacked by the PPM)  
336 were reduced in presence of birch. This finding is consistent with previous studies conducted on  
337 ORPHEE experiment (Castagneyrol et al. 2014c; Damien et al. 2016) and with observational or  
338 experimental studies in the same area (Jactel et al. 2011; Dulaurent et al. 2012; Castagneyrol et al.  
339 2014a). Associational resistance conveyed by birch can be explained by fast growing non-host trees  
340 disrupting host recognition by PPM (Jactel et al. 2011, 2015; Damien et al. 2016). This phenomenon  
341 has been found to be dependent on the relative size of pines *vs.* broadleaved species, whereby a  
342 stronger protection was provided by broadleaved trees taller than pines (Dulaurent et al. 2012;  
343 Damien et al. 2016). Consistently, we reported that, for a given pine density, the presence of birch in  
344 experimental plots reduced pine apparency.

345 Associational resistance conveyed by birch faded with time. This finding mirrors the regular increase  
346 in pine apparency in every plots, including two-species mixtures associating pines with birch (*i.e.*,  
347 densest mixed plots). Such a general increase in pine apparency can explain why associational  
348 resistance provided by birch faded with time: pines having eventually grown higher than birches, they  
349 were less physically hidden and may have been more easily found by gravid PPM females foraging  
350 for oviposition sites. However, although the strength of associational resistance decreased with time,  
351 plots associating pines with birch remained less attacked than plots of comparable pine density in  
352 which birch was absent. Although birch did not contribute to reduce pine physical apparency anymore  
353 after pines grew taller, they may have continued contributing to the reduction of pine chemical  
354 apparency. Specifically, the maintenance of associational resistance may be explained by birch still  
355 releasing volatile organic compounds interfering with the mating behaviour and host searching  
356 behaviour of PPM adults (Jactel et al. 2011, 2015). Further studies should aim at quantifying the  
357 relative importance of the physical and chemical disruptive cues emitted by broadleaved species.

358 The presence of birch reduced the probability that the same pines were repeatedly attacked by the  
359 PPM. Non-hosts act upon host colonisation by herbivores through a two-steps process involving first  
360 patch selection and then resource selection within patches (Finch and Collier 2000; Hambäck et al.  
361 2014; Verschut et al. 2016). It is therefore conceivable that birch altered pine colonisation both among  
362 and within patches, thus increasing year-to-year variability in individual pine attack rate. The  
363 occurrence of repeated attacks on the same tree has detrimental effects on pine growth (Jacquet et al.  
364 2013). Our finding therefore suggests that although the effect of birch on PPM infestation at the stand  
365 level weakened as pines grew, birch may have long-lasting beneficial effects on pines by reducing  
366 the number of repeated attacks. The presence of this fast growing non-host species may allow  
367 individual trees to recover from previous PPM attack, thus improving the resilience of mixed pine  
368 plantations to PPM attacks. To the best of our knowledge, the risk of repeated attacks by herbivores  
369 has never been studied so far and its consequences in terms of damage and tree growth would clearly  
370 deserve further attention.

## 371 Pine density had opposite effects on PPM density 372 and PPM attack rate

373 PPM density increased with pine density. Yet, needle biomass also obviously increased with pine  
374 density, regardless of presence or absence of birch in experimental plots. This result is therefore fully  
375 in line with the resource concentration hypothesis that predicts an increase in (specialist) herbivore  
376 density with an increase in herbivore's resource concentration (Root 1973; Hambäck and Englund  
377 2005). It can be explained by plots with higher pine density emitting a greater amount of attracting  
378 cues, therefore recruiting more herbivores. Alternatively, we cannot rule out the hypothesis that the  
379 higher PPM density in plots with higher pine density was simply the result of a passive interception  
380 of flying PPM females whereby more pines would have intercepted more moths.

381 At the contrary, PPM attack rate decreased with increasing pine density. This result indicates that  
382 although denser pine stands attracted or arrested more PPM females, the greater number of individuals  
383 was spread among an even greater number of pine trees, thus causing the dilution of herbivores among  
384 more abundant food items. Similarly, in less dense pine stands, PPM attacks may have concentrated  
385 on the fewer pine individuals (i.e., resource dilution hypothesis, Otway et al. 2005; Bañuelos and  
386 Kollmann 2011). This result is compatible with the observation that the number of repeated attacks  
387 decreased with pine density.

388 The effect of pine density on PPM density weakened with time while its effect on PPM attack rate  
389 strengthened with time. Although pine density remained roughly constant through time, PPM  
390 resource (i.e., needle biomass) consistently increased with time, regardless of pine density or  
391 presence/absence of birch. However, the increase in needle biomass was markedly stronger in denser  
392 plots (i.e., two-species mixtures), which may have strengthened the resource dilution effect of PPM  
393 attack rate. A possible mechanism explaining these trends is that tree canopies closed faster in pure  
394 pine stands (with high pine density) in such a way that the whole plot may be perceived by flying  
395 PPM females as a single patch of resource. By contrast, in low pine density plots, individual pine  
396 trees that are still spatially isolated but with large crown size may be detected as several host patches  
397 by PPM moths responding to a silhouette effect. More individual trees would thus be attacked in low  
398 pine density plots with time, resulting in higher percentage of attacked trees (attack rate), whereas the  
399 number of PPM nests would be more equally distributed across plots (within a block), resulting in  
400 more uniform PPM abundance variation along the pine density gradient. This suggests that spatial  
401 among vs. within patch host selection is another important dimension that has to be better taken into  
402 account in further studies to understand associational resistance mechanisms (Bommarco and Banks  
403 2003; Hambäck et al. 2014). In particular, they should address at which spatial scale host choice is  
404 made by gravid OPM females and whether the same cues act equally on males and mated vs. unmated  
405 females.

## 406 Conclusion and implication 407 for the management of mixed forests

408 With this study, we for the first time demonstrated that tree diversity effects on insect herbivores show  
409 directional changes as the forest grows. Associational resistance faded while effects of host density  
410 strengthened with time. Not only our findings question the ability of short-term studies conducted on  
411 young tree diversity experiments to draw general conclusions about associational effects (including  
412 ours, Castagneyrol et al. 2013; Setiawan et al. 2014; Wein et al. 2016), they also have potential  
413 implications for the long-term management of planted forests.

414 In the context of planted forests, our results demonstrate that the relative growth rate of associated  
415 tree species is a key driver of the observed temporal dynamics of associational effects. In particular,

416 initial associational resistance triggered by fast growing species can be offset following height  
417 dominance shift in forest structure. A management option could thus consist in planting fast growing  
418 non-host trees before planting the target species in order to prolong associational resistance. However,  
419 such a strategy may come with increased competition for light and nutrients. Further quantification  
420 of herbivory consequences on the yield of the target species in mixtures vs. monocultures is therefore  
421 needed to evaluate critically costs and benefits of such tree mixing strategies. Finally, whether the  
422 same processes are at play in less intensively managed forests is still an open question that should be  
423 considered by future studies addressing the biodiversity-resistance relationship.

424

## 425 **Acknowledgements**

426 BC was supported by the GIP-ECOFOR programme from the French ministry of agriculture (project  
427 BIOPICC ECOFOR-2014-15). MT, CP and HJ received support from the French National Research  
428 agency (project DiPTiCC, ANR-16-CE32-0003-01). M.V.K. was supported by the Academy of  
429 Finland (projects 311929 and 316182). We thank people who contributed to count PPM nests since  
430 2013 (with no particular order): Maxime Damien, Inge van Halder, Margot Régoloni, Céline  
431 Meredieu, Fabrice Vétillard, Lucile Perrot, Angelina Ceballos-Escalera, Yasmine Kadiri, Christophe  
432 Poilleux, Victor Rebillard. Authors acknowledge UEFP 0570, INRA, 69 route d'Arcachon, 33612,  
433 CESTAS for the management of the ORPHEE experiment.

## 434 **Compliance with ethical standards**

435 Conflict of interest: The authors declare no conflicts of interest.

436 Ethical approval: This article does not contain any studies with animals performed by any of the  
437 authors.

438

## 439 **Data archiving**

440 Data will be archived as supplementary material, provided the paper is accepted

## 441 **References**

442

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443

## 444 Tables

445 **Table 1.** Summary of (generalised) mixed effect models testing the effects of pine age, pine density  
 446 and presence/absence of birch on PPM density and attack rate and on pine apparency and resource  
 447 concentration. <sup>a</sup> Density corresponds to realised pine density a given year for PPM density and attack  
 448 rate (i.e., accounting for pine mortality), while it refers to initial planting density (three-levels factor)  
 449 for pine apparency and resource concentration. <sup>b</sup> Marginal ( $R_m^2$ ) and conditional ( $R_c^2$ )  $R^2$  are given for  
 450 the simplified models. Characters in bold font refer to significant effects.

451

Explanatory variable	PPM density (No. nests per plot)		PPM attack rate (% attacked trees)		Pine apparency		Resource concentration (needle biomass)	
	$\chi^2$	<i>P</i> -value	$\chi^2$	<i>P</i> -value	$\chi^2$	<i>P</i> -value	$\chi^2$	<i>P</i> -value
Age	<b>2.03</b>	0.154	1.71	0.191	5604.07	< <b>0.001</b>	3082.70	< <b>0.01</b>



Birch	<b>39.90 &lt; 0.003</b>	28.61 < <b>0.001</b>	293.70 < <b>0.001</b>	209.88 < <b>0.001</b>
Tree density <sup>a</sup>	<b>3.920.048</b>	50.56 < <b>0.001</b>	233.41 < <b>0.001</b>	82.36 < <b>0.001</b>
Age × Birch	<b>23.39 &lt; 0.001</b>	12.72 <b>0.001</b>	74.33 < <b>0.001</b>	8.22 <b>0.004</b>
Age × Tree density	<b>40.61 &lt; 0.001</b>	45.30 < <b>0.001</b>	207.50 < <b>0.001</b>	6.23 <b>0.044</b>
Tree density × Birch	< <b>0.01</b> 0.979	3.98 <b>0.046</b>	24.09 < <b>0.001</b>	1.160.560
Age × Tree density × Birch	0.420.514	0.010.900	20.65 < <b>0.001</b>	0.860.649
Rm <sup>2</sup> (Rc <sup>2</sup> ) <sup>b</sup>	0.30 (0.86)	0.07 (0.23)	0.81 (0.98)	0.80 (0.96)

452

453

## 454 **Figure captions**

455 **Figure 1. PPM population dynamics in the ORPHEE experiment.** Dots represent the total number  
456 of PPM nests counted on pines. Within brackets, numbers refer to the percentage of pines with at least  
457 one PPM nest.

458 **Figure 2. Temporal changes in the effect of presence of birch and pine density on PPM density**  
459 **(A) and PPM attack rate (B).** Dots represent PPM density and attack rate at the plot level in presence  
460 (grey) or absence (black) of birch. Solid and dashed lines represent predictions of the simplified  
461 model. Ages above panels correspond to time after planting.

462 **Figure 3. Effects of pine density and presence of birch on the probability of repeated attacks.**  
463 Dots represent individual plots in presence (grey) or absence (black) of birch. Solid and dashed lines  
464 represent the predictions of the simplified model and their standard error, respectively.

465 **Figure 4. Pine apparency (A) and resource concentration (B) in plots with initial density of 25,**  
466 **33 or 50 pines per plot in presence (+ birch) or absence (- birch) of birch for four consecutive**  
467 **years.** Pine apparency (cm) is the mean difference between mean pine height and the mean height of  
468 each associated species in mixture. Resource concentration (kg) is the estimated needle biomass at  
469 the plot scale. Dots and error bars represent means  $\pm$  SD.

Figure 1

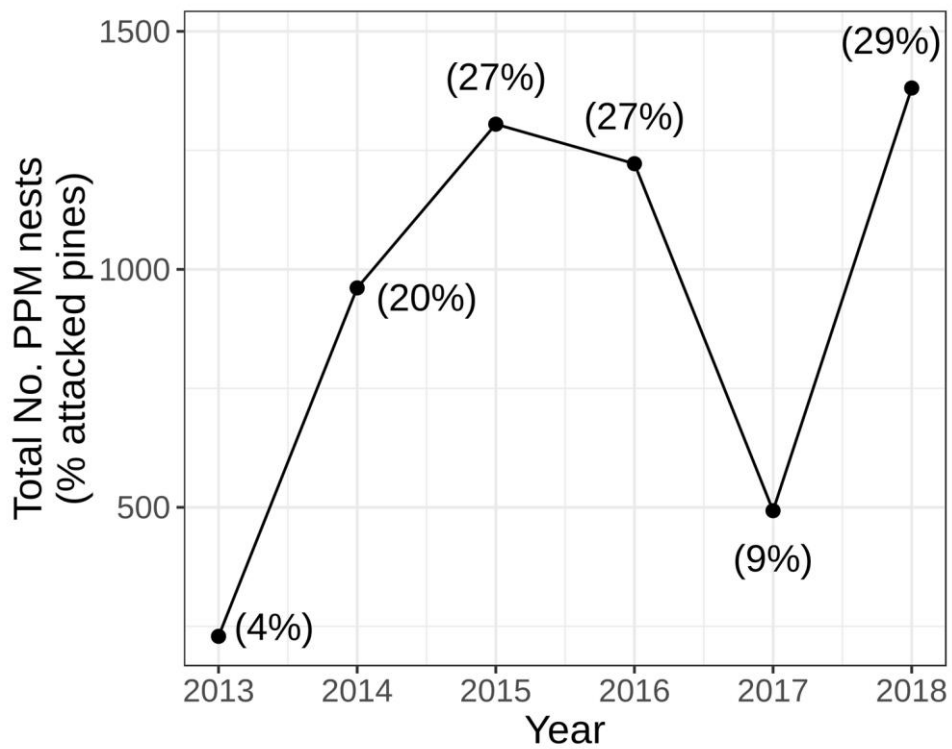


Figure 2

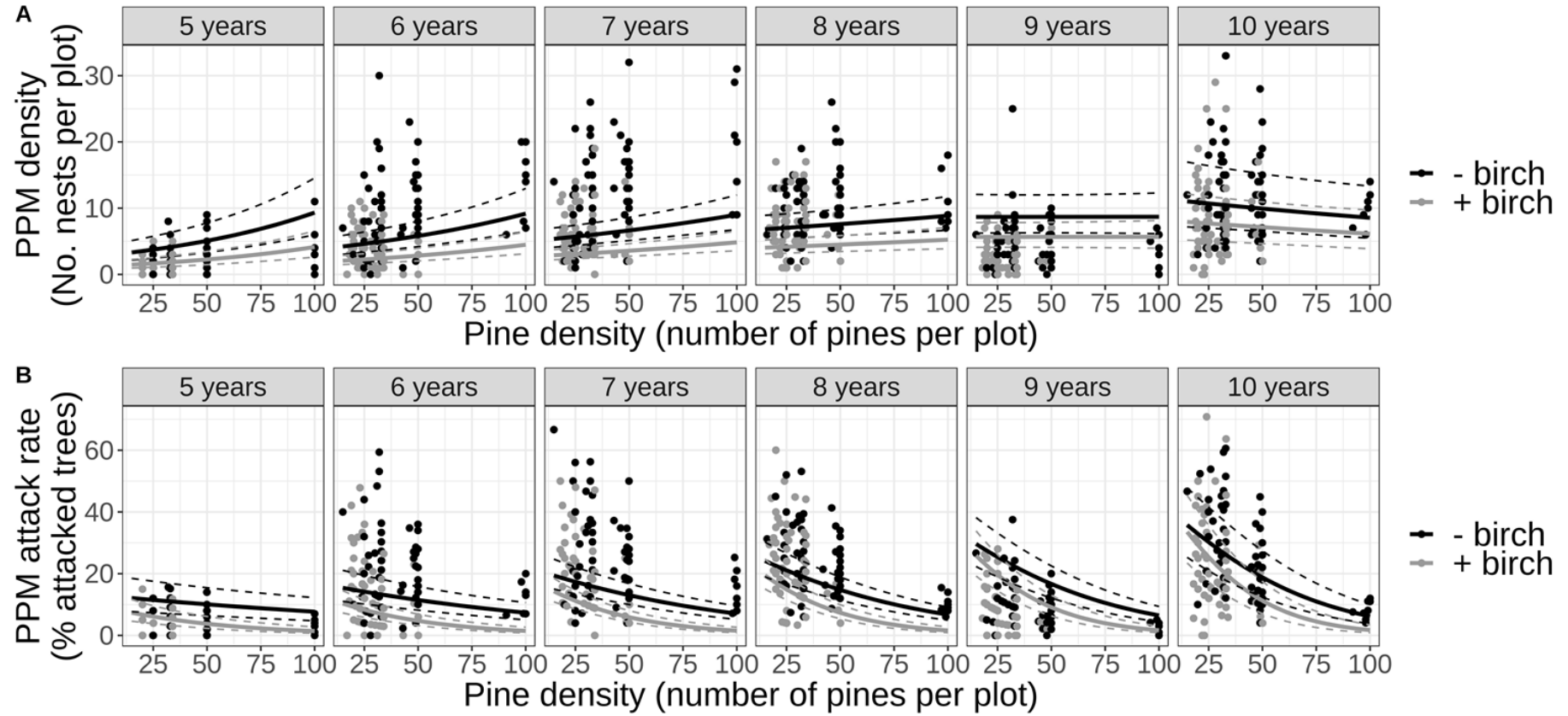


Figure 3

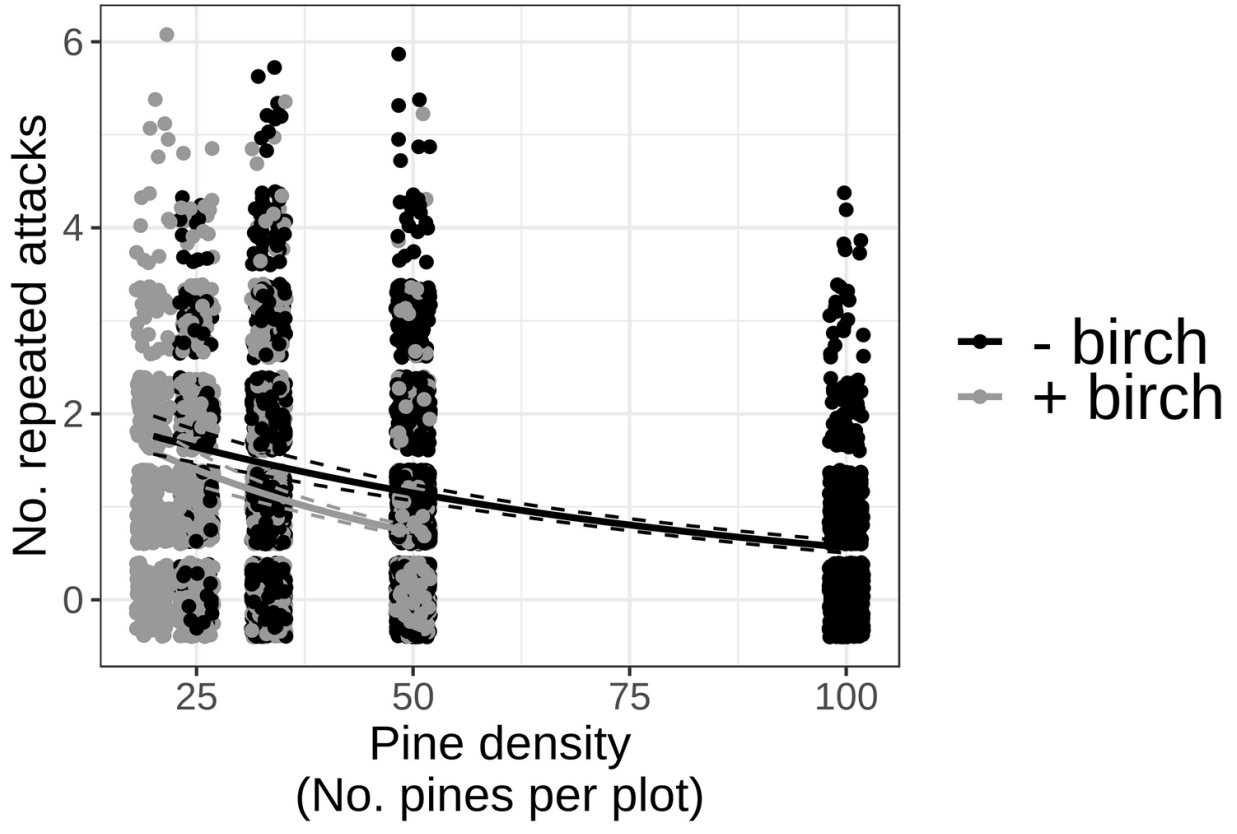


Figure 4

