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1 **Tree diversity reduces pine infestation by mistletoe**

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3 Inge van Halder*¹, Bastien Castagneyrol ¹, Cristóbal Ordóñez ^{2,4}, Felipe Bravo ^{2,4}, Miren del Río ^{2,3},

4 Lucile Perrot¹, Hervé Jactel¹

5

6 1 BIOGECO, INRA, Univ. Bordeaux, 33610, Cestas, France

7 2 Sustainable Forest Management Research Institute, University of Valladolid & INIA, Av. Madrid 44,

8 Palencia 34004, Spain

9 3 Department of Silviculture and Forest Management, INIA, Forest Research Centre, Ctra. A Coruña,

10 km 7.5, Madrid 28040, Spain

11 4 Departamento de Producción Vegetal y Recursos Forestales, E.T.S de Ingenierías Agrarias,

12 Universidad de Valladolid, Palencia, Spain

13

14 * **Corresponding author:** inge.van-halder@inra.fr

15

16 **Abstract**

17 The pattern that a given tree species suffers less damage when growing with heterospecific

18 neighbors than amongst conspecific plants, i.e. associational resistance, is common for insect

19 herbivores and many fungal pathogens. However, associational resistance to parasitic plants has

20 never been tested in a replicated study. Using paired forest plots, we investigated whether tree

21 diversity triggered associational resistance to a tree parasite, the European mistletoe *Viscum album*

22 ssp. *austriacum*, by comparing pure stands of Scots pine (*Pinus sylvestris*) with mixtures of Scots pine

23 and Maritime pine (*Pinus pinaster*) in northern Spain. Maritime pine, with 1.2% of trees being

24 infested, was considered a non-host species in the study area. The infestation level of Scots pines

25 was significantly higher in pure plots (45.1%) than in mixed plots of Scots pines and Maritime pines

26 (25.4 %). Our study is the first to quantify associational resistance to a plant parasite in mixed vs.

27 pure forest stands and suggests that mechanisms proposed to explain associational resistance to
28 insects and pathogens also apply to plant parasites. Scots pine trees that were taller than the
29 surrounding trees had a higher infestation probability, in both pure and mixed stands. Scots pine
30 trees growing in mixtures were slightly lower than Maritime pines, suggesting that associational
31 resistance was partly driven by reduced relative tree height. However, the effect of plot type (pure
32 vs. mixed) remained significant after the effect of tree height was accounted for, thus indicating that
33 other factors also contributed to lower mistletoe infestation in mixed plots. In particular, the
34 behavior of birds dispersing mistletoe seeds might differ in mixed vs. pure stands.

35

36 **Keywords** : Associational resistance; Biodiversity; Forest management; Mistletoe; *Pinus pinaster*;
37 *Pinus sylvestris*; *Viscum album*

38

39 **1. Introduction**

40 Increasing evidence is showing that tree diversity contributes to forest ecosystem functioning and
41 the provision of ecosystem services (Brocknerhoff et al., 2017). Mixed-species forests exhibit higher
42 productivity, plant and animal biodiversity, resistance to disturbances and less insect damage than
43 tree monocultures (Castagneyrol et al., 2014; Jactel and Brocknerhoff, 2007; Jactel et al., 2018, 2017).
44 Associational resistance, i.e. the fact that a given tree suffers less damage when growing with
45 heterospecific neighbors than amongst conspecific trees (Barbosa et al., 2009) is a common pattern
46 for herbivore insects (Castagneyrol et al., 2014) and root pathogens (Jactel et al., 2017), while for
47 foliar pathogens the effect of mixed stands seems more variable (Jactel et al., 2017). The effect of
48 tree diversity on insect herbivores and pathogens can be attributed to two, often non-independent,
49 processes: a lower density of host plants in mixtures or a pure associational effect (Hambäck et al.,
50 2014). Two theories explain the relationship between host density and insect/pathogen abundance
51 in pure vs. mixed stands. The resource concentration hypothesis (Root, 1973) predicts higher

52 herbivore abundance in pure stands because insects are more likely to find, remain and reproduce
53 on host trees that are more abundant in such stands. On the contrary, when host density is low in
54 mixed stands, herbivores may concentrate on the few available hosts, leading to a higher infestation
55 level per tree (resource dilution hypothesis (Damien et al. 2016; Otway et al., 2005)). Non-host trees
56 can also trigger associational resistance independently of host density. For example, reduced
57 apparency of focal tree species, whereby non-host trees in the mixture disrupt visual and chemical
58 cues emitted by host trees, can explain associational resistance to actively dispersing herbivores and
59 insect vectored pathogens (Castagneyrol et al., 2013). For airborne pathogens or those dispersing
60 through root contact the presence of non-host trees can provide a physical barrier to contamination
61 of neighboring host trees, leading to lower infestation levels in mixed stands (Jactel et al., 2017). The
62 presence of non-host trees can also promote the presence and abundance of natural enemies
63 providing biological control of insect herbivores (Jactel and Brockerhoff, 2007) or pathogens (Jactel et
64 al., 2017). While these resistance effects of tree diversity have frequently been observed for pest
65 insects and, to a lower extent, for pathogens, they have very rarely been studied for parasitic plants
66 such as mistletoes. In this study, we examined the prevalence of European mistletoe (*Viscum album*
67 *ssp. austriacum*) in pure vs. mixed pine forests.

68

69 Mistletoes are hemi-parasitic plants, with about 1300 species from five families within the Santales
70 (Watson, 2001). The European mistletoe, *Viscum album*, is a perennial, hemi-parasitic plant that only
71 lives on woody plants (Zuber and Widmer, 2009) and extracts water and minerals from its host. In
72 Europe four subspecies occur that differ in distribution and host range (Zuber, 2004). *V. album ssp.*
73 *austriacum* occurs in Spain and Central Europe, mainly on *Pinus* species and rarely on *Larix* and *Picea*
74 (Zuber, 2004; Zuber and Widmer, 2009). *V. album* is a species of interest because it is a host for
75 several specialized insect species, a food source for birds and it contains pharmacological substances
76 (Briggs, 2011; Lázaro-González et al., 2017; Zuber, 2004). However, high levels of *V. album* infestation
77 have negative effects on tree growth (Noetzli et al., 2003; Rigling et al., 2010; Sangüesa-Barreda et

78 al., 2013) and contribute to tree death especially when associated with drought stress (Dobbertin
79 and Rigling, 2006; Mutlu et al., 2016; Tsopelas et al., 2004). The relationship with drought stress
80 indicates that with climate change the damage caused by *V. album* will probably increase in the
81 future. Moreover, *V. album* is expanding its range. An upward shift in altitude has been observed in
82 the last century, which seems linked with global warming (Dobbertin et al., 2005).

83 As for many other mistletoe species, the seeds of *V. album* are dispersed by birds. Seed dispersal, the
84 first step in the infestation process, seems an essential process in explaining *V. album* infestation and
85 spatial distribution and bird behavior may lead to a higher seed deposition on certain trees, for
86 example on tall trees or on trees at stand edges (Durand-Gillmann et al., 2014; Vallauri, 1998). The
87 most important dispersers of *V. album* seeds are mistle thrush (*Turdus viscivorus*), other *Turdus*
88 species, waxwing (*Bombycilla garrula*) and blackcap (*Sylvia atricapilla*) (Mellado and Zamora, 2014;
89 Zuber, 2004). The most effective dispersers of *V. album* in southern Europe are thrushes (Mellado and
90 Zamora, 2014). Thrushes eat the berries and defecate the seeds. With a transit time of about half an
91 hour the seeds can be dispersed over distances of more than 20 km by migrating birds (Frochot and
92 Sallé, 1980). However, most seed dispersal occurs at shorter distances by thrushes foraging in areas
93 with *V. album* infested trees or by thrushes holding and defending territories of groups of *V. album*
94 infested trees (Skórka and Wójcik, 2005; Snow and Snow, 1984). Blackcaps, another seed disperser,
95 disperse the seeds at even closer distances, mainly within the same tree, as they feed on the skin of
96 the berry and leave the seed on a shoot nearby the *V. album* shrub (Zuber, 2004). The behavior of
97 birds to spend more time on infested hosts than non-infested hosts thus leads to an aggregation of
98 mistletoes within hosts (Aukema and Martinez de Rio, 2002).

99

100 The effects of tree diversity on mistletoe infestation, including effects of host density and of pure
101 associational effects of the accompanying tree species, can be multiple, since tree diversity can
102 influence both the behavior of seed dispersing birds and mistletoe-host interactions (see Figure 1).
103 Birds are active seed dispersers and it is likely that processes generating associational effects for

104 insect herbivores also act upon birds, such as disruption of host finding cues. Mistletoe infestation is
105 often higher on taller trees as observed for *V. album* (Durand-Gillmann et al., 2014; Kolodziejek and
106 Kolodziejek, 2013) and for several other mistletoe species (Aukema and Martínez del Rio, 2002;
107 Donohue, 1995; Roxburgh and Nicolson, 2008; Shaw et al., 2005; Smith and Reid, 2000; Teodoro et
108 al., 2010). This pattern was proposed to result mainly from bird preferences for more apparent trees
109 rather than to differences in host tree suitability (Aukema and Martínez del Rio, 2002; Roxburgh and
110 Nicolson, 2008). In mixed stands, where infested trees can be partly hidden by non-infested
111 neighbours, birds foraging for mistletoe fruits may have greater difficulty to find their resource. Birds
112 can also react to local mistletoe abundance. The behavior of birds to spend more time in groups of
113 trees with high mistletoe abundance gives that in those areas both infested and uninfested hosts
114 have a higher exposure to seed dispersers than in areas with a low infestation level (Aukema, 2003).
115 This mechanism may lead to a direct effect of the non-host density in mixtures as birds will
116 encounter less mistletoe hosts in these stands and shorten probably their foraging time.
117 Tree diversity can also affect host-mistletoe interactions. Host plants have developed structural and
118 biochemical defenses to mistletoe infestation (Aukema, 2003) and the expression of tree defensive
119 traits have been shown to be influenced by the identity of neighboring trees (Castagneyrol et al.,
120 2018; Rosado-Sánchez et al., 2018). Trees may also differ in quality for mistletoes. For example, in
121 areas where water is limiting, mistletoes are more likely to establish on host trees with better access
122 to water (Watson, 2009). This process probably differs between pure and mixed stands, with drought
123 responses of tree species varying according to the composition of mixtures (Forrester and Bauhus,
124 2016; Grossiord, 2018).

125

126 The objective of our study was to evaluate the effect of mixed vs. pure stands on the infestation level
127 by *V. album* and to identify tree and stand characteristics linked to associational resistance or
128 susceptibility. We studied the presence of *V. album* ssp. *austriacum* in pure Scots pine (*Pinus*
129 *sylvestris*) forests and mixed forests of Scots pine and Maritime pine (*P. pinaster*) in northern Spain.

130 Preliminary observations in the study area indicated that Scots pine was much more sensitive to *V.*
131 *album ssp. austriacum* than Maritime pine that could be considered a non-host. As such,
132 associational effects in mixed stands of Scots pine and Maritime pine would result from a
133 combination of both host density effects, whereby Scots pine density is lower in mixtures as
134 compared to monocultures, and pure associational effects whereby, for a given Scots pine density,
135 the presence of Maritime pines might reduce the probability of infestation on neighboring Scots
136 pines.

137 In particular, our study aimed to answer the following questions:

- 138 i) does *V. album* infestation level of Scots pines differ between pure and mixed stands?
- 139 ii) does the presence of *V. album* depend on relative tree height (i.e. how much a given tree is
140 higher than its neighbors) ?
- 141 iii) what are the relative effects of host and non-host density on *V. album* infestation?

142

143

144 2. Material and methods

145

146 2.1 Study area and plots

147 The study was conducted in northern Spain, in an area of approximately 50,000 ha covered with
148 Mediterranean forests of Scots pine and Maritime pine. The area covers the transition zone between
149 the natural Scots pine (higher elevation) and Maritime pine (lower elevation) forests in the Northern
150 Iberian mountain range, belonging to the provenance regions “Montaña Soriano Burgalesa” and
151 “Montaña de Soria Burgos” respectively (Martín et al 1998). Mean annual temperature of the area is
152 9.0 °C, mean annual precipitation ranges from 715 to 888 mm and elevation ranges from 1090 to
153 1277 m a.s.l.. To study the effect of species mixture on forest productivity and structure in this area,
154 Riofrio et al. (2017) selected in 2014-2015 36 circular plots with a radius of 15 m. Plots were selected
155 as representative parts of forest composition and structure in the surrounding area. Plots were

156 grouped into 12 triplets of mixed plots and the corresponding pure plots of Scots pine and Maritime
157 pine (i.e. 36 plots in total). All triplets were situated in an area of 40 km length by 20 km width, with
158 coordinates of plots between 41°46'15.2"N - 41°53'46.6"N and 2°55'39.9"W - 3°20'43.4"W. Distance
159 between plots within the same triplet was always shorter than 1 km. Tree age of plots ranged
160 between 38 and 139 years. For Scots pines, the median difference in age between the pure and
161 mixed plot of a triplet was 7.5 years, with a minimum of 2 years for the triplet with the youngest
162 plots and a maximum of 38 years for the triplet with the oldest plots. For Maritime pine the median
163 value was 8 years, and varied between 2 years to 34 years for the oldest triplet. Additional
164 information about stand characteristics are included in Riofrío et al (2017, Supplementary Material).
165 For each tree, the diameter at breast height and the height were measured (see for more details on
166 forest management, plot selection, and measurements Riofrío et al. (2017).

167 Preliminary observations on Maritime pine trees in pure Maritime pine stands and in mixed stands
168 revealed that *V. album* was nearly absent on Maritime pine in this area, in sharp contrast with the
169 high prevalence on Scots pine. We therefore considered Maritime pine as non-host and did not
170 survey pure Maritime pine plots. The study was thus based on *V. album* infestation in 12 pairs of
171 pure stands of *P. sylvestris* and mixtures of *P. sylvestris* and *P. pinaster*. Mixed plots had varying
172 proportions of tree species, with *P. sylvestris* representing 37-77% of the total number of trees and
173 32-71% of total basal area. In plots classified as pure plots, *P. sylvestris* accounted for at least 91% of
174 the total number of trees and 85% of total basal area (**Table 1**). Other plot characteristics are
175 indicated in **Table 1** and **Appendix A (Fig. A.1 and A.2; Table A.1)**. Since the average total number of
176 trees was the same in mixed and pure plots and Maritime pine thus partly replaced Scots pine in
177 mixed plots, the number of trees of the two species was negatively correlated for the 24 plots ($r = -$
178 0.54) as was their basal area ($r = -0.74$, Appendix **Fig. A.1**).

179 In March 2017, two observers, positioned at different sides of the tree, assessed together the
180 presence/absence of *V. album* on each tree inspecting the complete tree crown and stem with
181 binoculars. A total of 255 Maritime pines and 843 Scots pines were inspected in the 12 pairs of plots.

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Table 1. Compositional and structural characteristics of the mixed and pure plots. For each tree species, mean (minimum, maximum) values per plot are given for the number of trees (expressed per plot and per hectare), DBH (Diameter at Breast Height), tree height, basal area and % trees calculated for the total number of trees (N) or basal area (BA).

	mixed plots (N=12)		pure <i>P. sylvestris</i> plots (N=12)	
	<i>P. sylvestris</i>	<i>P. pinaster</i>	<i>P. sylvestris</i>	<i>P. pinaster</i>
number of trees / plot	26.3 (14, 42)	19.7 (9, 36)	45.3 (26, 76)	1.6 (0, 6)
number of trees / ha	372.5 (198.1, 594.2)	278.2 (127.3, 509.3)	640.2 (367.8, 1075.2)	22.4 (0.0, 84.9)
DBH (cm)	29.6 (20.2, 40.3)	37.5 (23.5, 47.7)	30.3 (20.4, 39.8)	42.0 (26.0, 56.7)
tree height (m)	19.3 (14.0, 24.7)	20.4 (14.9, 26.9)	20.1 (14.8, 24.5)	21.2 (15.3, 26.3)
basal area (m ² /ha)	26.2 (13.0, 45.9)	30.8 (11.1, 48.7)	45.8 (29.3, 59.1)	2.6 (0.0, 7.1)
% trees (N)	57.4 (36.8, 76.9)	42.6 (23.1, 63.2)	97.0 (90.9, 100.0)	3.0 (0.0, 9.1)
% trees (BA)	46.3 (31.9, 71.4)	53.7 (28.6, 68.1)	94.4 (85.0, 100.0)	5.6 (0.0, 15.0)

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 189

190 2.2 Statistical analyses

191 Data were analyzed at the plot level and at the individual tree level. At the plot level, we analyzed the
 192 proportion of Scots pine trees infested with *V. album* using three sets of explanatory variables. In the
 193 first model, we used plot type (pure vs. mixed plots) as explanatory categorical variable. Since a
 194 possible effect of plot type may be driven by either a dilution of Scots pine and/or an increase in
 195 Maritime pine, we ran two other models by substituting plot type by i) the basal area of Scots pine +
 196 the basal area of Maritime pine + their interaction or ii) the number of Scots pine trees + the number
 197 of Maritime pine trees + their interaction. Combining both Scots pine and Maritime pine abundance
 198 in the same model allowed addressing both the effect of host concentration (here Scots pine) and
 199 the pure effect of the associated species (here the abundance of Maritime pine). For these three
 200 models we used generalized linear mixed models (GLMM) with a binomial error and a *logit* link
 201 function on a response variable consisting of the number of infested Scots pine trees vs. the number

202 of non-infested Scots pine trees per plot. To take into account the structure of the dataset with
203 paired plots we used Pair identity (12 pairs of plots) as a random factor.

204 We used the same general approach to analyze the probability of mistletoe infestation at the level of
205 individual trees, but further accounted for tree-level covariates. For the analyses at the tree level we
206 first estimated the individual relative tree height (ΔH), which indicates how much taller or lower a
207 tree is as compared to its neighbors (Castagneyrol et al., 2013; Damien et al., 2016). We calculated
208 for each Scots pine tree its ΔH by subtracting from the height of the tree the mean height of the trees
209 in the corresponding plot. As such, $\Delta H > 0$ indicates that a tree is higher than the mean canopy
210 height. In order to verify if ΔH was independent of the sampling design, we first tested if the height
211 and ΔH of Scots pine trees differed between mixed and pure plots using linear mixed models (LMM)
212 with plot type as explanatory variable. Next we analyzed the probability of a Scots pine tree being
213 infested by *V. album* by using three sets of explanatory variables. In the first model, we analyzed the
214 effect of ΔH , plot type (pure vs. mixed) and their interaction on the presence/absence of *V. album* on
215 individual Scots pine trees using a GLMM with binomial error and a *logit* link function. As for the
216 analyses at the plot level, we replaced plot type by i) the basal area of Scots pine, of Maritime pine
217 and their interaction and ii) the number of trees of each species and their interaction. For all models
218 at the tree level we used as random factors Plot identity nested within Pair identity to account for
219 the nested structure of the dataset where trees were incorporated in a plot, that belonged to a pair
220 of plots (Schielzeth and Nakagawa, 2013).

221 For all models, both at the plot and tree level, we applied a model simplification procedure by
222 comparing nested models, with vs. without the variable of interest. We sequentially removed
223 predictors, starting with the least significant, while applying marginality principle where the principal
224 effects were not removed if involved in a significant interaction. Significance of effects was tested by
225 comparing models with and without the term with type II Wald chi-square tests on log likelihood
226 ratios. For model validation we visually checked model residuals. For the simplified models, R^2 values
227 were calculated to estimate the variance explained by fixed effects (marginal R^2 , R^2_m), and by fixed

228 plus random effects (conditional R^2 , R^2_c)(Nakagawa and Schielzeth, 2013). Variables were scaled
229 before analyses.
230 All analyses were carried out in R (R Core Team, 2019). The following functions and libraries were
231 used: glmer function from lme4 package (Bates et al., 2015), r.squaredGLMM from MuMin package
232 (Barton, 2018), Anova from car package (Fox and Weisberg, 2011) and simulateResiduals from
233 DHARMA package (Hartig, 2019) for residual plots.

234

235 **3. Results**

236 The overall *V. album* infestation level was 35.8 % for Scots pine trees (n= 843 trees) and 1.2 % for
237 Maritime pine trees (n= 255 trees), confirming that Maritime pine can be considered a non-host
238 species for *V. album* ssp. *austriacum* in the study area.

239 The infestation level of Scots pines was almost twice as high in pure plots as in mixed plots ($X^2 = 37.2$,
240 $df = 1$, $P < 0.001$), with a mean infestation level of 45.1 ± 8.4 % (\pm SE) in pure plots vs. 25.4 ± 6.8 % in
241 mixed plots (**Fig. 2**). However, plot type *per se* only explained a limited amount of variance in *V.*
242 *album* infestation ($R^2_m = 0.062$, $R^2_c = 0.390$).

243

244 For the model using basal area of both tree species as explanatory variables, only the basal area of
245 Scots pine trees was selected in the final model, showing an increase in infestation level with
246 increasing Scots pine basal area (**Table 2**). On the contrary, for the model using number of trees only
247 the number of Maritime pine trees was selected, showing an increase in infestation level with
248 decreasing number of Maritime pine trees (**Table 2**). Therefore, although they did not retain the
249 same variables as significant predictors, both models yielded consistent results whereby mistletoe
250 infestation was higher where host-trees were more abundant and where non-host trees were less
251 abundant. The model using basal area of Scots pines as an explanatory variable explained more
252 variance in *V. album* infestation ($R^2_m = 0.14$, Table 2) than the model using the number of Maritime
253 pine trees ($R^2_m = 0.07$, Table 2).

254

255 **Table 2.** Summary of models testing the effects of basal area (BA) and tree number (N) of *P. sylvestris* and *P.*
 256 *pinaster* on *V. album* infestation level of *P. sylvestris* at the plot level. Explanatory variables in bold had a
 257 significant effect (at $P < 0.05$). R^2m and R^2c are marginal and conditional R^2 , respectively, and are calculated for
 258 the final model resulting from model simplification.

Response	Predictors	Estimate (\pm SE)	χ^2	Df	P-value	R^2m (R^2c)
infestation level	BA <i>P. sylvestris</i>	1.32 (\pm 0.36)	13.48	1	< 0.001	0.14 (0.41)
	BA <i>P. pinaster</i>	0.40 (\pm 0.29)	1.76	1	0.185	
	BA <i>Ps</i> x BA <i>Pp</i>	0.21 (\pm 0.26)	0.68	1	0.411	
infestation level	N <i>P. sylvestris</i>	0.38 (\pm 0.23)	1.61	1	0.204	
	N <i>P. pinaster</i>	-0.43 (\pm 0.16)	14.43	1	< 0.001	0.07 (0.40)
	N <i>Ps</i> x N <i>Pp</i>	0.25 (\pm 0.25)	1.04	1	0.307	

259

260

261 The height of Scots pine trees was not statistically different between mixed and pure plots ($\chi^2 = 1.43$,
 262 $df = 1$, $P = 0.230$). However, ΔH (i.e. the difference between individual Scots pine tree height and
 263 mean plot height) was slightly, but significantly lower in mixed plots than in pure plots ($\chi^2 = 8.62$, $df =$
 264 1 , $P = 0.003$), with a mean ΔH of -0.45 m in mixed plots and -0.003 m in pure plots, indicating that
 265 Scots pines were on average lower than Maritime pines in mixed plots.

266

267 At the individual tree level, both ΔH and plot type had significant and independent effects on *V.*
 268 *album* infestation probability (**Table 3**). The probability of individual Scots pines being infested
 269 increased with increasing ΔH and was higher in pure than in mixed plots (**Fig. 3**). The fact that plot
 270 type remained significant after the effect of ΔH was accounted for, and conversely, indicates that
 271 factors other than those related to relative tree height additionally contributed to the effect of plot
 272 type on *V. album* infestation probability. When plot type was replaced by the basal area of the two
 273 tree species, ΔH and basal area of Scots pine were selected in the final model (**Table 3**). The
 274 infestation probability increased with ΔH and with the basal area of Scots pines in the plot. For the

275 model including ΔH and the number of trees of each species, ΔH and the number of Maritime pines
 276 were selected (**Table 3**), leading to a higher infestation probability with increasing ΔH and decreasing
 277 number of Maritime pine trees per plot.

278
 279

280 **Table 3.** Summary of models testing the effects of the individual relative tree height of *P. sylvestris* (ΔH) and
 281 plot composition on infestation probability by *Viscum album* of individual *P. sylvestris* trees. The effect of the
 282 following predictors on *V. album* infestation probability of individual *P. sylvestris* trees were tested in separate
 283 models: 1) relative tree height (ΔH), plot type (pure or mixed) and their interaction, 2) ΔH , basal area (BA) of *P.*
 284 *sylvestris* and of *P. pinaster* and their interaction and 3) ΔH , tree number (N) of *P. sylvestris* and of *P. pinaster*
 285 and their interaction. Explanatory variables in bold characters had a significant effect (at $P < 0.05$). R^2_m and R^2_c
 286 are marginal and conditional R^2 , respectively, and are calculated for the final model resulting from model
 287 simplification.

Model tested	Predictors	Estimate (\pm SE)	X^2	Df	P-value	R^2_m (R^2_c)
Model 1	ΔH	0.96 (\pm 0.19)	87.07	1	< 0.001	0.23 (0.58)
	plot type	1.17 (\pm 0.32)	13.88	1	< 0.001	
	$\Delta H \times$ plot type	0.31 (\pm 0.25)	1.64	1	0.201	
Model 2	ΔH	1.14 (\pm 0.12)	85.26	1	< 0.001	0.30 (0.57)
	BA <i>P. sylvestris</i>	1.31 (\pm 0.43)	10.39	1	0.001	
	BA <i>P. pinaster</i>	0.50 (\pm 0.33)	1.52	1	0.217	
	BA <i>Ps</i> \times BA <i>Pp</i>	0.38 (\pm 0.30)	1.61	1	0.205	
Model 3	ΔH	1.18 (\pm 0.12)	90.05	1	< 0.001	0.25 (0.58)
	N <i>P. sylvestris</i>	0.17 (\pm 0.33)	0.01	1	0.931	
	N <i>P. pinaster</i>	-0.33 (\pm 0.32)	11.15	1	< 0.001	
	N <i>Ps</i> \times N <i>Pp</i>	0.51 (\pm 0.37)	1.89	1	0.169	

288

289

290 4. Discussion

291 We showed that the infestation level of Scots pines by *V. album* was almost twice as high in pure
292 Scots pine plots compared to mixed plots of Scots pine and Maritime pine. Our study is the first to
293 reveal and quantify associational resistance to a plant parasite in mixed vs. pure forest stands.
294 Despite the correlative nature of our study, we can speculate that mechanisms proposed to explain
295 tree diversity effects on resistance to insects and pathogens also apply to plant parasites. The
296 observation that tree diversity reduces *V. album* infestation level may be related to i) changes in
297 behavior or abundance of seed dispersing birds and/or to ii) changes in *V. album*-tree interactions.
298 Both processes are potentially influenced by the density of the host tree (Scots pine) and the density
299 of the associated, non-host species (Maritime pine).

300

301 **4.1 Effect of host and non-host densities on mistletoe infestation**

302 We analyzed in the same model the effect of Scots pine and Maritime pine abundance on *V. album*
303 infestation level. The use of number of trees indicated a pure associational effect of Maritime pine
304 whereby *V. album* infestation decreased with increasing abundance of the non-host species, whereas
305 analysis based on host and non-host basal area suggested an effect of host cover, whereby *V. album*
306 infestation increased with increasing Scots pine basal area. These findings suggest that both the
307 proportion and density of the host tree can account for the effect of mixture on *V. album* infestation.
308 However, because the experimental plots were based on a replacement of one species by the other
309 and the number of trees or the basal area of the two species were correlated negatively, we could
310 not quantify the relative importance of these two mechanisms. To demonstrate a pure associational
311 effect one should compare plots with the same Scots pine density but with absence or presence of
312 Maritime pines (Damien et al., 2016; Hambäck et al., 2014). Concerning the effect of Scots pine
313 abundance in our plots it seems that the *V. album* infestation depended more on Scots pine basal
314 area than on the number of Scots pine trees, possibly because seed dispersing birds, such as Mistle
315 trushes, may react more to the species space occupancy in the stand (particularly crown surface
316 where birds land) than to the number of trees. Kolodziejek and Kolodziejek (2013) observed in

317 Poland, in pure Scots pine stands, a higher prevalence of *V. album* in low density stands compared to
318 high density stands. This pattern corresponds to the resource dilution hypothesis where infestations
319 are more concentrated on a more diluted resource of host trees (Otway et al., 2005). Likewise,
320 Mellado and Zamora (2016) showed an increase in visits of frugivorous birds and *V. album* seed
321 abundance in lower density *Pinus nigra* stands. However, effects of tree density, basal area, crown
322 cover and tree height may have been confounded in this or other studies, which complicates their
323 interpretation (Donohue, 1995; Kolodziejek and Kolodziejek, 2013). Low tree density can correspond
324 to taller trees with a larger crown affecting possibly bird behavior. Moreover, Kolodziejek and
325 Kolodziejek (2013) studied pure Scots pine stands whereas our results are based on pure and mixed
326 stands, explaining that we did not observe the same pattern. We therefore encourage future studies
327 to uncouple the effects of stand density and tree dimensions to move the understanding of
328 associational effects on mistletoe toward a more mechanistic framework.

329

330 **4.2 Mistletoe infestation increased with relative host size**

331 We showed that Scots pine trees that were higher than the surrounding trees had a higher *V. album*
332 infestation probability, both in mixed and pure plots. Many studies have shown a higher infestation
333 by mistletoe species in taller trees (Aukema and Martínez del Rio, 2002; Donohue, 1995; Kolodziejek
334 and Kolodziejek, 2013; Norton et al., 1997; Roxburgh and Nicolson, 2008; Shaw et al., 2005; Smith
335 and Reid, 2000; Teodoro et al., 2010) and some could attribute this effect to preferences of birds for
336 visiting taller trees, either in open landscape or forest (Aukema and Martínez del Rio, 2002; Monteiro
337 et al., 1992; Roxburgh and Nicolson, 2008). In our mixed plots, Scots pines were slightly lower than
338 Maritime pines, making them possibly less attractive for birds and thus leading to a lower seed
339 deposition on Scots pines in mixed stands compared to pure stands. Reduced host apparency is a
340 pure associational effect that has been found to diminish insect attacks on trees (Castagneyrol et al.,
341 2013; Damien et al., 2016; Dulaurent et al., 2012) and can thus likewise reduce *V. album* seed
342 deposition by birds on partially hidden trees. Taller trees may not only be more apparent to birds,

343 they also offer a larger crown surface to land on, which could increase their infestation probability.

344 Taller trees may also be a more suitable host for *V. album*, which is a light demanding species (Zuber,
345 2004). *V. album* survival may be thus better in dominant, sun-exposed trees. Taller trees, in the same
346 taxon, may also provide a more reliable water supply because of their deeper rooting system and
347 thereby offering a higher survival to mistletoe species (Norton et al., 1997; Roxburgh and Nicolson,
348 2008).

349 Additionally, we showed that for the same relative tree height in a considered stand, individual Scots
350 pine trees had a lower infestation probability in mixed stands than in pure stands, indicating that
351 other mechanisms than relative tree height play a role for the observed lower infestation level in
352 mixed stands. In mixed stands birds may land on Scots pines and Maritime pines and a part of the
353 seeds will be dropped and thus lost on Maritime pine. Future studies on bird behavior in relation to
354 host proportion may show if this mechanism is important. Pure Scots pine stands also represent
355 areas with higher *V. album* densities for birds, as host tree density is higher and trees have a higher
356 infestation level than in mixed stands. Birds feeding on *V. album* may stay longer or be more
357 abundant in pure Scots pine stands where they can find a higher amount of resources (Skórka and
358 Wójcik, 2005; Snow and Snow, 1984; Telleria et al., 2008;2014), thereby increasing seed deposition in
359 already infested stands. Aukema (2003) and Martinez del Rio et al. (1996), documented a local
360 aggregation of mistletoe for respectively a desert mistletoe in North America and a cactus mistletoe
361 in Chili. They could link this pattern with bird behavior as the percentage of non-parasitized hosts
362 receiving seeds increased with the percentage of mistletoe-infested hosts in the neighborhood. This
363 created a positive feedback as infected neighborhoods become even more heavily infected. Likewise,
364 Morales et al. (2012) showed, for a mistletoe species dispersed by a marsupial, a reduction in seed
365 dispersal distances when the neighborhood had a high mistletoe density.

366 Altogether, it seems probable that the observed higher mistletoe infestation in pure Scots pine
367 stands is related to bird preferences for apparent trees and for areas with higher infestation levels.
368 However, we cannot exclude that physiological (like chemical defenses, e.g. Lazaro-Gonzalez et al.

369 2019) or anatomical traits of Scots pines (e.g. bark thickness) may be different between pure and
370 mixed stands and that these traits could explain the rate of mistletoe establishment and growth.
371 Further research is therefore needed to determine which mechanism is most important.

372

373 **4.3 Consequences for forest management**

374 Since high densities of *V. album* reduce tree growth and contribute to tree mortality, different
375 methods for controlling this parasitic plant have been proposed. The most effective one is
376 mechanical control, such as pruning of infested branches, or removing infested trees (Varga et al.,
377 2012). This may be applicable in infested orchards, but seems less applicable in extensive forests with
378 tall trees. Moreover, removing infested trees may render remaining host trees more prone to
379 infestation (Vallauri, 1998). However, this may not be the case in our mixed stands where lower host
380 abundance seems to decrease infestation level. We showed that in mixed pine stands the infestation
381 level of Scots pine was on average 44 % lower compared to pure stands. Conservation pest
382 management, that is the use of tree diversity to keep *V. album* infestation at a low level, has to our
383 knowledge only been tested by Oliva & Colinas (2010), who showed that *Abies* stands with a low
384 level of *V. album* infestation had a higher proportion of accompanying tree species than stands with
385 a high infestation level. However, they observed no differences between highly infested and non-
386 infested stands, probably because of confounding factors for the non-infested stands.

387 Management of tree species diversity in forest stands for associational resistance shows several
388 advantages. It not only allows diminishing the negative effects of *V. album* on tree growth and
389 mortality, but may also permit an overall higher stand productivity (Riofrío et al., 2016; 2017). Lower
390 *V. album* infestation can be even one of the factors related to higher productivity in mixed stands
391 and would merit further research.

392

393 **4.4 Conclusion and perspectives**

394 We showed that tree diversity can reduce Scots pine infestation by a plant parasite, the mistletoe *V.*
395 *album*. Although literature on mixed forest resistance to herbivorous insects and fungal pathogens
396 may help to identify possible mechanisms underlying mixed forest resistance to this plant parasite,
397 further dedicated research is needed to clarify them. In particular, mistletoe is actively dispersed by
398 birds. Studies on bird behavior and abundance in relation to stand composition and *V. album*
399 infestation level may allow to precise their role in the observed reduced infestation in mixed stands.
400 Moreover, it will be useful to evaluate the effect of different tree species mixtures on *V. album*
401 infestation levels and in different regions, as host preferences of *V. album* may vary regionally. This
402 will also allow generalizing our results and recommendations to other forest systems and ecological
403 conditions.

404

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409

410 **Author Contributions**

411 IVH and HJ conceived the mistletoe study. MdR and FB set up the forest triplets, and CO measured
412 the trees. IVH, HJ and LP performed the mistletoe field survey, IVH and BC analyzed the data, IVH
413 drafted the first version of the manuscript. All authors contributed to the writing of the present
414 version of the manuscript.

415

416 **Appendix A. Supplementary material**

417 Supplementary material to this article can be found online at

418

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593

594 **Figure captions:**

595

596 **Fig. 1.** Possible effects of tree diversity on mistletoe (*Viscum album*) infestation. The solid arrows
597 represent the mistletoe cycle (seed consumption and dispersion by birds, seed germination and plant
598 establishment on the host tree, here Scots pine). The dashed arrows represent possible effects of a
599 non-host tree species (here Maritime pine) on mistletoe infestation of Scots pines growing in a mixed
600 stand.

601

602 **Fig. 2.** Mean percentage (\pm SE) of Scots pines infested with *V. album* in mixed vs. pure plots.

603

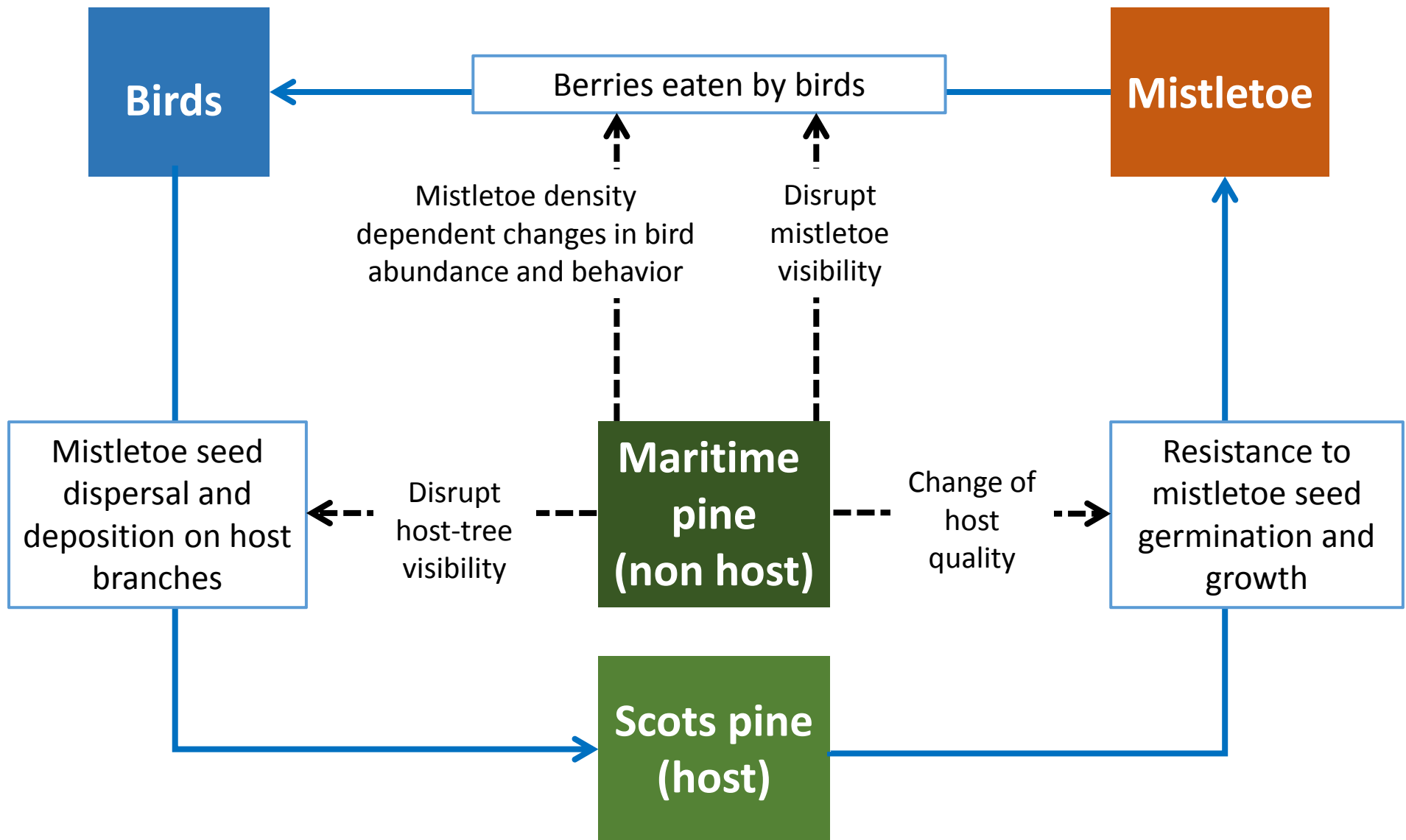
604

605 **Fig. 3.** Effect of individual relative tree height (ΔH), which indicates how much taller or lower an
606 individual *P. sylvestris* tree is as compared to its neighbors within the plot, in mixed and pure plots,
607 on the probability of individual *P. sylvestris* trees being infested by *Viscum album* (i.e. model 1 of
608 Table 3). The dashed vertical line at $\Delta H = 0$ indicates the cases in which *P. sylvestris* are on average as
609 tall as the other trees in the plot. Light green and dark green vertical bars at $y = 0$ and $y = 1$ represent
610 observed ΔH in mixed and pure stands, respectively. Logistic curves represent predictions from
611 models (solid lines) and their standard errors (dashed lines).

612

613

614



% infested *P. sylvestris* per plot

