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Abstract

The pattern that a given tree species suffers less damage when growing with heterospecific neighbors than amongst conspecific plants, i.e. associational resistance, is common for insect herbivores and many fungal pathogens. However, associational resistance to parasitic plants has never been tested in a replicated study. Using paired forest plots, we investigated whether tree diversity triggered associational resistance to a tree parasite, the European mistletoe *Viscum album* ssp. *austriacum*, by comparing pure stands of Scots pine (*Pinus sylvestris)* with mixtures of Scots pine and Maritime pine (*Pinus pinaster)* in northern Spain. Maritime pine, with 1.2% of trees being infested, was considered a non-host species in the study area. The infestation level of Scots pines was significantly higher in pure plots (45.1%) than in mixed plots of Scots pines and Maritime pines (25.4 %). Our study is the first to quantify associational resistance to a plant parasite in mixed *vs*.

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

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

1. Introduction

Increasing evidence is showing that tree diversity contributes to forest ecosystem functioning and the provision of ecosystem services (Brockerhoff et al., 2017). Mixed-species forests exhibit higher productivity, plant and animal biodiversity, resistance to disturbances and less insect damage than tree monocultures (Castagneyrol et al., 2014; Jactel and Brockerhoff, 2007; Jactel et al., 2018, 2017). Associational resistance, i.e. the fact that a given tree suffers less damage when growing with heterospecific neighbors than amongst conspecific trees (Barbosa et al., 2009) is a common pattern for herbivore insects (Castagneyrol et al., 2014) and root pathogens (Jactel et al., 2017), while for foliar pathogens the effect of mixed stands seems more variable (Jactel et al., 2017). The effect of tree diversity on insect herbivores and pathogens can be attributed to two, often non-independent, processes: a lower density of host plants in mixtures or a pure associational effect (Hambäck et al., 2014). Two theories explain the relationship between host density and insect/pathogen abundance in pure *vs*. mixed stands. The resource concentration hypothesis (Root, 1973) predicts higher herbivore abundance in pure stands because insects are more likely to find, remain and reproduce on host trees that are more abundant in such stands. On the contrary, when host density is low in mixed stands, herbivores may concentrate on the few available hosts, leading to a higher infestation level per tree (resource dilution hypothesis (Damien et al. 2016; Otway et al., 2005)). Non-host trees can also trigger associational resistance independently of host density. For example, reduced apparency of focal tree species, whereby non-host trees in the mixture disrupt visual and chemical cues emitted by host trees, can explain associational resistance to actively dispersing herbivores and insect vectored pathogens (Castagneyrol et al., 2013). For airborne pathogens or those dispersing through root contact the presence of non-host trees can provide a physical barrier to contamination of neighboring host trees, leading to lower infestation levels in mixed stands (Jactel et al., 2017). The presence of non-host trees can also promote the presence and abundance of natural enemies providing biological control of insect herbivores (Jactel and Brockerhoff, 2007) or pathogens (Jactel et al., 2017). While these resistance effects of tree diversity have frequently been observed for pest insects and, to a lower extent, for pathogens, they have very rarely been studied for parasitic plants such as mistletoes. In this study, we examined the prevalence of European mistletoe (*Viscum album* ssp. *austriacum*) in pure *vs.* mixed pine forests.

Mistletoes are hemi-parasitic plants, with about 1300 species from five families within the Santales (Watson, 2001). The European mistletoe, *Viscum album,* is a perennial, hemi-parasitic plant that only lives on woody plants (Zuber and Widmer, 2009) and extracts water and minerals from its host. In Europe four subspecies occur that differ in distribution and host range (Zuber, 2004). V. *album* ssp. *austriacum* occurs in Spain and Central Europe, mainly on *Pinus* species and rarely on *Larix* and *Picea* (Zuber, 2004; Zuber and Widmer, 2009). *V. album* is a species of interest because it is a host for several specialized insect species, a food source for birds and it contains pharmacological substances (Briggs, 2011; Lázaro-González et al., 2017; Zuber, 2004). However, high levels of *V. album* infestation have negative effects on tree growth (Noetzli et al., 2003; Rigling et al., 2010; Sangüesa-Barreda et al., 2013) and contribute to tree death especially when associated with drought stress (Dobbertin and Rigling, 2006; Mutlu et al., 2016; Tsopelas et al., 2004). The relationship with drought stress indicates that with climate change the damage caused by *V. album* will probably increase in the future. Moreover, *V. album* is expanding its range. An upward shift in altitude has been observed in the last century, which seems linked with global warming (Dobbertin et al., 2005).

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

The effects of tree diversity on mistletoe infestation, including effects of host density and of pure associational effects of the accompanying tree species, can be multiple, since tree diversity can influence both the behavior of seed dispersing birds and mistletoe-host interactions (see Figure 1). Birds are active seed dispersers and it is likely that processes generating associational effects for insect herbivores also act upon birds, such as disruption of host finding cues. Mistletoe infestation is often higher on taller trees as observed for *V. album* (Durand-Gillmann et al., 2014; Kolodziejek and Kolodziejek, 2013) and for several other mistletoe species (Aukema and Martínez del Rio, 2002; Donohue, 1995; Roxburgh and Nicolson, 2008; Shaw et al., 2005; Smith and Reid, 2000; Teodoro et al., 2010). This pattern was proposed to result mainly from bird preferences for more apparent trees rather than to differences in host tree suitability (Aukema and Martínez del Rio, 2002; Roxburgh and Nicolson, 2008). In mixed stands, where infested trees can be partly hidden by non-infested neighbours, birds foraging for mistletoe fruits may have greater difficulty to find their resource. Birds can also react to local mistletoe abundance. The behavior of birds to spend more time in groups of trees with high mistletoe abundance gives that in those areas both infested and uninfested hosts have a higher exposure to seed dispersers than in areas with a low infestation level (Aukema, 2003). This mechanism may lead to a direct effect of the non-host density in mixtures as birds will encounter less mistletoe hosts in these stands and shorten probably their foraging time.

Tree diversity can also affect host-mistletoe interactions. Host plants have developed structural and biochemical defenses to mistletoe infestation (Aukema, 2003) and the expression of tree defensive traits have been shown to be influenced by the identity of neighboring trees (Castagneyrol et al., 2018; Rosado-Sánchez et al., 2018). Trees may also differ in quality for mistletoes. For example, in areas where water is limiting, mistletoes are more likely to establish on host trees with better access to water (Watson, 2009). This process probably differs between pure and mixed stands, with drought responses of tree species varying according to the composition of mixtures (Forrester and Bauhus, 2016; Grossiord, 2018).

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

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

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

i) does *V. album* infestation level of Scots pines differ between pure and mixed stands?

ii) does the presence of *V. album* depend on relative tree height (i.e. how much a given tree is higher than its neighbors) ?

iii) what are the relative effects of host and non-host density on *V. album* infestation?

2. Material and methods

2.1 Study area and plots

The study was conducted in northern Spain, in an area of approximately 50,000 ha covered with Mediterranean forests of Scots pine and Maritime pine. The area covers the transition zone between the natural Scots pine (higher elevation) and Maritime pine (lower elevation) forests in the Northern Iberian mountain range, belonging to the provenance regions “Montaña Soriano Burgalesa” and “Montaña de Soria Burgos” respectively (Martín et al 1998). Mean annual temperature of the area is 9.0 °C, mean annual precipitation ranges from 715 to 888 mm and elevation ranges from 1090 to 1277 m a.s.l.. To study the effect of species mixture on forest productivity and structure in this area, Riofrio et al. (2017) selected in 2014-2015 36 circular plots with a radius of 15 m. Plots were selected as representative parts of forest composition and structure in the surrounding area. Plots were grouped into 12 triplets of mixed plots and the corresponding pure plots of Scots pine and Maritime pine (i.e. 36 plots in total). All triplets were situated in an area of 40 km length by 20 km width, with 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 between plots within the same triplet was always shorter than 1 km. Tree age of plots ranged between 38 and 139 years. For Scots pines, the median difference in age between the pure and mixed plot of a triplet was 7.5 years, with a minimum of 2 years for the triplet with the youngest plots and a maximum of 38 years for the triplet with the oldest plots. For Maritime pine the median value was 8 years, and varied between 2 years to 34 years for the oldest triplet. Additional information about stand characteristics are included in Riofrío et al (2017, Supplementary Material). For each tree, the diameter at breast height and the height were measured (see for more details on forest management, plot selection, and measurements Riofrio et al. (2017).

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

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

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 *P. sylvestris* plots (N=12)**	
	P. sylvestris	***P. pinaster***	***P. sylvestris***	***P. pinaster***
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)

2.2 Statistical analyses

Data were analyzed at the plot level and at the individual tree level. At the plot level, we analyzed the proportion of Scots pine trees infested with *V. album* using three sets of explanatory variables. In the first model, we used plot type (pure *vs*. mixed plots) as explanatory categorical variable. Since a possible effect of plot type may be driven by either a dilution of Scots pine and/or an increase in Maritime pine, we ran two other models by substituting plot type by i) the basal area of Scots pine + the basal area of Maritime pine + their interaction or ii) the number of Scots pine trees + the number of Maritime pine trees + their interaction. Combining both Scots pine and Maritime pine abundance in the same model allowed addressing both the effect of host concentration (here Scots pine) and the pure effect of the associated species (here the abundance of Maritime pine). For these three models we used generalized linear mixed models (GLMM) with a binomial error and a *logit* link function on a response variable consisting of the number of infested Scots pine trees *vs.* the number of non-infested Scots pine trees per plot. To take into account the structure of the dataset with paired plots we used Pair identity (12 pairs of plots) as a random factor.

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

For all models, both at the plot and tree level, we applied a model simplification procedure by comparing nested models, with *vs*. without the variable of interest. We sequentially removed predictors, starting with the least significant, while applying marginality principle where the principal effects were not removed if involved in a significant interaction. Significance of effects was tested by comparing models with and without the term with type II Wald chi-square tests on log likelihood ratios. For model validation we visually checked model residuals. For the simplified models, R^2 values were calculated to estimate the variance explained by fixed effects (marginal R^2, R^2_m), and by fixed plus random effects (conditional R^2, R^2_c)(Nakagawa and Schielzeth, 2013). Variables were scaled before analyses.

All analyses were carried out in R (R Core Team, 2019). The following functions and libraries were used: glmer function from lme4 package (Bates et al., 2015), r.squaredGLMM from MuMin package (Barton, 2018), Anova from car package (Fox and Weisberg, 2011) and simulateResiduals from DHARMa package (Hartig, 2019) for residual plots.

3. Results

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

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

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

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

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

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

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

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

Model tested	**Predictors**	**Estimate (± SE)**	**X^2**	**Df**	**P-value**	**R^2m (R^2c)**
Model 1	**ΔH**	0.96 (± 0.19)	87.07	1	< 0.001	0.23 (0.58)
	plot type	1.17 (± 0.32)	13.88	1	< 0.001	
	ΔH × plot type	0.31 (± 0.25)	1.64	1	0.201	
Model 2	**ΔH**	1.14 (± 0.12)	85.26	1	< 0.001	0.30 (0.57)
	BA *P. sylvestris*	1.31 (± 0.43)	10.39	1	0.001	
	BA *P. pinaster*	0.50 (± 0.33)	1.52	1	0.217	
	BA *Ps* x BA *Pp*	0.38 (± 0.30)	1.61	1	0.205	
Model 3	**ΔH**	1.18 (± 0.12)	90.05	1	< 0.001	0.25 (0.58)
	N *P. sylvestris*	0.17 (± 0.33)	0.01	1	0.931	
	N *P. pinaster*	-0.33 (± 0.32)	11.15	1	< 0.001	
	N *Ps* x N *Pp*	0.51 (± 0.37)	1.89	1	0.169	

4. Discussion

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

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

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

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

4.2 Mistletoe infestation increased with relative host size

We showed that Scots pine trees that were higher than the surrounding trees had a higher *V. album* infestation probability, both in mixed and pure plots. Many studies have shown a higher infestation by mistletoe species in taller trees (Aukema and Martínez del Rio, 2002; Donohue, 1995; Kolodziejek and Kolodziejek, 2013; Norton et al., 1997; Roxburgh and Nicolson, 2008; Shaw et al., 2005; Smith and Reid, 2000; Teodoro et al., 2010) and some could attribute this effect to preferences of birds for visiting taller trees, either in open landscape or forest (Aukema and Martínez del Rio, 2002; Monteiro et al., 1992; Roxburgh and Nicolson, 2008). In our mixed plots, Scots pines were slightly lower than Maritime pines, making them possibly less attractive for birds and thus leading to a lower seed deposition on Scots pines in mixed stands compared to pure stands. Reduced host apparency is a pure associational effect that has been found to diminish insect attacks on trees (Castagneyrol et al., 2013; Damien et al., 2016; Dulaurent et al., 2012) and can thus likewise reduce *V. album* seed deposition by birds on partially hidden trees. Taller trees may not only be more apparent to birds, they also offer a larger crown surface to land on, which could increase their infestation probability. Taller trees may also be a more suitable host for *V. album*, which is a light demanding species (Zuber, 2004). *V. album* survival may be thus better in dominant, sun-exposed trees. Taller trees, in the same taxon, may also provide a more reliable water supply because of their deeper rooting system and thereby offering a higher survival to mistletoe species (Norton et al., 1997; Roxburgh and Nicolson, 2008).

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

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

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

4.3 Consequences for forest management

Since high densities of *V. album* reduce tree growth and contribute to tree mortality, different methods for controlling this parasitic plant have been proposed. The most effective one is mechanical control, such as pruning of infested branches, or removing infested trees (Varga et al., 2012). This may be applicable in infested orchards, but seems less applicable in extensive forests with tall trees. Moreover, removing infested trees may render remaining host trees more prone to infestation (Vallauri, 1998). However, this may not be the case in our mixed stands where lower host abundance seems to decrease infestation level. We showed that in mixed pine stands the infestation level of Scots pine was on average 44 % lower compared to pure stands. Conservation pest management, that is the use of tree diversity to keep *V. album* infestation at a low level, has to our knowledge only been tested by Oliva & Colinas (2010), who showed that *Abies* stands with a low level of *V. album* infestation had a higher proportion of accompanying tree species than stands with a high infestation level. However, they observed no differences between highly infested and non-infested stands, probably because of confounding factors for the non-infested stands.
Management of tree species diversity in forest stands for associational resistance shows several advantages. It not only allows diminishing the negative effects of *V. album* on tree growth and mortality, but may also permit an overall higher stand productivity (Riofrío et al., 2016; 2017). Lower *V. album* infestation can be even one of the factors related to higher productivity in mixed stands and would merit further research.

4.4 Conclusion and perspectives

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

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Author Contributions

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

Appendix A. Supplementary material

Supplementary material to this article can be found online at …..

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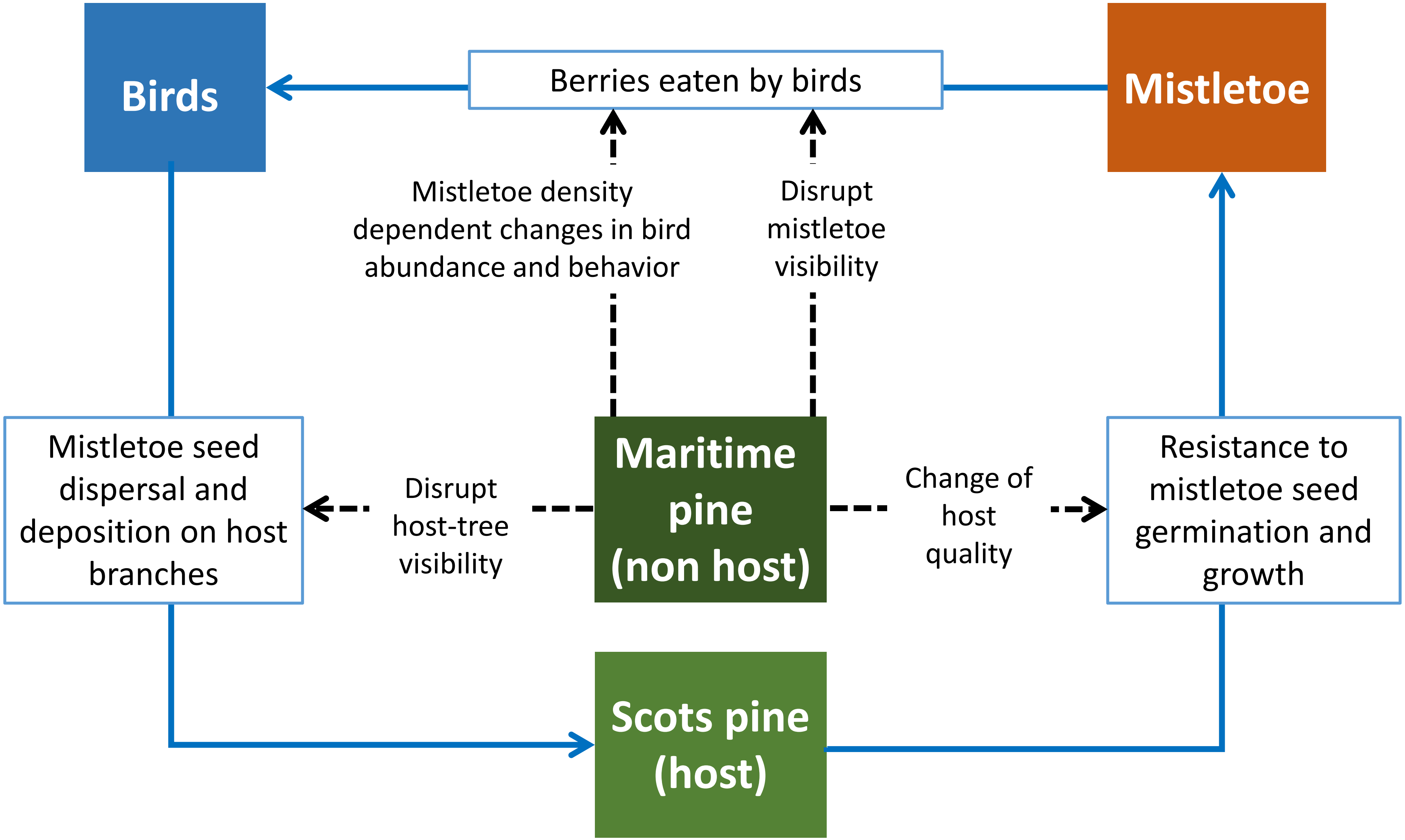
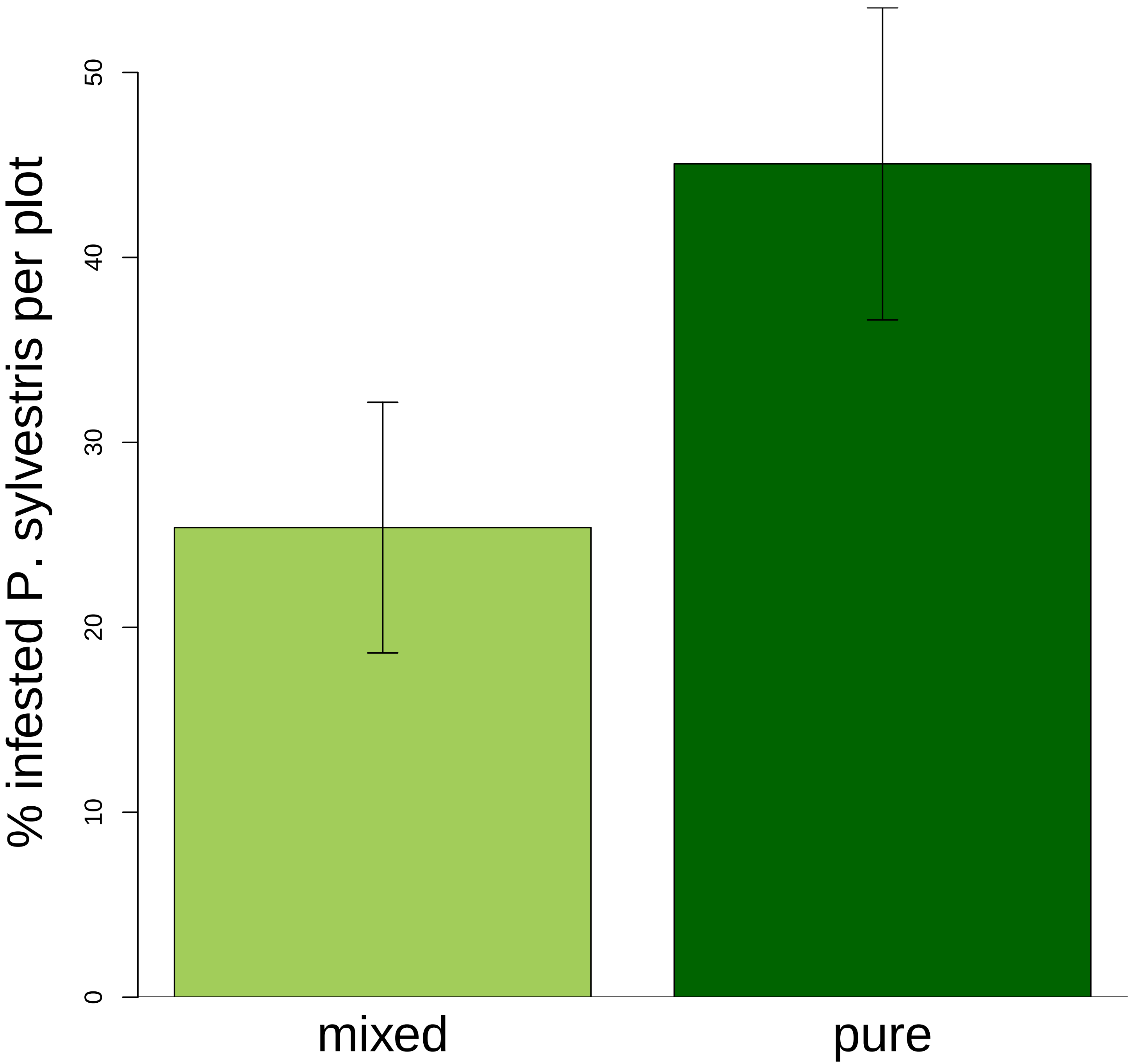
Figure captions:

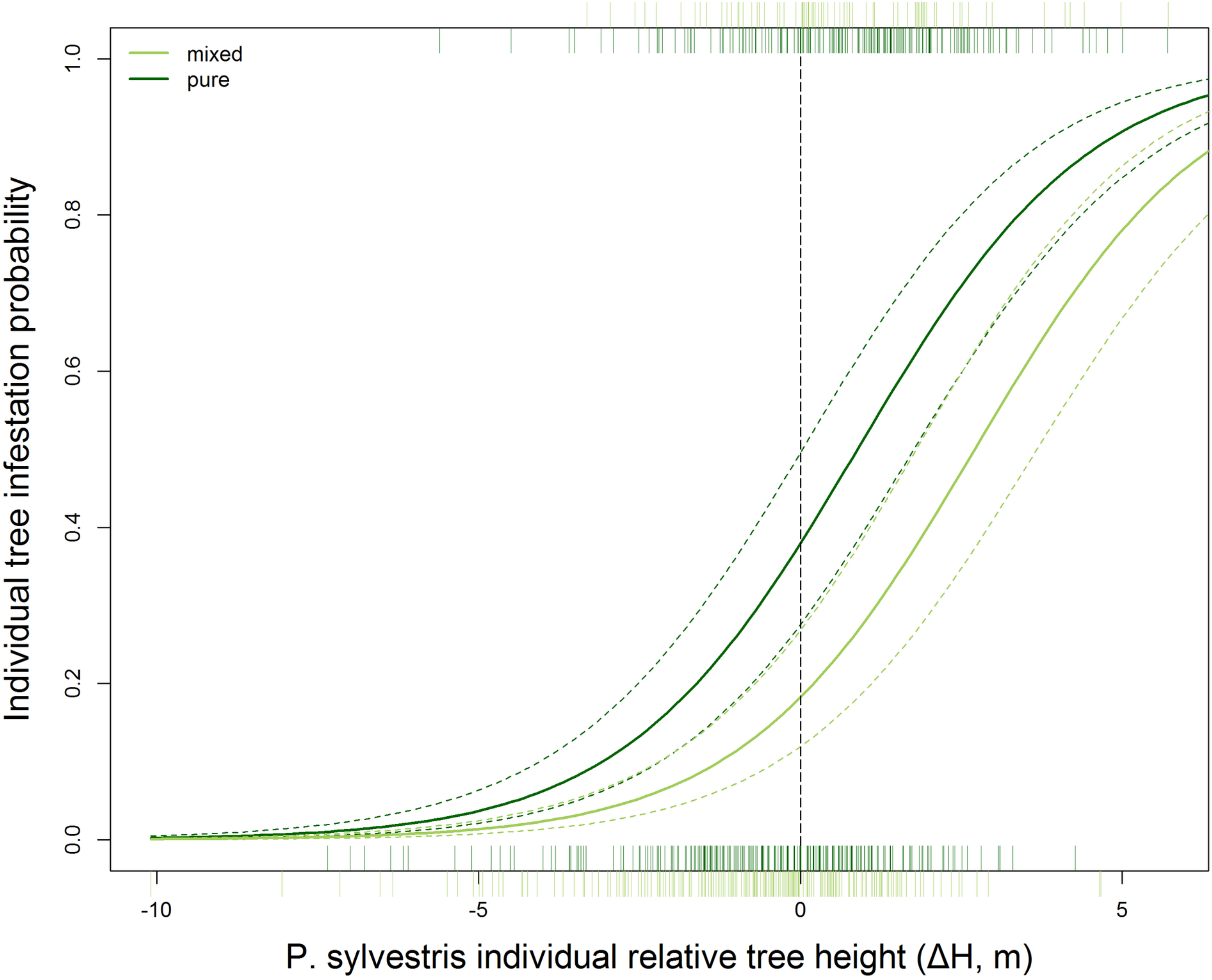
Fig. 1. Possible effects of tree diversity on mistletoe (*Viscum album*) infestation. The solid arrows represent the mistletoe cycle (seed consumption and dispersion by birds, seed germination and plant establishment on the host tree, here Scots pine). The dashed arrows represent possible effects of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

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

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


Birds
Berries eaten by birds
Mistletoe
Mistletoe density dependent changes in bird abundance and behavior
Disrupt mistletoe visibility
Mistletoe seed dispersal and deposition on host branches
Disrupt host-tree visibility
Maritime pine (non host)
Change of host quality
Resistance to mistletoe seed germination and growth
Scots pine (host)


% infested P. sylvestris per plot
0
10
20
30
40
50
mixed
pure


mixed
pure
Individual tree infestation probability
0.0
0.2
0.4
0.6
0.8
1.0
-10
-5
0
5
P. sylvestris individual relative tree height (ΔH, m)