Using associational effects of European beech on Norway spruce to mitigate damage by a forest regeneration pest, the pine weevil *Hylobius abietis*

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A B S T R A C T

Forest regeneration can be compromised by insect damage to newly-planted conifer seedlings, with the pine weevil, *Hylobius abietis*, being the most economically important pest in Europe. Seedling protection strategies include physical barriers, silvicultural measures and insecticides, while the potential benefits of Associational Effects (AE) have been little explored. Associational Resistance (AR) or Susceptibility (AS) arise when neighbouring plants decrease or increase, respectively, the likelihood and extent of attack on a focal plant. We investigated the potential of European beech, *Fagus sylvatica*, to mediate AE for Norway spruce, *Picea abies*, seedlings against pine weevil damage. First, we examined the effects of neighbor identity on damage to *P. abies* at a small scale, using choice arenas in the lab. Then, in the field, we examined these effects at a larger scale using plots containing only Norway spruce, or both species. We found that *P. abies* seedlings were attacked and damaged less by weevils when beech was their close neighbor, relative to having another Norway spruce as a neighbor in the lab. Yet, no difference in damage between only spruce and mixed seedling plots was found in the field. Our results indicate that the susceptibility of *P. abies* to *H. abietis* can be influenced by neighbor identity, and effects can vary with inter-plant distance. In close proximity, the presence of the non-host *F. sylvatica* can alter pine weevil feeding behaviour and thus, has the potential to mediate AR. However, these associational effects appear not to provide enhanced seedling protection at a larger scale.

1. Introduction

Insects represent a constant threat to European forests and their damage results in large losses to forest production systems (Day and Leather 1997). Several types of insect pests attack trees at different stages of the forestry rotation period, and these include defoliators, sap-suckers and stem and root feeders, among others. Their feeding can have negative consequences for tree growth, susceptibility to other pests and disturbances, wood quality and total biomass harvested (Kulman 1971, Brown and Gange, 1990, Gonda-King et al. 2014). Among the most vulnerable stages to insect damage is the forest regeneration phase. Seedling establishment and survival are the basis for successful reforestation, and in Europe the major threat to achieving this in coniferous forests is the pine weevil, *Hylobius abietis* (L.).

Pine weevils use the roots of recently-dead or dying conifer trees as breeding substrate, and are thus attracted by conifer volatiles from stumps of freshly-felled trees (Nordlander et al. 1986). They can easily locate and migrate by flight to forest areas which have been recently harvested (Solbreck 1980). The adult weevils feed on tender bark on roots, stems and branches of conifer trees, but once reforestation occurs, they can feed on the stem bark of planted seedlings (Fedderwitz et al., 2018). They often remove an entire ring of bark from around the stem, which disrupts or halts nutrient transport and usually results in plant death. Without any preventive measures, *H. abietis* can cause very high levels of mortality and compromise reforestation (Örlander and Nilsson, 1999). Traditionally, seedlings have been protected by prophylactic treatment with insecticides such as synthetic pyrethroids and neonicotinoids, but their use has become increasingly controversial. In Sweden, insecticide treatment has now been largely replaced by physical protection through stem coatings applied in the nursery (Nordlander et al., 2009; Skogsstyrelsen, 2020). This direct protection of seedlings is usually combined with silvicultural measures that diminish the

likelihood of damage, especially site preparation followed by planting in mineral soil (Nordlander et al., 2011). Depending on local conditions and silvicultural practices, the applicability and efficacy of various protective measures may, however, vary (Luoranen et al. 2017, Willoughby et al. 2020). Thus, long term and sustainable approaches to seedling protection against this pest are still in demand.

An overlooked ecological concept to aid in the improvement of forest seedling protection is associational effects. Associational effects emerge when the interaction between a resource and a consumer can be influenced by the identity or diversity of neighbouring individuals (Underwood et al. 2014). In the case of plant-insect interactions, it would entail how neighbouring plants affect the likelihood and extent of herbivore attack on a focal plant. Neighbours of a different species, or of a different genotype of the same species, can mediate associational resistance or susceptibility to an insect pest, relative to when the focal plant does not occur with such a neighbour. Several studies have shown that the association of certain plant species can be used as a means to indirectly lessen herbivory (Barbosa et al., 2009; Jactel et al., 2021). For example, Jactel et al. (2011) have shown that the association of maritime pine (*Pinus pinaster*) with birch (*Betula pendula*) can reduce damage by the pine processionary moth (*Thaumetopoea pityocampa*), a serious defoliator of several pine species. Likewise, density of green leaf weevils (*Polydrusus flavipes*) on birch (*B. pendula*) was reduced by the co-occurrence of the non-host shrub *Rhododendron tomentosum* in the field, and in choice experiments the autumnal moth larvae (*Epirrita autumnata*) preferred non-exposed over *R. tomentosum*-exposed birch leaves (Himanen et al., 2010). Thus, by associating the focal herbivore-susceptible plant with a herbivore-resistant or herbivore-deterring species, associational effects could be used to enhance plant protection.

Associational effects could mitigate damage caused by insect pests through different mechanisms. These mechanisms include various ways in which neighbours can interfere with the availability or quality of the focal plant. For example, non-hosts can release substances that 'mask' focal plants, as these are intercepted by the herbivore first and can hinder the pest from identifying or locating their target plant (Agrawal et al. 2006, Kim 2017). Focal plants can also perceive the volatiles of their herbivore-attacked neighbours and prepare their own defenses; thus, resulting in increased resistance and being less attractive to subsequent pest attack (Heil and Silva Bueno, 2007, Arimura et al. 2009). Furthermore, perceiving and capturing of repellent volatiles from a neighbouring plant can cause re-emission of such volatiles (Himanen et al. 2015), therefore increasing the susceptible plant's resistance against the herbivore. Finally, associational resistance could also be mediated through natural enemies of the pest herbivores. The composition of neighbouring plants can change the community of natural enemies, and have effects on the abundance of insect pests and damage to focal plants (Riihimäki et al., 2005; Jactel et al., 2011).

Associational effects of potential relevance for forest protection have mainly been studied in mature forests and at the larger stand and landscape scale (e.g., Guyot et al., 2016, 2019; Jactel et al., 2017). Far less is known about such effects during forest regeneration, and the few studies examining associational effects on forest seedlings have almost exclusively focused on mammalian herbivory (reviewed by Ruttan and Lortie 2015). In the case of the pine weevil, attraction to conifer volatiles has been shown to be inhibited or reduced by various non-host volatiles, e.g. methyl salicylate, which can be emitted by deciduous trees (Azeem et al. 2015, 2020). Associational effects have, however, been investigated only with respect to ant-mediated effects on plant resistance (Maňák et al. 2017). The authors found that Norway spruce (*Picea abies*) seedlings that neighboured ant-attended seedlings of the same species, harbored a lower number of weevils compared to those near ant-excluded seedlings. However, how inter-specific associational effects may directly influence levels of pine weevil damage on seedlings, has not been previously addressed.

In this context, we conducted a lab and field experiment to examine if European beech (*Fagus sylvatica*) has the potential to mediate associational effects (associational susceptibility or resistance) on the focal plant Norway spruce (*P. abies*), with respect to pine weevil damage. We chose to focus on *F. sylvatica* since it was noted that in reforestation areas where European beech and Norway spruce occurred together, the focal spruce plants tended to experience less damage (A. Tudoran and I. Oltean, personal observations). Furthermore, beech is an ecologically and economically important species in Central Europe (Merino et al. 2007), and there is increasing interest in the performance of conifer-beech stands under different pest and climate change scenarios (Griess and Knoke 2011, Neuner et al. 2015, Rukh et al. 2020). More specifically, we aimed to answer in a laboratory and field experiment: Do Norway spruce seedlings receive less damage by the pine weevil *Hylobius abietis* when they have European beech as neighbors, in contrast to when they occur with other Norway spruce plants?

2. Materials and methods

2.1. Plant and insect material

The plant materials used in both the laboratory and field experiments were obtained from the same sources. Norway spruce seedlings (1.5 years old, 25–35 cm in height) were purchased from a commercial Swedish plant nursery, Stora Enso Plantor AB (Nässja, Sweden); while the European beech seedlings (1 year old, 30–50 cm in height in the lab and up to 50–80 cm in the field) were obtained from a Dutch plant nursery, Plants Online BV (Nistelrode, Netherlands). Once received, the seedlings for the lab tests were planted in plastic pots (diameter = 13 cm) with commercial planting soil (S-JORD, Hasselfors Garden, Sweden) and kept in a greenhouse (16L:8D, 20 °C day, 18 °C night) until the start of the experiments. Plants intended for field tests were purchased a few days before field planting, and kept moist in plug trays under the same greenhouse conditions.

The pine weevils used in the laboratory test were collected during their spring migration in 2018 and 2019 at a sawmill (Balungstrands Sågverk AB) in Enviken, Sweden. They were kept in a cold room (10 °C) in darkness and fed with young Scots pine (*Pinus sylvestris*) stems and branches. One week prior to being used in lab tests, they were placed at room temperature (~20 °C, 14L/10D) for acclimatization, in a plastic bucket supplied with water and Scots pine branches.

2.2. Associational effects in the lab

To examine associational effects of European beech on pine weevil damage received by Norway spruce seedlings, we first set up a choice experiment using circular arenas in the lab. The multi-choice test arena (diameter = 1 m) was made out of dark-grey Perspex® acrylic (thickness = 5 mm) and contained 6 locations with round openings, each being 8 cm in diameter. To eliminate visual cues from the surrounding environment and prevent weevils from escaping, a 38 cm high layer of cardboard covered with a thin nylon net on top, surrounded the arena. In each of the 6 arena positions, a pair of plants was inserted from below through the opening. These plants were planted together in one pot in close proximity (1–1.5 cm between stems) and their soil was covered with aluminum foil. Thus, on the arena, only the aboveground parts of the two plants were available to the pine weevils. Plant height and stem diameter were measured at the start of the experiment. Moreover, before inserting the pairs into the arena openings, the stem bark of each plant (both Norway spruce and European beech) was lightly scraped with a scalpel close to the base. From previous studies (e.g., Nordlander 1991) it is known that pine weevils can be strongly attracted to the first plant being damaged, as it emits more attractive volatiles than undamaged plants. Thus, to avoid this bias, all plants were mechanically damaged previous to exposure.

A total of 24 pine weevils of mixed sexes (previously starved for 48H) were released in the middle of the arena, and these were able to choose among: (1) a Norway spruce seedling planted with another Norway

spruce plant (treatment SS); (2) a European beech seedling planted with another European beech plant (treatment BB); and (3) a Norway spruce seedling planted in pair with a European beech seedling (treatment SB). Since the arena contained 6 positions, each of these treatments was replicated twice and randomly assigned to these positions. Pine weevils were allowed to remain in the arena for 48H. We made observations twice every day, and recorded the number of pine weevils, and if they were feeding or not, on the plants in each treatment. Once pine weevils had been removed, we measured the total stem area debarked on each plant using millimeter paper.

Due to a shortage of arenas, we replicated the experiment consecutively in time. After each run in the arena, the arena was cleaned and a new round was conducted (treatment positions in the arena were randomized every time) for a total of 14 runs (n = 2 arenas per run, March-July 2019). For each run, a new set of plants and pine weevils were used. All runs were conducted in the Pine weevil lab at the Department of Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden. The lab counts with a light control mechanism, and all runs were at room temperature with a dark/light period of 10 and 14H, respectively.

2.3. Associational effects in the field

In order to test associational effects of European beech on pine weevil damage received by Norway spruce seedlings under natural attack conditions, we set up a field experiment in a forest clear-cut. A non-scarified clear-cut (7 ha, harvested autumn 2018, dominated by Scots pine) near Tierp in central Sweden (60°21′N, 17°26′E), was chosen for the experiment. Here, on June 28th 2019, we planted a total of 640 seedlings (160 European beech seedlings and 480 Norway spruce seedlings) in 5 blocks. Each block consisted of a plot with only Norway spruce seedlings (treatment SS), and a plot with Norway spruce and European beech seedlings together (treatment SB). We spread out the location of these 5 blocks across the clear-cut, but chose areas that were as similar as possible. We avoided creating blocks that included stumps or piles of branches remaining from the harvest, larger rocks or boulders, or remaining standing trees. We aimed for uniform non-slope areas with low vegetation, and a minimum distance of 10 m between blocks. Each plot within a block was 8 × 8 m in size, and seedlings were planted in rows at 50 cm from each other, for a total of 64 seedlings per plot. In plots with Norway spruce and European beech, seedlings from each species alternated each other at every position. As for the lab experiment, the stems of each plant (both Norway spruce and European beech) were lightly scraped with a scalpel just before planting. All plants were planted on the same day using commercial planting tubes (Planting tube 55, Pottiputki, Finland), and plant diameter and height were recorded.

Pine weevil damage was recorded every 10 days on the focal Norway spruce plants until levels no longer changed (total = 4 assessment points, between July-September 2019). At each assessment we recorded whether or not the plant had been attacked, total stem area debarked, survival and whether or not the plant had been girdled (entire ring of bark removed around the stem). This type of damage on the stem bark is distinctive for the pine pine weevil, and can only rarely be confounded by any other damage, e.g., by *Hylastes* spp. bark beetles which mainly feed on the roots. For European beech, we only noted if the plant had been damaged or not. To calculate total area debarked we measured the following variables: (1) Debarked height - the height from the ground (right above the root collar) up to the upper side of the last pine weevil feeding scar found on the stem, and (2) Percentage debarked - the proportion of stem area damaged (%) in relation to the total surface area up to the debarked height described in (1). Using these measurements and the equation for calculating the circumference of a circle (perimeter of the seedling stem), we estimated the debarked area (cm^2) for each plant as: Total area debarked = Circumference ($\pi\cdot d$) × (debarked height × percentage debarked).

2.4. Statistical analyses

All analyses were conducted in R version 3.6.3 (R Core team, 2020) using R studio 1.2.5033 (R studio team, 2016), and all graphs were plotted using the *ggplot2* package (Wickham 2016). For both the laboratory and field experiments, Bayesian statistics were used through the *brms* package in R (Bürkner 2017). We first fitted our models with a frequentist approach, but found that these models often did not converge, especially for the field data; thus, a Bayesian approach enabled more flexible model fitting. For those models that did converge, results were the same for both approaches. Models were fitted using the *Rstan* package (Stan Development Team 2020), which is integrated in the *brms* package and uses a Markov Chain Monte Carlo (MCMC) sampler. For each model, we ran four MCMC chains, each with 2000 iterations, and used the default priors specified in *brms*. For the fixed effects, the *brms* package uses flat improper priors. For the intercept, residual standard deviation and block effect, it uses weakly informative half student-t priors with three degrees of freedom and a minimal scale parameter of 10. If the Gamma family was used in models, the package uses an additional inverse gamma prior for the shape. Model fit was assessed by comparing the posterior predictive distribution (*posterior_epred.brmsfit* command) with the raw data. To test the significance of fixed effects and conduct comparisons among treatments, we obtained 95% credible intervals (CI) estimates from the models. If the upper and lower interval limits of the estimates (or of differences between treatment estimates) did not overlap with zero, these were considered statistically significant.

For the lab experiment, we examined the effect of treatment on levels of pine weevil damage on the focal Norway spruce plants by fitting a mixed model using the *brm* command (*brms* package). The model included the fixed effect of treatment (treatment SS, Norway spruce + Norway spruce; treatment SB, Norway spruce + European beech), and arena nested in run as a random effect (n = 2 arenas, replicated in 14 runs). Plant height was used as a continuous covariate, and the response variable examined was area debarked by pine weevils. A Hurdle model was used, which examines the effects of treatment on damage in two parts: first, on whether the plant received any damage or not (binary component); and secondly, the effect of treatment on the plants that were damaged (continuous data) with a Gamma distribution. We used a Hurdle model both for the lab and field experiments due to the presence of zeroes in the data, especially for the first and second field assessments of damage. For the number of pine weevils found feeding on each plant, a mixed model was also fitted with the same fixed and random effects as for pine weevil damage on Norway spruce. Since the number of pine weevils was averaged across observation periods for each plant, they were treated as continuous data and the model was fitted with a Gamma distribution. Damage and number of pine weevils on European beech were analyzed separately, using the same random and fixed effects as for the Norway spruce models, but including treatment BB (European beech + European beech) instead of SS.

For the field experiment, we examined the effect of treatment in a similar way as for the lab experiment. A Hurdle mixed model, including the same fixed factors as for the laboratory experiment (treatments SS and SB) was fitted to test the effect of pine weevil damage on focal Norway spruce plants. Plot nested within block (n = 10) was included as a random factor and plant height as a continuous covariate. In addition to debarked area, mortality (alive or dead), attack rate (plant attacked or not) and girdling (girdled or not) were explored as response variables at each assessment time point, using the same mixed model described above but with a Bernoulli distribution.

3. Results

3.1. Associational resistance in the lab

In the lab experiment, we found that pine weevil damage to *P. abies*

differed depending on its neighboring plant. Norway spruce seedlings received approximately 48% less feeding damage per plant when they occurred together with a European beech seedling, compared to being planted with another Norway spruce seedling (Fig. 1a, Table 1). Moreover, the mean number of pine weevils per plant found on *P. abies* seedlings of treatment SB (Norway spruce + European beech) was 53% lower than for seedlings in treatment SS (Norway spruce + Norway spruce) (Fig. 1c, Table 1). On the other hand, we found no statistically significant difference in the amount of damage, or mean number of pine weevils feeding on European beech seedlings when planted together with another *F. sylvatica* seedling, compared to the mixed species treatment (Fig. 1b and 1d, Table 1).

Table 1

Estimated difference in mean area debarked (cm^2) by pine weevils, and number of weevils found feeding per plant for Norway spruce or European beech seedlings, between treatments in the lab experiment. Treatments are abbreviated as follows: Treatment SS (Norway spruce + Norway spruce), BB (European beech + European beech) and SB (Norway spruce + European beech). Lower and upper limits of 95% credible intervals are shown for each difference estimate. If these limits do not overlap with zero, then the difference between estimates is statistically significant (shown in bold).

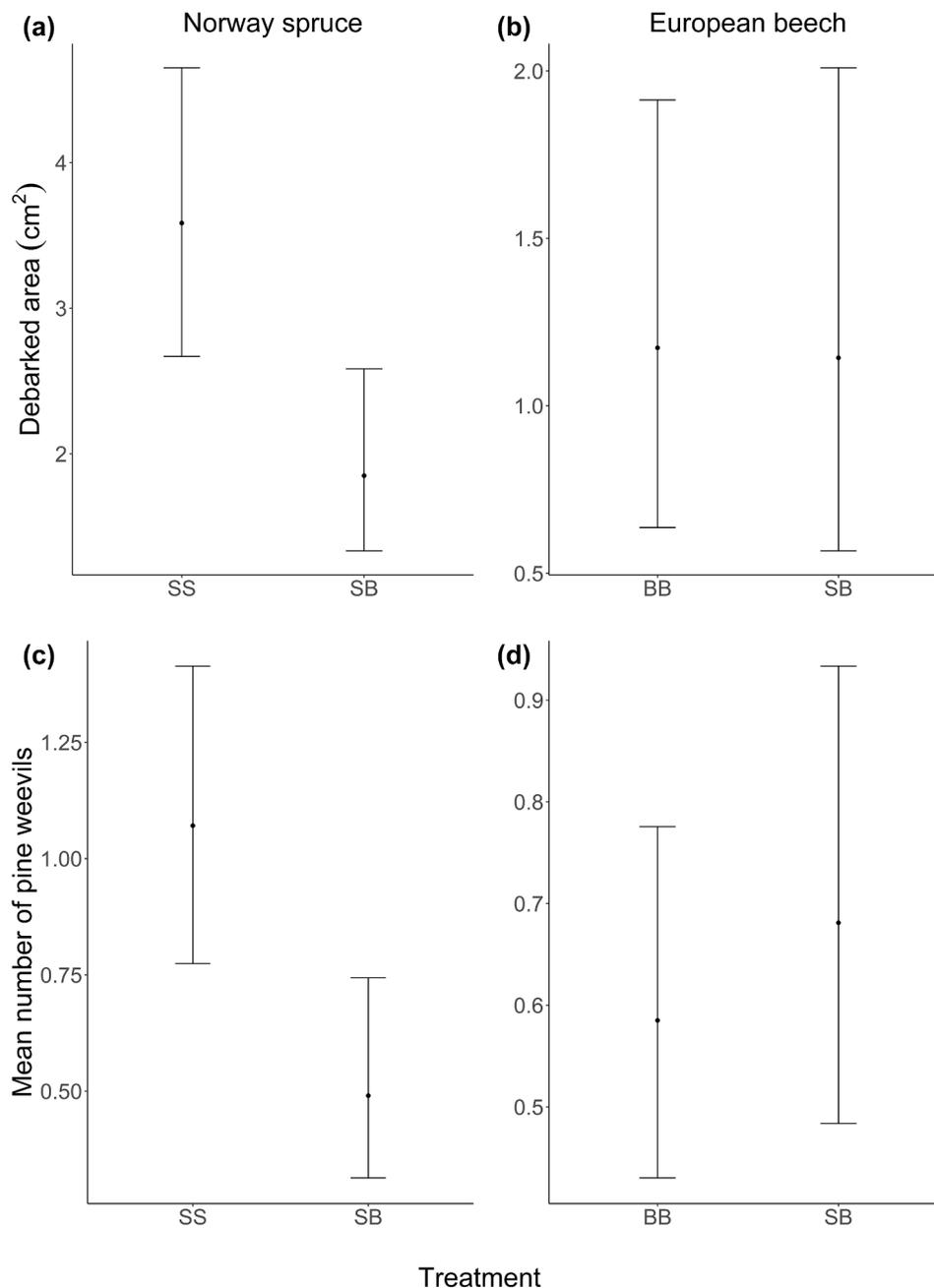| Difference	Debarked area (cm^2)			Number of weevils feeding		
	Estimate	Lower limit	Upper limit	Estimate	Lower limit	Upper limit
SS-SB	**1.76**	**0.56**	**3.73**	**0.597**	**0.193**	**1.24**
BB-SB	0.01	−0.74	0.67	−0.097	−0.365	0.09

Fig. 1. Estimated mean area debarked (cm^2) by pine weevils, and mean number of pine weevils per plant (±95% credible intervals) for **(a, c)** Norway spruce and **(b, d)** European beech seedlings in each of the treatments in the lab experiment. Treatments are abbreviated as follows: Treatment SS (Norway spruce + Norway spruce), BB (European beech + European beech) and SB (Norway spruce + European beech).

3.2. Associational resistance in the field

Unlike the lab experiment, we found no statistically significant difference in pine weevil feeding damage to *P. abies* plants across treatments in the field (Table 2). Norway spruce plants in the SS (Norway spruce + Norway spruce) and SB treatments (Norway spruce + European beech) received similar levels of damage across the whole assessment period (Fig. 2a). Damaged increased steadily for plants in both treatments, until all plants in our experimental plots were damaged (Fig. 2a and b). Some trends were observed though for attack (whether the plant was damaged or not) and girdling (whether the plant was girdled or not) frequency, even though these were not statistically significant (Table 2). During the first field assessments, attack and girdling rates were slightly lower (7.3 and 4.5% lower, respectively) for Norway spruce plants in the SB treatment relative to those in the SS treatment; however this difference diminished with time (Fig. 2b and c). In terms of total Norway spruce seedling mortality (averaged across all assessments), a reduction was observed for plants in treatment SB (mean mortality: 97%) compared to plants in treatment SS (mean mortality: 93%), but this difference was not statistically significant (estimated difference between treatments SS-SB: 0.04; lower and upper credible interval limits, respectively: −0.011, 0.135). Lastly, we found that European beech seedlings were little damaged by pine weevils, with about 10% of seedlings being attacked across all blocks and over the entire field season.

4. Discussion

We found that neighbor identity appears to affect the levels of pine weevil damage received by focal *P. abies* plants, however these effects differed for the lab and field experiments. In the lab, Norway spruce seedlings were damaged less by pine weevils when they had *F. sylvatica* instead of *P. abies* as a close neighbor. Yet, in the field, we found that damage was similar for seedling plots with only Norway spruce or with European beech and Norway spruce, and mortality was high for both treatments. Our lab results indicate that pine weevil behaviour can be influenced by the neighbor identity of *P. abies* at a small scale; however, these associational effects did not result in plant protection benefits at a larger scale.

Results from the laboratory experiment showed that damage levels and the number of pine weevils found feeding on Norway spruce were significantly reduced for seedlings associated with European beech, relative to Norway spruce paired seedlings. This suggests that *F. sylvatica* can alter the interaction between the focal *P. abies* and *H. abietis*, and has the potential to mediate associational resistance for Norway spruce seedlings. The presence of *F. sylvatica* could have affected pine weevil behaviour, for instance, by diminishing the detectability or relative palatability of the focal plant (Hahn and Orrock 2016). In choice tests, adult pine weevils have been shown to preferentially feed on *Pinus sylvestris* or *P. abies* over various broad-leaved species such as *Betula pendula*, *Quercus robur*, *Fraxinus excelsior*, *F. sylvatica* and hybrid aspen (*Populus × wettsteinii* Hämet-Ahti) (Leather et al. 1994, Löf et al. 2004,

Toivonen & Viiri, 2006, Wallertz et al. 2014). Antifeedants that repel weevils away from plants or feeding deterrents that act when the bark is fed upon, are thought to completely prevent or limit pine weevil feeding to shallow nibbling on these alternative species (Månsson and Schlyter 2004). Moreover, the locomotion of pine weevils towards attractive conifer volatiles has been shown to be interrupted by various non-host volatiles (Azeem et al. 2015, 2020). Thus, the close proximity of non-hosts to a preferred food, such as Norway spruce, may alter weevil behaviour.

In line with our results, Leather et al. (1994) also found that area debarked by pine weevils on Scots pine was significantly reduced when it was paired with ash (*F. excelsior*), relative to when it was in combination with another conifer (Norway spruce). Unlike our experiment, they found that *F. excelsior* was not fed upon at all by the weevils, suggesting that lower conifer damage was not due to increased feeding on the alternative host and repellents likely played a role. In our study, *F. sylvatica* was fed upon by pine weevils in both the only beech and in the Norway spruce and beech combination treatment. The feeding damage, however, was superficial, with only the outer bark being removed. This suggests that *F. sylvatica* may not have strong bark volatiles that arrest/repel pine weevils, but instead bark feeding deterrents may be important as suggested by Månsson and Schlyter (2004). Probing or feeding may, thus, be needed for European beech to mediate associational resistance effects. Even though we are not able to discern the underlying mechanisms, it seems that properties of *F. sylvatica* may alter pine weevil feeding behaviour when it occurs in close proximity to *P. abies*.

Studies with other conifers and insect herbivores, albeit few, have shown that behaviour can be altered by the close presence of a non-host or non-conspecific neighbor. For example, Bognounou et al. (2017) found that balsam fir (*Abies balsamea*) can mediate associational resistance for black spruce (*Picea mariana*) at the beginning of an outbreak of spruce budworm (Choristoneura fumiferana), but these effects are reversed by the end of the outbreak. Similarly, Castagneyrol et al. (2020) found that the presence of birch (*Betula pendula*) can reduce damage and the likelihood of repeated attack by pine processionary moth (*Thaumetopoea pityocampato*) to *Pinus pinaster*. However, as pines outgrew birch trees in height, these associational effects disappeared. On the other hand, mixtures of *B. pendula*, *P. pinaster* and *Quercus robur*, resulted in greater levels of insect damage relative to plots containing trees of only one of these species (i.e., associational susceptibility), but these effects were only observed under drought conditions (Castagneyrol et al. 2017). It is worth noting that most studies on associational effects have examined defoliators/chewers (Jactel et al. 2021). In conifers, they often involve Lepidopteran females searching for oviposition sites under a short-time window in older trees stands, and not seedlings. One of the few studies we found in younger trees examined associational effects among saplings of broad-leaved and conifer trees with respect to leaf-chewing insects (Wein et al. 2016). The authors find strong associational susceptibility for heterospecific mixtures relative to monocultures (plots composed of only one species), however, these effects were predominant for generalist herbivores (Wein et al. 2016). Associational

Table 2
Estimated difference in mean area debarked (cm^2) by pine weevils, attack and girdling rate (proportion of plants attacked or girdled) for Norway spruce seedlings, between treatments in the field experiment. Assessments of damage were conducted at four time points (Assessments 1 to 4; first assessment: July 8th 2019, with 10 days between assessments). Treatments are abbreviated as follows: Treatment SS (Norway spruce + Norway spruce), and SB (Norway spruce + European beech). Lower and upper limits of 95% credible intervals are shown for each difference estimate. If these limits do not overlap with zero, then the difference between estimates is statistically significant.

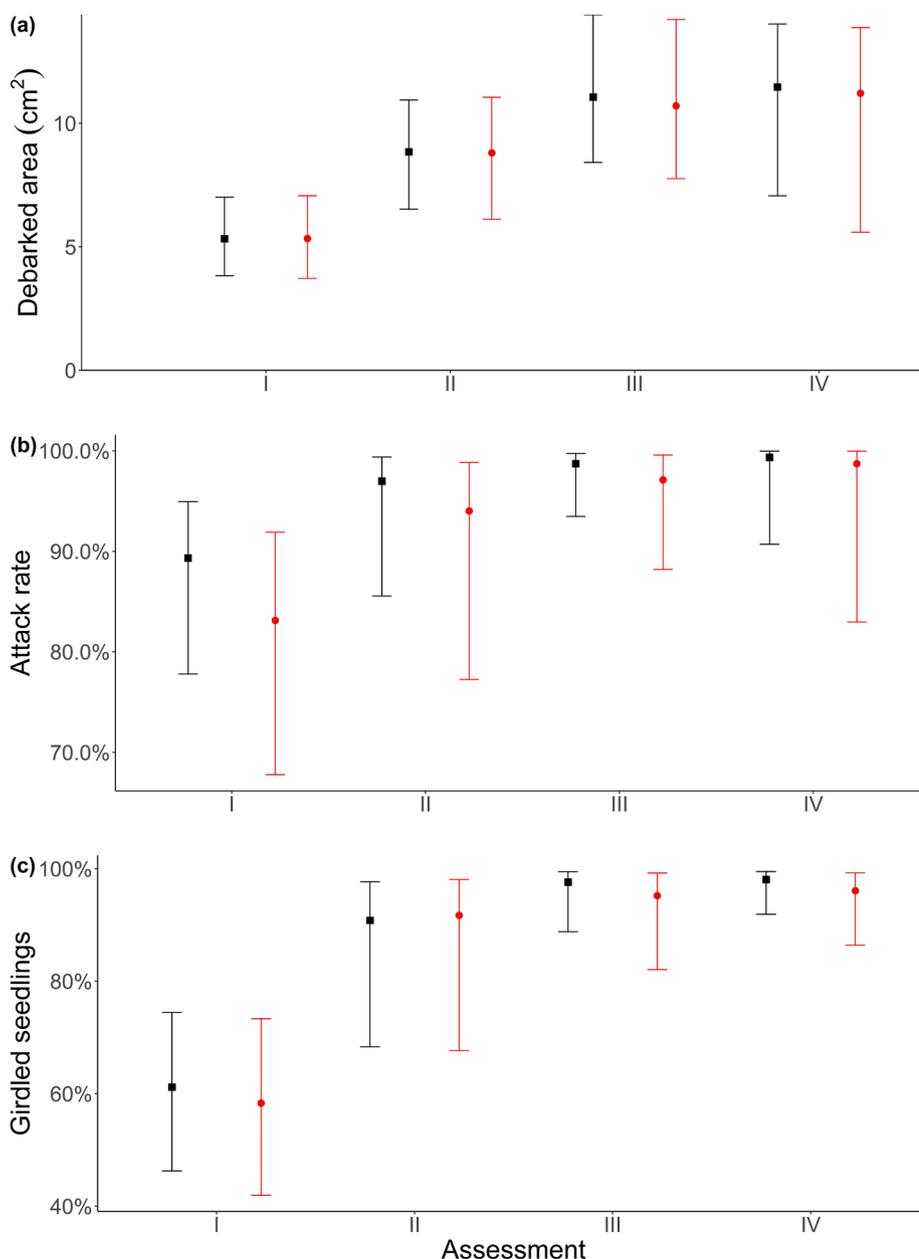| Assessment	Difference	Debarked area (cm^2)			Attack rate			Girdling rate		
		Estimate	Lower limit	Upper limit	Estimate	Lower limit	Upper limit	Estimate	Lower limit	Upper limit
1	SS-SB	−0.016	−1.85	1.88	0.063	−0.047	0.210	0.027	−0.132	0.179
2	SS-SB	0.025	−1.96	2.23	0.034	−0.052	0.183	−0.006	−0.151	0.138
3	SS-SB	0.327	−1.75	2.50	0.017	−0.039	0.103	0.027	−0.058	0.151
4	SS-SB	0.200	−1.75	2.22	0.008	−0.057	0.101	0.021	−0.037	0.998

Fig. 2. Estimated **(a)** mean area debarked (cm²) by pine weevils, **(b)** proportion (%) of seedlings attacked by pine weevils, and **(c)** proportion (%) of girdled seedlings (±95% credible intervals), for Norway spruce in each of the treatments and assessments of damage in the field experiment (Assessments 1 to 4; first assessment: July 8th 2019, with 10 days between assessments). Treatment SS (Norway spruce + Norway spruce) is represented by black filled squares, and treatment SB (Norway spruce + European beech) is represented by red filled circles. Note that the y-axes for attack and girdling rate do not start at zero. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

effects are, thus, not always consistent in direction and can vary with time, the species mix examined, herbivore diet breadth and abiotic factors.

Even though we found that pine weevils were affected by the presence of *F. sylvatica* in close proximity, at the larger plot scale these effects did not hold. In the field experiment, plants were placed 50 cm apart from each other and arranged in blocks, while in the lab they were found in pairs set 1–2 cm apart from each other. We found that attack rate was somewhat lower for mixed Norway spruce and European beech plots, but these effects disappeared with time and no difference in total damage was observed (Fig. 2b). Associational effects can occur at two spatial scales: neighbors can affect the likelihood of herbivores finding, arriving and leaving a patch, but they can also affect food selection among plants within a patch (Hambäck et al. 2014). Previous studies have found that associational effects can vary depending on the scale examined (Bommarco and Banks 2003). For example, Bergvall et al. (2008) observed that neighbors mattered for the food choice of fallow deer only at short distances among experimental (cut) tree branches, and not when branches were more spread out. In contrast, no

associational effects occurred among the plant species *Opuntia humifusa* and *O. stricta* with respect to damage by the cacti moth (*Cactoblastis cactorum*) at short inter-plant distances; yet, effects may be observed at larger scales in sites with widely separated plant patches (Stiling et al., 2004; Jezorek et al., 2012). In another study, Emerson et al. (2012) found that both associational susceptibility and resistance can occur for squirrel predation of palatable and non-palatable seeds at the among-patch scale, but effects disappeared at the within-patch scale. Thus, our results are both in line and in contrast to previous studies, and they suggest that *F. sylvatica* appears to not mediate associational resistance at larger scales and/or inter-plant distances.

The occurrence of associational effects at different scales depends on the focal plant-herbivore system, and the cues involved in host detection and selection. It has been suggested that for some insects, food selectivity increases when different plant resources grow in close proximity, and decreases when resources grow across larger spatial distances (Hambäck et al. 2009). However, this can vary depending on the organizational level at which consumers perceive their plant resources (Hambäck et al., 2014; Verschut et al., 2018; Kim, 2017). The pine

weevil is able to identify and migrate to freshly-felled forest areas, from a long distance and at a larger stand scale, in search of suitable oviposition substrate (Solbreck 1980). However, a few weeks after arrival their flight muscles regress and they remain on the ground for the rest of the season (Nordenhem 1989). Adult weevils walk around in search of food items, and several factors can influence location and choice of food. Visual and olfactory cues play an important role, but also soil type at the site (humus or mineral soil), and their decision to attack or not a conifer seedling is taken in very close vicinity (<2.5 cm) to the plant (Nordlander 1991, Björklund et al. 2003, Björklund et al. 2005). They have also been shown, for example, to distinguish between insecticide-treated vs. non-treated food items even when no consumption of the treated food occurs (Rose et al. 2005). Moreover, palatability plays a role, and pine weevils will often probe or try most of the food resources available before selection (Månsson and Schlyter 2004). Thus, when it comes to their feeding preferences, *H. abietis* appear to be guided by cues that act at lower organizational levels. Therefore, for repellent or anti-feeding associational effects to occur against pine weevil damage, close proximity of focal plants to the less preferred item, may be required.

It is important to note that associational effects can be confounded with resource density effects. Patches with a high abundance of host plants should harbor greater herbivore loads than those with lower abundance (Resource concentration hypothesis; Root 1973). These effects are expected to be more prominent for specialist herbivores, which often find, reproduce and stay where host resources are concentrated such as tree stands composed mostly by one species (e.g., monocultures). However, within stands, a greater abundance of hosts can also result in a lower likelihood of individual trees being attacked (i.e., dilution of attacks; Hambäck and Englund 2005, Andersson et al. 2013). For example, Damien et al. (2016) found that the density of pine processionary moth increased across a low- to high-density gradient of *P. pinaster*; yet, the proportion of attacked trees was lower at higher densities (lowest attack rate in patches with 100% pine). The effects of resource density on damage levels to a focal plant can, thus, vary depending on whether insect host-finding or post patch-colonization processes are examined. At long distances, concentrated resources may easily attract many herbivores; but, within a patch, if suitable hosts occur at a low density, aggregation of attacks on these few preferred plants might occur (Otway et al. 2005). In our experiment, the density of Norway spruce seedlings in the mixed plots was half of that found in the only spruce plots. Even though there was a slight tendency for lower attack frequency in the mixed plots at the beginning of the season (7% difference between SB and SS treatments at assessment 1; Fig. 2b), both plot types were similarly attacked by pine weevils by the end of the season, which does not indicate resource dilution or concentration effects. Most previous studies examining associational susceptibility and resource density effects have focused on flying insects searching for suitable breeding sites, while our study focuses on walking adult insects for which perception of resources is likely different.

Another important aspect that could explain differences between the lab and field experiment is the potential effects of close interaction or communication between *F. sylvatica* and *P. abies*. Plants can communicate both through the root system (Baluška et al. 2010) and aboveground airborne signals (Heil and Karban 2009). In the lab experiment, plants were closely planted together in the same pot, which could lead to strong interactions both above and belowground. Airborne signals from damaged trees can 'warn' undamaged neighbors and even trigger defense response (Baldwin and Schultz 1983). To minimize these effects, we lightly damaged the stem of all seedlings with a scalpel at the start of the lab and field experiments. However, we cannot rule out that belowground communication occurred in the lab experiment and could have played a role in the associational effects observed. Plants in the field were planted together for a longer period of time, but not in such close proximity.

In addition to plant communication, other factors that differed between the lab and field experiments were pine weevil pressure and the

duration of experiments. Very low or very high densities of herbivores may reduce the likelihood of detecting associational effects (Jezorek et al., 2012). As underlined by Merwin et al. (2017), damage to a focal plant can increase with consumer density, suggesting a dynamic relationship between insect populations and neighborhood effects. For instance, Smit et al. (2007) found that when deciduous and conifer saplings where planted under or inside the canopy of shrubs of *Rosa rubiginosa*, sapling survival was high at low cattle grazing pressure; while at high grazing pressure, the shrubs were unable to 'protect' the saplings and did not reduce mortality. In our experiment, we did not measure or estimate pine weevil density directly; however, we planted in a fresh non-scarified forest clear-cut, which we know attracts a high number of pine weevils (Örlander et al. 1997), and no other plants were planted. Moreover, the frequency of attacked plants was very high (<80%) just 10 days after planting. Such high pressure could have dampened any benefits of the non-host *F. sylvatica* on pine weevil damage to Norway spruce seedlings. Moreover, plants in the field experiment were followed over a longer period of time than those in the lab experiment, which can also contribute to differences in results. Lastly, there could be other factors that differ between the lab and field environments, and we are able to hold more variables constant in the lab compared to the field.

5. Conclusion

In conclusion, neighbor identity may influence pine weevil damage to focal Norway spruce plants. However, the associational effects mediated by European beech, appear to lose their efficacy at larger inter-plant distances, under higher consumer pressure or longer time periods. To better understand variation across scales and improve forest protection against this pest, future studies should examine different among-plant distances and other non-preferred hosts that could mediate associational effects against the pine weevil.

CRediT authorship contribution statement

Amelia Tudoran: Conceptualization, Methodology, Formal analysis, Investigation, Resources, Writing - original draft, Visualization. **Helena Bylund:** Conceptualization, Methodology, Writing - review & editing. **Göran Nordlander:** Conceptualization, Methodology, Writing - review & editing. **Ion Oltean:** Conceptualization, Investigation. **Adriana Puentes:** Conceptualization, Methodology, Formal analysis, Writing - original draft, Writing - review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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