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# Experimental Evidence for Associational Resistance against the European Pine Sawfly in Mixed Tree Stands

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This study examined whether the saplings of Scots pine (*Pinus sylvestris*) exhibit associational resistance against the European pine sawfly *Neodiprion sertifer* (Hymenoptera, Diprionidae) when grown in a mixture with 50% silver birch (*Betula pendula*). The number of sawflies on pine trees in pure and mixed stands was manipulated at two experimental sites during two years. Survival of larvae and eggs was monitored, and the numbers of presumed sawfly predators were counted. A lower proportion of sawfly larvae and eggs survived on pines grown in the mixture with birch as compared with pure pine stands. Lower survival of sawfly larvae in the mixed stands was associated with the higher abundance of ants in these stands. The numbers of other sawfly predators (e.g. spiders and predatory heteropterans) differed between the study sites and were negatively associated with the presence of ants, which suggests possible interference between these groups. Although sawfly survival was lower on pines in the mixed stands, providing evidence of associational resistance, a related study shows the same trees had a higher number of ant-tended aphid colonies as compared with pines in the pure stands. Therefore, instead of considering resistance against individual herbivore species, it seems more practical to use associational resistance as a trait representing the resistance of larger systems, such as whole tree stands, against the total damage caused by herbivores in general.

**Keywords** natural enemies, species diversity, stand structure, tri-trophic interactions

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# 1 Introduction

Diverse plant communities may be less susceptible to herbivores because they can provide plant species with “associational resistance”, in addition to the resistance of species themselves. Associational resistance refers to the reduction in herbivory experienced by a plant associated with taxonomically diverse plant species (Tahvanainen and Root 1972), and is based on interactions involving the plant, its herbivores and the plant species forming the surrounding community. The underlying mechanisms may be diverse and include factors such as higher abundance and diversity of natural enemies, lower density and nutritional quality of host plants, and chemical and physical interference between the plant species of the community (Finch and Collier 2000, Hambäck and Beckerman 2003, Stiling et al. 2003). Experimental evidence for associational resistance has been obtained in many agricultural systems where crop diversification is successfully used for pest and disease control (Andow 1991, Trenbath 1993, Mundt 2002).

In forest ecosystems, few rigorously experimental comparisons between the incidence of herbivory, diseases and stand diversity have been conducted, and it is thus not possible to ascertain a causal relationship between the diversity of tree species and herbivory and pathogen levels (Watt 1992, Koricheva et al. 2006). Yet, it is widely believed that forest monocultures are prone to herbivore outbreaks and disease epidemics, and many authors have recommended stand diversification as a means of controlling herbivores and pathogens (Belyea 1923, Graham 1959, Klimetzek 1990). Nevertheless, it is obvious that the assumptions concerning the relationship between diversity and herbivore incidence in forest communities need to be confirmed with a range of experimental studies designed for the purpose.

In the present study, we tested the existence of associational resistance by experimentally infesting the saplings of Scots pine (*Pinus sylvestris*) with eggs and larvae of the European pine sawfly (*Neodiprion sertifer*) in experimental stands consisting either of pure pine monocultures or 50%-50% mixtures with silver birch (*Betula pendula*). In addition, the size of pine crowns and its connection with the occurrence of potential predators within the canopy was measured as a specific form of resistance. This was based on the facts that crown size is likely to indicate the structural complexity of trees, and that the structural complexity of a habitat, in turn, may play an important role in the predator-prey dynamics (e.g. Hawkins 1988, Halaj et al. 2000), as indicated also by a recent synthesis of experiments (Langellotto and Denno 2004).

# 2 Materials and Methods

## 2.1 Study Species

*N. sertifer* occurs mainly in the boreal and subboreal regions of the northern hemisphere and feeds on many *Pinus* sp. species. It can be frequently found on pine stands of all ages and also has irregular and sometimes wide-spread outbreaks (Juutinen 1967, Larsson and Tenow 1984). A female lays in August–September approximately 50 eggs (Juutinen 1967) by placing them in rows inside the current-year needles, and the eggs hatch in May–July in the next year. Gregarious *N. sertifer* larvae defend themselves as a group against enemies (Codella and Raffa 1995) by hooking their bodies and extracting resin droplets from their mouth. In late June–early July the larvae stop feeding and pupate in the litter layer of soil. The adults hatch from pupae in late August. *N. sertifer* is a haplodiploid species, diploid females develop from fertilized eggs and haploid males from unfertilized eggs.

## 2.2 Study Sites

The study was conducted at two separate sites (hereafter Area 1 and Area 2), 15 km apart, in western Finland (approximately 61°41´N, 21°50´E). These sites belong to the Satakunta tree species diversity experiment described in Scherer-Lorenzen et al. (2005). The sites are managed forest sites that were clear-cut in winter 1998 to 1999 and then planted in spring 1999 with one-year-old seedlings obtained from a local tree nursery. Each area contains thirty-eight

20 m × 20 m plots in which seedlings of Scots pine, Norway spruce (*Picea abies*), Siberian larch (*Larix sibirica*), silver birch, and black alder (*Alnus glutinosa*) were planted alone or in combinations. Plots within each area were randomly allocated to 19 treatments: monocultures of each of the 5 tree species, 7 different 2-species mixtures, 6 different 3-species mixtures and one 5-species mixture. Each particular species combination was replicated twice within each area. The treatments were substitutive, i.e. the number of tree saplings was the same in all treatments (169/plot). Planting interval of seedlings was 1.5 m. Originally, the study sites were Myrtillus type forests with a mixture of spruce, birch and pine. The surrounding areas consist mainly of 40 to 60 years old spruce-dominated mixed stands where birch is the second and pine is the third abundant species.

In the present study, plots where Scots pine was planted either as a monoculture or as a 50%-50% mixture with the silver birch were utilised. Accordingly, there were two plots of each type within both sites. A low and random proportion of naturally regenerated saplings was also present in the plots, and included additional species such as aspen (*Populus tremula*), mountain ash (*Sorbus aucuparia*) and pubescent birch (*B. pubescens*). The canopy of stands was open, and measurements of photosynthetic photon-flux density suggested that pine crowns received a comparable level of radiation in both monocultures and pine-birch mixtures (P. Kaitaniemi, unpublished data). Vegetation surrounding the trees was typical of a clear-cut area with a dominance of herbs and grasses. The two types of study plots represent habitats that are widely available for *N. sertifer.*

## 2.3 Survival Experiment

The number of *N. sertifer* sawflies was experimentally manipulated in a sample of planted trees to study the effect of stand structure on sawfly performance. In total, 139 experimental pine trees (10 per plot in 2002, 7–8 per plot in 2003) were used in the study. The trees were chosen haphazardly within the central 15 m × 15 m part of the plots to avoid possible edge effects.

In 2002, the experiment was started on 13 June when each of the trees was infested with 10 sawfly larvae in Area 1 and 15 larvae in Area 2. The larvae placed on the trees were collected wild from Kankaanpää, about 30 km NE from the study sites, and were mainly in the third instar. Each original larval brood was divided and distributed among two or three trees, because the experimental pines were small, less than 150 cm tall, had a basal diameter less than 5 cm and, consequently, also had low needle biomass (Cienciala et al. 2006) in relation to brood size. A paint brush was used to place the larve individually on a single shoot such that they always remained in a group. If larvae dropped during the transfer they were placed back with a paint brush. In 2002, some larval groups were attached on pines also with their original feeding shoots (~10 cm long) using a thin metal wire.

In August 2002, after pupation of sawflies, each of the experimental pines was infested by enclosing a female in a mesh bag and allowing it to oviposit on the tree. To achieve partial control for potential differences in the sex ratio of offspring, one male was enclosed in the mesh bag of half of the trees to fertilize the female. These adults originated from survived experimental larvae, and they were randomly reallocated to new host trees. The bags with males were distributed evenly among the sites and treatments. In 2003, the first larvae used in the survival study hatched from the eggs on 10 June.

During both years, survival of larvae on the study trees was monitored at about three day intervals by counting the number of larvae present on the trees. The frequent counts were used to assess the timing of larval disapperance so that potential differences in the timing of predator activity and composition of predatory groups between the stand types could be assessed. Final survival was assessed as the proportion of larvae that survived on the study trees until the start of the pupation period when the first ones of the remaining larvae were observed to start pupation. The remaining larvae were then collected to check potential parasitism, but the level of parasitism was found negligible. In spring 2003, the proportion of eggs that successfully hatched was counted and used as an estimate of survival of overwintered eggs.

To assess the potential impact of different predators on the survival of larvae, the number of ants (mainly *Formica rufa* group) and ant-tended aphid colonies on the trees was counted when the larvae were in the middle of their larval period. At the same time, the number of spiders, harvestmen (Opiliones) and predatory heteropterans was also counted from each tree. All these arthropod groups are known to prey on sawfly larvae (Benson 1950, Ives 1967, Juutinen 1967, Olofsson 1992, Lindstedt et al. 2006). Representative data on harvestmen and heteropterans were obtained only in 2002 because their numbers were very low at the time of counting in 2003.

To examine the effects of different predator groups in more detail, half of the trees were applied with a glue ring (Stikem-Special®, Seabright Laboratories, Emeryville, California, USA) at the base of the stem in spring 2003 to reduce the access by ants and other walking invertebrates. Previous evidence suggests that spiders are not affected by this treatment (Tanhuanpää et al. 2001).

## 2.4 The Abundance of Predators

An additional group of trees from the same plots was used to further examine the abundance of the two most common predatory groups, ants and spiders, on the pine trees. Up to 10 trees per plot were investigated both in early June and early August in 2002 and 2003. The number of spiders was directly counted. The abundance of ants was estimated on a five-step scale ranging from zero (no individuals) and one (only single individuals present) to four (individuals present at all parts of canopy). High abundance of ants was always related to a high abundance of ant-tended aphid (*Cinara pinea*) colonies. Only seedlings that originated from the plantings in 1999 were used, and all the pines that had been damaged by browsing vertebrates or by drought before the monitoring took place were excluded from the data.

In addition, to test for the potential interactive effects of tree size and predator incidence on sawfly larval survival, the size of the study trees was quantified by measuring the basal diameter of stems in both years. In Scots pine, as in trees in general, the basal diameter shows a positive allometric relationship with other measures of size such as tree height and needle biomass (Cienciala et al. 2006).

## 2.5 Statistical Analysis

The probability of larvae to survive on the study trees until the end of the experiment was analyzed with a logistic regression model using a binomial distribution and logit link function. Besides the main treatment effect (stand composition), there was a large number of potential but possibly confounding explanatory variables (the incidence of different predator groups, study area, year and glue ring treatment) as well as their interactions. It was not meaningful to include all these effects in a single model, and hence the alternative models were ranked on the basis of their AIC (Akaike's Information Criterion) values to identify the best explanatory variables. A variable was excluded from the model if its exclusion reduced $|\text{AIC}|$ by at least 2. The individual tree was nested within the study area and year, and defined as the repeated subject, i.e. the true replicate, in the models. The analyses were conducted with the PROC GENMOD in SAS statistical software (version 8.2, SAS Institute Inc., Cary, USA).

The timing of larval mortality was assessed with a survival analysis. The proportional hazard model (Cox 1972) was applied using the PHREG procedure in SAS (Allison 1995). The dependent variable was survival time, i.e. the number of days elapsing after the larva was placed in a tree until it disappeared or was collected. The explanatory variables in the model were stand composition, study area, glue ring treatment and year. After the final model with these variables was attained, the numbers of spiders and ants were also entered to check for their explanatory power as well, even though this procedure maybe incorrectly assumed that the numbers measured at a single point in time were representative of the whole larval period. The survival times of larvae collected from the trees were recorded as right-censored observations, because larval fate on the trees would not have been known after that point. The EXACT ties handling method was used because the actual larval survival time is continuous, i.e. death can occur at any point in time.

The effect of stand composition on the basal diameter of pine, as well as on survival of *N. sertifer* eggs, was tested with a two-way analysis of variance with both study area and stand composition as the explanatory variables. Normality of residuals was verified with a Kruskall-Wallis test and the homogeneity of variances with a Levene's test. The relationship between stem diameter and the incidence of natural enemies on the pine trees was assessed with Spearman correlation coefficients. Spearman correlations were also used to investigate the associations of different predator groups with each other, and with the tree-specific survival of the experimental sawflies.

## 3 Results

The final logistic regression model suggested that both ants and spiders were associated with the survival of experimental sawfly larvae but in a manner that was dependent on the tree composition of the stand (Table 1). The corresponding interaction terms were both significant, and more larvae remained on the trees growing in pure pine stands than in pine-birch mixture (Fig. 1). The number of sawflies seemed to decrease as the number of ants increased, because the average number of ants per tree was highest in the pine-birch mixtures (Fig. 1). The effect of ants on sawfly incidence was strong enough to be significant also on its own (Table 1). Spider numbers did not show any clear response with respect to the stand type (Fig. 1).

**Table 1.** Factors in the logistic regression model that best explained the final survival of experimental *Neodiprion sertifer* sawfly larvae on Scots pine saplings in the western Finland. Stand composition indicates either a pine-birch mixture (50%-50%) or a pure pine stand. Area and year refer to two study areas and years, respectively. Ants and spiders are continuous variables that indicate the numbers found on the study trees.

| Source | df | $\chi^2$ | P |
|---|---|---|---|
| Stand composition | 1 | 2.25 | 0.1337 |
| Area | 1 | 3.90 | 0.0482 |
| Year | 1 | 13.33 | 0.0003 |
| Ants | 1 | 5.87 | 0.0154 |
| Spiders | 1 | 0.14 | 0.7040 |
| Ants × Stand composition | 1 | 3.94 | 0.0470 |
| Spiders × Stand composition | 1 | 4.96 | 0.0260 |
| Area × Year | 1 | 4.48 | 0.0342 |

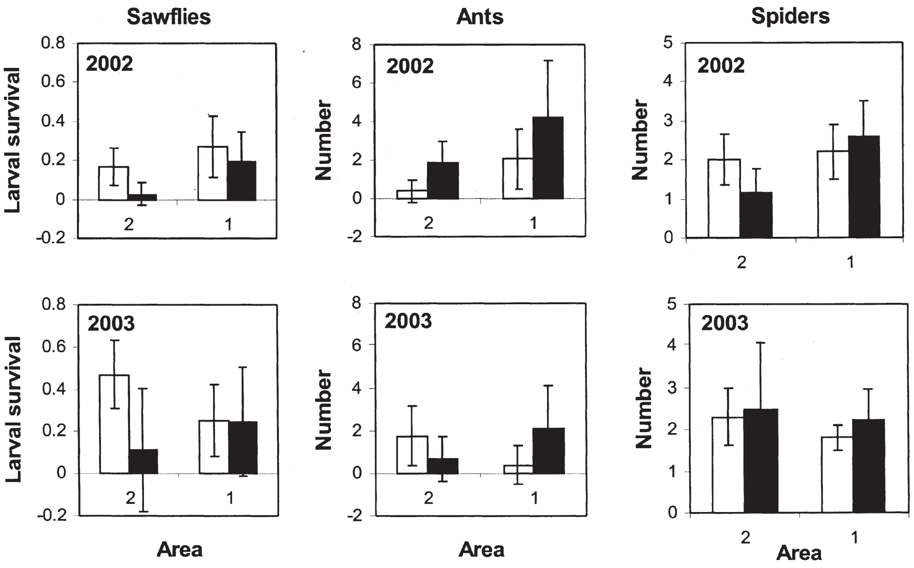

**Fig. 1.** The leftmost figures show the average proportion of *Neodiprion sertifer* larvae that survived on the experimental trees during two study years and at two different study sites. The average numbers of ants and spiders found on the same trees are shown by the two rightmost figures. White bars indicate pure pine stands whereas the black bars refer to mixtures of pine and silver birch. 95% confidence intervals are also shown.

Differences in the timing of larval mortality (graphs not shown) also indicated that factors related to stand composition affect the fate of sawfly larvae. In accordance with Fig. 1, a high rate of mortality at the beginning of experiment was typically associated with lowered final survival, as was the case with pine-birch mixtures ($\chi^2=5.2$, $P=0.02$) and year 2002 ($\chi^2=270.6$, $P<0.0001$). Similarly, the effect of stand composition was different on the two study areas as suggested by the significant area by stand composition interaction ($\chi^2=33.2$, $P<0.0001$). The effect of glue ring was also different between the two areas ($\chi^2=5.8$, $P=0.02$). When the numbers of spiders and ants were entered into the model, the main effect of stand composition disappeared and was replaced with significant interactions ant number by area, ant number by stand composition, spider number by area, and spider number by stand composition ($P<0.02$ in all cases).

In the model of final survival (Table 1), also the collective terms *area*, *year*, and their interaction remained, and indicated the effect of yet unidentified factors on sawfly larvae. The two years were included in the final logistic regression model, because the analysis of 2002 data alone did not warrant the inclusion in the model of harvestmen and heteropterans that were virtually absent in the 2003 data. A separate analysis on the incidence of these other predator groups, however, seemed to provide a partial explanation for the differences between the two areas in 2002. A much lower proportion of larvae survived to pupation on the trees of Area 2 than on the trees of Area 1 in 2002, but in 2003 the difference was reversed (Fig. 1). In contrast, it was found that, similar to ants and spiders (Fig. 1), the harvestmen also had a somewhat higher abundance (Kruskall-Wallis test, $\chi^2=2.8$, $P=0.09$, df=1) on Area 1 (mean 0.13, confidence limits 0.02 to 0.23) than on Area 2 in 2002 (mean 0.03, confidence limits –0.03 to 0.08). Heteropterans were not detected at all on Area 1.

There was also a negative correlation between the incidence of ants and heteropterans on Area 2 ($r_s=-0.32$, $P=0.04$, $N=40$), as well as between ants and spiders in both areas (Area 2: $r_s=-0.40$, $P=0.01$, $N=40$, Area 1: $r_s=-0.29$, $P=0.07$, $N=40$). The number of spiders was positively correlated with the basal diameter of trees on Area 2 ($r_s=0.34$, $P=0.03$, $N=40$). Other correlations between the predator groups were not detected, and neither were there any direct correlations with sawfly incidence.

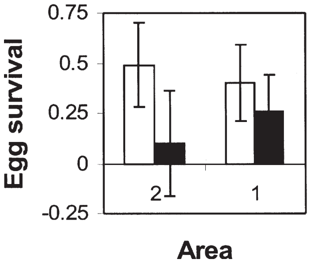

**Fig. 2.** Survival of the overwintering eggs of the *Neodiprion sertifer* sawfly on the experimental trees during winter 2002 to 2003. White bars indicate pure pine stands whereas the black bars refer to mixtures of pine and silver birch. 95% confidence intervals are also shown.

Stand composition had a similar effect on sawfly egg survival as it had on the larvae (Fig. 2). A much higher proportion of eggs hatched on the pines in pure stands than on those in the pine-birch mixtures ($F_{1,51}=6.17$, $P=0.02$). The two areas did not differ from each other in egg survival ($F_{1,51}=0.13$, $P=0.72$).

It should be noted that some of the differences between the years (Table 1) were obviously caused by differences in the duration of the experiment as the experiment was started with the third instar larvae in 2002 whereas the whole larval period was covered in 2003. A glue ring treatment was also used in 2003, and the initial number of larvae per tree was more variable in 2003. Separate analyses for the two years suggested comparable results and hence both years were included in the final model. The glue ring treatment in 2003 reduced the number of ants by 40% with $P=0.06$.

The crown size of pine as estimated by the basal diameter of the main stem was not affected by stand composition ($F_{1,28}=0.39$, $P=0.54$). The mean basal diameter of trees (± one standard deviation) was smallest in Area 2 in both pine monocultures (2.4 ± 0.9 cm vs. 3.3 ± 1.0 cm at Area 1) and in pine-birch mixtures (2.1 ± 0.7 cm vs. 3.2 ± 0.7 cm). Similar to the trees of the survival experiment, basal diameter in Area 2 was positively correlated with the incidence of spiders in both 2002 ($r_S=0.84$, $P<0.0001$, $N=21$) and 2003 ($r_S=0.47$, $P=0.005$, $N=34$).

# 4 Discussion

The study indicated that the pine saplings growing in the more diverse stand gained associational resistance against their sawfly herbivores via the effect of the third trophic level. This lends experimental evidence for the earlier observations in the central France, which have shown that tree mortality rates following severe sawfly defoliation are lower in mixed stands than in pure Scots pine stands (Geri 1988). Similarly, at the landscape level, areas of pure Scots pine have experienced the most severe, the earliest, and the longest infestations (Geri 1988). On the basis of these observations, it has been suggested that forest management should attempt to mix pines with deciduous trees, and large areas of pure pine should be avoided (Geri 1988). Our results give probably the first experimental support for this idea, and show that stand composition has at least potential for providing resistance against sawflies, although the results should be confirmed at a larger geographical scale, with more diverse stand sizes, and with stands covering a range of developmental stages. In our stands, further support for the results was received in 2006, when the number of trees with naturally occurring sawflies was twice as large in monocultures as in pine-birch mixtures (J. Riihimäki, unpublished data).

Stand composition together with the abundance of ants and spiders was associated with the incidence of sawfly larvae and survival of sawfly eggs, but a correlative analysis suggested the underlying mechanisms may have been largely different between the two areas investigated. Ants were the only predator group that was consistently associated with the lower survival of sawfly larvae on both areas, and hence responded correspondingly to the stand composition. The role of ants as predators of sawfly larvae has been reported also previously (Olofsson 1992). Other predator groups were negatively associated with the presence of ants, which suggests possible interference between these groups (Halaj et al. 1997). Similar to the analysis of final survival, the analysis of the timing of survival suggested that different predators were acting on the two areas, because there was a highly significant interaction between the area and stand composition.

In particular, interference between predators was suggested in 2002 when most comprehensive data were available, because fewer sawflies remained on the study trees of Area 2, where ants were also less abundant than on Area 1. Instead of ants, there were more harvestmen and heteropterans at this site, and the latter also showed a negative relationship with the ants. On the other hand, there were no direct correlations between the abundance of these groups and sawfly survival within Area 2, which leaves open the question whether these groups were directly responsible for poorer performance of sawflies. Although all the heteropterans were predatory ones, it is not known if they all used *N. sertifer* as a prey. In any case, the predatory genus *Podisus* sp. was frequently found preying upon the experimental sawfly larvae during both years at Area 2. *Picromerus bidens,* which has been reported to prey on pine sawfly larvae (Benson 1950), was also present. Factors behind the lower survival of sawfly eggs on the mixed stands remained unresolved, but the holes found on the eggs suggest that attacks by sucking insects have taken place (Ives 1967). Our correlative results suggest that it was unlikely that the small size of larval groups affected the outcome of the study, because the original group size was equal in both stand types (see also Lindstedt et al. 2006).

The relationship between spiders and sawfly larvae was complicated, and to be fully resolved, it will require information about the predatory habits of individual spider species, as well as experimental evidence about their interactions with the other predators. In any case, spiders may form part of the explanation, because there was a negative correlation between the numbers of ants and spiders on both areas. Individual larvae were also regularly found trapped in spider webs. Juutinen (1967) reported that two spiders (*Theridion sisyphium* and *Entelecara* sp.) trapped about 10% of the sawfly larvae at the site of his study.

Spiders were more abundant on larger trees. Considering the predatory role of spiders, this suggests that the dynamically changing size of tree crowns may form an additional factor that determines the outcome of the interplay between the predators, herbivores, and their host plant (Kaitaniemi et al. 2004). Tree size may provide a partial explanation for the presence of the outbreaks of some sawfly species on mainly young trees and other species on mainly mature trees (De Somviele et al. 2004). On the other hand, in contrast to *N. sertifer* that mainly infests relatively young stands especially in the central Europe, large and mature trees seem to more often experience outbreaks of the common pine sawfly *Diprion pini* (De Somviele et al. 2004). This suggests that the relationship between the increase of predator numbers and tree size, as observed in the present study, is not a simple explanation for predator efficiency.

As the species composition of tree canopies changes with increased architectural complexity (Lawton 1983), it is likely that the species and interactions responsible for the regulation of sawfly numbers also change. The structural complexity of mature pines may also act as a shelter for sawfly larvae, like it does for larvae feeding on the mountain birch (Kaitaniemi and Ruohomäki 2001, Kaitaniemi et al. 2004). A factor that is associated with the amount of growth in pines, and hence potentially also with the architectural complexity of crowns, is the level of host plant resin acids (Björkman et al. 1991), which clearly can also contribute to the observed patterns.

In the present study, the plots were only 20m × 20m in size which suggests that stand composition may have an effect on sawfly incidence even at a fine spatial scale. A similar effect at fine spatial scale was observed in another study where survival of the lepidopteran *Epirrita autumnata* larvae was lowest in pine-birch mixtures compared with three other stand types with the same plot size (Riihimäki et al. 2005).

Altogether, our results are in accordance with the idea of associational resistance and suggest that the species composition of trees within a stand, together with tree size, can determine the composition of predatory community attacking pine sawflies. However, what is associational resistance against one species may not be against another. At the same time as the number of sawflies decreased in the pines growing in mixed stands with birch, the number of ants and ant-tended aphid colonies increased in the same trees (Riihimäki et al. 2005). The predator community which appeared to be underlying resistance also differed between the study sites. Without further experimentation and long-term data, it is impossible to judge, whether the net benefit for pines was positive or not. At least there was no detectable effect on pine diameter yet. However, as a whole, the stands with pine and birch mixed may benefit from the associational resistance as the birches within the same mixed plots also experienced associational resistance (Riihimäki et al. 2005). Thus, following the original formulations (Root 1973), it may be practical to use the concept of associational resistance as a trait characterizing the resistance of whole communities against damage by herbivores in general, instead of concentrating only on some specific interactions.

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