Interactions between Ants and Pine Weevils

Effects on Forest Regeneration

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Abstract

Ants interact with plants in various ways and ant presence on plants can decrease local abundance or activity of herbivores, which in turn increases plant fitness. Red wood ants (*Formica rufa* group) are common species in forests of northern Europe. A large part of their diet consists of honeydew produced by ant-tended arboreal aphids and ants have been shown to affect a wide range of herbivores both in tree canopies and undergrowth. The pine weevil, *Hylobius abietis* (L.), is an economically important forest pest species. Adult beetles feed on stem bark of transplanted conifer seedlings and cause severe seedling mortality in forest regeneration areas. In this thesis, interactions between ants and pine weevils were investigated to evaluate whether ants can affect weevils' damage to conifer seedlings. The results showed that pine weevil damage to conifer seedlings with a food source attended by ants was significantly lower (by ca. 30%) compared to control seedlings. This effect was mainly ascribed to non-consumptive interactions i.e., the presence of ants distracted pine weevils from feeding. Observations of ant-weevil interactions supported this hypothesis, as ants frequently attacked pine weevils close to ant-attended seedlings and weevils' locomotion behaviour increased during ant attacks. The effects of ant-attendance may be generalized to other aggressive ant species, as ant-attended seedlings visited by *Lasius* ants suffered lower damage by weevils compared to ant-excluded seedlings. Differences in ant abundance on the ground, however, did not affect damage to unbaited spruce seedlings, because similar feeding damage was recorded in areas with high and low abundance of red wood ants. Further, weevils' damage to seedlings that were planted in close proximity to ant-attended seedlings was comparable to that of ant-excluded seedlings. This suggests that seedling protection by ants is probably mainly related to the ants' protection of food sources whereas abundance of ants has less effect on weevils' feeding. Understanding the role of ants may have important implications for future strategies aiming to control pine weevil damage.

Keywords: ants, associational resistance, conifer seedlings, forest regeneration, *Formica rufa* group, herbivores, *Hylobius abietis*, integrated pest management, *Lasius,* non-consumptive effects, trait-mediated interactions, trophic cascade

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Contents

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Maňák, V., Nordenhem, H., Björklund, N., Lenoir, L. & Nordlander, G. (2013). Ants protect conifer seedlings from feeding damage by the pine weevil *Hylobius abietis*. *Agricultural and Forest Entomology,* 15(1), 98-105.

II Maňák, V., Björklund, N., Lenoir, L., Knape, J. & Nordlander, G. Behavioural responses of pine weevils as a result of non-consumptive interactions with red wood ants (manuscript).

III Maňák, V., Björklund, N., Lenoir, L. & Nordlander, G. (in press). The effect of red wood ant abundance on feeding damage by the pine weevil *Hylobius abietis*. *Agricultural and Forest Entomology*. Published online 18 October 2014: http://dx.doi.org/10.1111/afe.12080

IV Maňák, V., Björklund, N., Lenoir, L. & Nordlander, G. Testing associational resistance against pine weevils mediated by *Lasius* ants attending conifer seedlings (manuscript).

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The contribution of Vítězslav Maňák to the papers included in this thesis was as follows:

I Idea and hypothesis (10%), planning of work (30%), performance of work (70%), analysis and summary of results (90%), writing of manuscript (80%)

II Idea and hypothesis (50%), planning of work (70%), performance of work (90%), analysis and summary of results (90%), writing of manuscript (80%)

III Idea and hypothesis (30%), planning of work (50%), performance of work (90%), analysis and summary of results (90%), writing of manuscript (80%)

IV Idea and hypothesis (50%), planning of work (50%), Performance of work (100%), Analysis and summary of results (90%), writing of manuscript (80%)

1 Introduction

1.1 Background

Ants (Hymenoptera, Formicidae) are abundant in most terrestrial ecosystems and they influence their environment in various ways. They are, for example, important predators, herbivores or affect plant dispersal (Hölldobler & Wilson, 1990). Plant defence by ants has received considerable attention in scientific literature and several ant species have been found beneficial in agroecosystems as they consume pest species that cause damage to crops (Way & Khoo, 1992; Rico-Gray & Oliveira, 2007). Ants can be attracted to plants directly by plant rewards (extrafloral nectaries, food bodies and domatia) or indirectly, through interactions with honey-dew producing Homoptera on the plants (Way, 1963; Heil & McKey, 2003). Ants protecting such food resources on plants have generally negative effect on abundance and activity of herbivores, which in turn benefits the plants (Styrsky & Eubanks, 2007; Chamberlain & Holland, 2009; Rosumek et al., 2009).

In general, interactions between herbivores and their natural enemies that result in decrease of herbivore damage to the plants have been formalized in the concept of trophic cascades (Schmitz et al., 2000). Natural enemies can suppress herbivore activity by direct consumption of herbivores (density-mediated effects) or by changing behaviour or physiology of herbivores, i.e. non-consumptive (trait-mediated) effects (Hairston et al., 1960; Schmitz et al., 2004). The effects of non-consumptive interactions have been shown in many cases to be comparable to those of direct predation (Werner & Peacor, 2003; Preisser et al., 2005). Ants are known primarily for their predatory activities, but non-consumptive effects on other arthropods have also been documented (Rudgers et al., 2003; Hawes et al., 2013; Mestre et al., 2014). There is a growing number of cases where non-consumptive effects supress the activity of economically important pests (Eubanks & Finke, 2014), but the importance of these effects needs to be further evaluated in both agro- and forest ecosystems. Further, natural enemies attracted to plants can affect herbivore activity not only on these plants but also on other plants that occur in close proximity. These effects, referred to as associational resistance, have been widely studied for their potential benefits in agroecosystems (Barbosa et al., 2009; Letourneau et al., 2011).

1.2 Ants in forests

Ant communities in forests of northern Europe consist of several ant species that can be classified into three groups based upon their aggressiveness and territoriality: (1) aggressive and territorial, (2) encounter (aggressive and non-territorial), and (3) submissive species (Savolainen et al., 1989). Red wood ants (*Formica rufa* group) are classified as aggressive and territorial ants that have strong influence on other territorial or encounter species (e.g. *Camponotus* and *Lasius*). Submissive ants (e.g. *Myrmica* and *Leptothorax*) are influenced by aggressive species but can coexist in their territories due to the utilization of different niches (Savolainen et al., 1989). This thesis focus mostly on red wood ants (Study I, II, III) but other ant species are also considered (Study I, IV).

Red wood ants inhabit forest habitats and build typical mounds that may contain several hundred thousand of individuals. Four species are typically included in the *F. rufa* group: *F. lugubris*, *F. rufa*, *F. polyctena* and *F. aquilonia* (Douwes et al., 2012). Red wood ant species are very similar in their morphology and the main characters used for species identification are numbers of erected hairs on different body parts (Douwes, 1981). Traditionally, red wood ants are divided into monogynous species, i.e. having one queen (*F. rufa* and *F. lugubris*) and polygynous species, i.e. having multiple queens (*F. polyctena* and *F. aquilonia*) (Hölldobler & Wilson, 1977; but see Sundström et al., 2005). Monogynous species disperse by flight and establish new colonies through temporary parasitism on other ant species, while polygynous ants can establish new colonies (by budding) close to a parental nest. Monogynous species often build smaller nests and inhabit younger forests whereas polygynous species build larger nests and inhabit close-canopy mature forest stands (Punttila, 1996).

Red wood ants occupy a territory of up to 60-80 meters around their nests and create trail systems that are stable over their active season (Buhl et al., 2009; Sorvari, 2009; Douwes et al., 2012). The trails frequently lead to foraging trees where the ants collect honeydew produced by mutualistic aphids in tree canopies (Domisch et al., 2011). Honeydew makes up a large part of the ants' diet, but the ants also prey on other arthropods, mainly aphids, Diptera and Lepidoptera larvae (Way, 1963; Skinner, 1980). Due to their predatory behaviour, red wood ants have long been regarded as potential biocontrol agents to reduce damage by forest pest species (Adlung, 1966). Accordingly, several studies have shown that ant-predation of herbivores positively affects the growth and performance of ant-attended trees (Whittaker & Warrington, 1985; Karhu, 1998; Moreira et al., 2012). These effects are dependent on several factors, e.g. intensity of ant-attendance (Kilpeläinen et al., 2009), plant physiology (Sipura, 2002) or interactions between ants and other predators (Mooney, 2007).

Ants can also affect insect predators on the ground such as ground beetles (Carabidae) that have been shown to be more numerous in areas with low ant abundance compared to areas with high ant abundance (Laakso & Setälä, 2000; Hawes et al., 2002; Reznikova & Dorosheva, 2004). These effects are probably caused by non-consumptive interactions, because ground beetles kept with red wood ants ceased to consume food items and increased their locomotion behaviour (Hawes et al., 2013). The effect of red wood ants on other arthropods on the forest ground may be constrained to specific species as some studies found no effect of red wood ants on spiders and other groups of ground dwelling arthropods (Brüning, 1991; Neuvonen et al., 2012).

Figure 1. Red wood ants (*Formica rufa* group) are territorial and aggressive ants that inhabit forests of northern Europe.

1.3 Effects of forest management

1.3.1 Effects of clear-cutting on ants

Forests in northern Europe are primarily managed for wood production. Mature forests are harvested by clear-cutting, a method that has been used in Sweden since 1950's (Lundmark et al., 2013). Ant communities of mature forests consist of rather few species (e.g. red wood ants, *Camponotus herculeanus* and *Myrmica ruginodis*) and these species may persist in the sites after clear-cutting (Punttila et al., 1994; Niemelä et al., 1996; Domisch et al., 2008). Other ant species (e.g., *Lasius* and other *Formica* species) start colonizing clear-cuts during first years after harvest (Punttila et al., 1991).

Figure 2. A clear-cut close to Uppsala the first season after harvest.

Clear-cutting has, however, mostly negative effects on red wood ants. The risk that red wood ants will abandon their nest is higher in clear-cuts compared to in mature forest stands (Punttila, 1996; Sorvari & Hakkarainen, 2007). Factors such as loss of aphid colonies, loss of visual cues for orientation or change in microclimate are considered to affect ants negatively in the clear-cuts (Rosengren & Pamilo, 1978; Rosengren, 1979). Recent research suggests, however, that the probability of nest survival and production of sexual offspring is higher close to the forest edge compared to that in the centre of clear-cut (Sorvari, 2013). Gibb and Johansson (2010) found that the rate of honey-dew harvesting by red wood ants in clear-cuts was similar to that in old growth stands and it was suggested that this may be a result of recent changes in forest management that improve the temporal continuity of forests for ants. Thus, silvicultural measures such as smaller sizes of clear-cuts or tree retention may increase the probability of survival of red wood ants in harvested areas. Red wood ants may be effective for pest control even in clear-cuts as they have been shown to predate on important forest herbivores e.g. autumnal moth (*Epirrita autumnata*) and pine sawflies (*Neodiprion sertifer*) in forest regeneration areas (Riihimäki et al., 2005; Kaitaniemi et al., 2007).

1.3.2 Pine weevil problem

Forests in Sweden are regenerated mostly by replanting, mainly by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*). The seedlings are grown in nurseries and transplanted in clear-cuts usually in spring or autumn any of the first three years after tree harvest (Nilsson et al., 2010).

The major recurring problem in forest regenerations is a mortality of conifer seedlings caused by the pine weevil *Hylobius abietis*. Adult pine weevils feed on thin bark of roots and branches (Örlander et al., 2000; Wallertz et al., 2006) and transplanted seedlings usually only form a smaller part of their food intake (Bylund et al., 2004). Newly planted seedlings, however, often do not resist the feeding damage caused by pine weevils, which can result in 90% mortality of transplanted seedlings in forest regenerations (Örlander et al., 1997; Petersson & Örlander, 2003).

Figure 3. The pine weevil (*Hylobius abietis*) is an economically important pest species because it feeds on bark of conifer seedlings and cause high seedling mortality in forest regenerations.

Clear-cutting areas provide a suitable habitat for pine weevil development. Weevils fly into newly harvested clear-cuts, orienting towards the volatiles released from freshly cut wood (Solbreck & Gyldberg, 1979; Räisänen et al., 2008). The density of pine weevils on a fresh-clear cuts was estimated to be higher than 10,000 individuals per ha^{-1} (Nordlander et al., 2003). After arriving to the clear-cuts, their flight muscles regress and pine weevils move mostly on the ground (Nordenhem, 1989). Roots of conifer stumps left after harvest serve as breeding material; weevils lay their eggs in proximity of the stumps and the larvae develop in the roots for 1.5 - 3 years, depending on latitude and temperature (Butovitsch & Heqvist, 1961; Eidmann, 1964; Nordlander et al., 1997). Most damage is caused by pine weevils during four years after clear-cutting, i.e. by pine weevils that immigrated into the clear-cuts but also by the generations of weevils emerging from the stumps in following years (Örlander et al., 1997; Örlander & Nilsson, 1999).

In the 1950's when the forestry intensified, insecticides became a main measure against pine weevil damage. DDT (dichlorodiphenyltrichloroethane) was widely used until it was banned in 1970's and synthetic pyrethroids, neonicotinoids and other insecticides have been used since then (Nilsson et al., 2010). Pesticides are still used today but their application will probably be phased out in Sweden during the next few years, mainly due to recent development of effective and environmentally friendly methods, e.g. sand or wax coating techniques (Nordlander et al., 2009; Nordlander et al., 2011; Giurca & von Stedingk, 2014).

Population density of pine weevils is mostly regulated by availability of breeding material, whereas effects of natural enemies are of less importance (Eidmann, 1977). The pine weevil has, however, a number of natural enemies among insects, fungi and nematodes. Among insects, two host-specific parasitic wasps (Hymenoptera, Braconidae) have been found to attack pine weevils. *Bracon hylobii* attacks larvae in the roots of conifer trees (Munro, 1914) whereas *Perilitus areolaris* attacks the adult weevils (Gerdin & Hedqvist, 1984). *Bracon hylobii* has been shown to cause locally large mortality of pine weevil larvae, but production of parasitic wasps is still expensive to use in forest protection (Leather et al., 1999). Entomopathogenic nematodes and fungi have also been tested to decrease the number of developing larvae and some promising results have been shown in both laboratory and field trials (Dillon et al., 2006; Williams et al., 2013). The effect of predators have rarely been investigated, but some cases of predation, by both vertebrate and invertebrate predators, have been documented (Collinge, 1915; Salisbury & Leather, 1998). Prior to this thesis, very little was known about ant-weevil interactions and their effect on conifer seedlings in forest regeneration areas.

2 Thesis aims

The aim of this thesis was to investigate whether interactions between ants and pine weevils will have an effect on pine weevil feeding on conifer seedlings and to understand the mechanisms underlying these interactions. This knowledge may provide new tools for seedling protection against pine weevils which may be applicable in future integrated forest pest management programs. The four specific aims of this thesis were to:

- Assess whether ants attracted to spruce seedling will reduce pine weevil damage compared to control seedlings and if these effects are influenced by other factors such as distance of seedlings from ant-hill or ant abundance in close vicinity of the seedlings.

- Investigate how ants influence movement behaviour of pine weevils in vicinity of ant-attended seedlings compared to unattended seedlings.

- Estimate the effects of high and low abundances of red wood ants on the ground on feeding damage of pine weevil to conifer seedlings.

- Evaluate whether *Lasius* ants affect pine weevil damage to conifer seedlings attended by the ants and whether neighbouring seedlings experience associational resistance.

3 Methods

Three field studies (Study I-III) and a laboratory experiment (Study IV) were conducted to study the effects of ants on pine weevils. Field studies were carried out on clear-cuts that were located in managed coniferous forest stands consisting mainly of Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*). The clear-cuts were distributed in the province of Uppland, central-eastern Sweden (N 60°, E 17°). The field experiments were designed to study the effect of red wood ants and study sites were therefore chosen around ant-hills that remained active in clear-cuts after harvest. Seedlings of Norway spruce, obtained from forest nurseries, were used in all four experiments.

Pine weevils feed on stem bark of conifer seedlings and seedling damage is thereby an important measure of pine weevil feeding activity (Figure 4). Feeding is typically located near the stem base and if the feeding scar covers the entire stem circumference, the seedlings become girdled and will not survive. To assess pine weevil feeding activity, we measured feeding-scar area on the seedlings (Study I, III, and IV). Moreover, proportions of attacked and killed seedlings were recorded (Study III).

Figure 4. Feeding damage on a spruce seedling caused by the pine weevil

Movement behaviour of pine weevils during their interactions with ants was also investigated (Study II). Pine weevils are large beetles with highly sclerotized cuticle that makes them a difficult prey for insect predators. Behavioural responses to the presence of or interactions with ants may be an important mechanism influencing pine weevil feeding activity on the seedlings. Four different pine weevil behaviours were recorded: standstill, locomotion, stationary movement (i.e. movement within the distance of beetle's body length) and digging. Interactions of pine weevils with ants were divided into three categories: no interactions, aggressive interactions in which ants bite pine weevils with their mandibles on different body parts and non-aggressive short interactions in which ants investigate the weevils with their antenna. Weevils were observed around seedlings within an area with a radius of 30 cm.

To examine the effects of ants, damage to the seedlings (Study I, IV) and pine weevil behaviour (Study II) was compared between seedlings attended by ants and seedlings without ants. Additionally, damage to (non-attended) seedlings was compared between areas where ants were abundant and areas with low ant abundance (Study III).

In order to attract ants, the seedlings were equipped with sugar baits (Study I and IV) or infested with aphids (Study II). The sugar bait consisted of plastic tube filled with sugar. The tube was attached to the seedling with the lid facing down and ants could access the bait through an opening in the lid of the tube. In the laboratory (Study IV), we used 1 M solution of sugar which was collected by ants from a piece of dish sponge soaked in the solution. In the field, sugar baits with hard consistency were used (table sugar mixed with egg white), so that the bait could be used by ants for a longer period of time. Aphids *Cinara piceicola* used in Study II were transferred to the seedlings from naturally infested branches of spruce trees in the beginning of spring when the aphids emerge from the overwintering eggs.

Abundance and activity of ants on the ground was measured using pitfall traps (Study I and III). The pitfall traps were placed close to the experimental seedlings for a short period of time to minimize interference with the activity of both ants and pine weevils. Further, ant activity on the seedlings was inspected visually (Study I, II) or estimated from consumption of sugar solution (Study IV).

3.1 Design and statistical analyses

Ant-attended and control seedlings were planted either in pairs (Study I) or individually around ant hills (Study II). Seedling groups, each containing sixteen seedlings, were planted in areas with high and low abundance of red wood ants (Study III). Laboratory experiments were done by using seedlings in box pairs, one of which was visited by ants and the other was closed for the ants (Study IV).

Generalized linear mixed models were used to analyse the data of feeding damage to the seedlings (Study I, III and IV). The response variable was feeding-scar area on the seedlings (Study I, III and IV) and proportions of attacked or killed seedlings (Study III). Analyses were carried out to test mainly the effect of treatment, i.e. ant-attendance (Study I and IV) or ant abundance (Study III). We also tested the effects of other factors such as distance of seedlings from ant-hills, abundance of ants in close vicinity of seedlings or differences among ant nests. Feeding damage to the seedlings was recorded on several occasions (Study I and III) and the feeding damage was analysed as repeated response variable. Random factors were used to take account for variation among seedling pairs (Study I), seedling groups (Study III) and box pairs (Study IV). The analyses were conducted in GLIMMIX procedure in SAS 9.2 (SAS Institute INC., Cary, North Carolina).

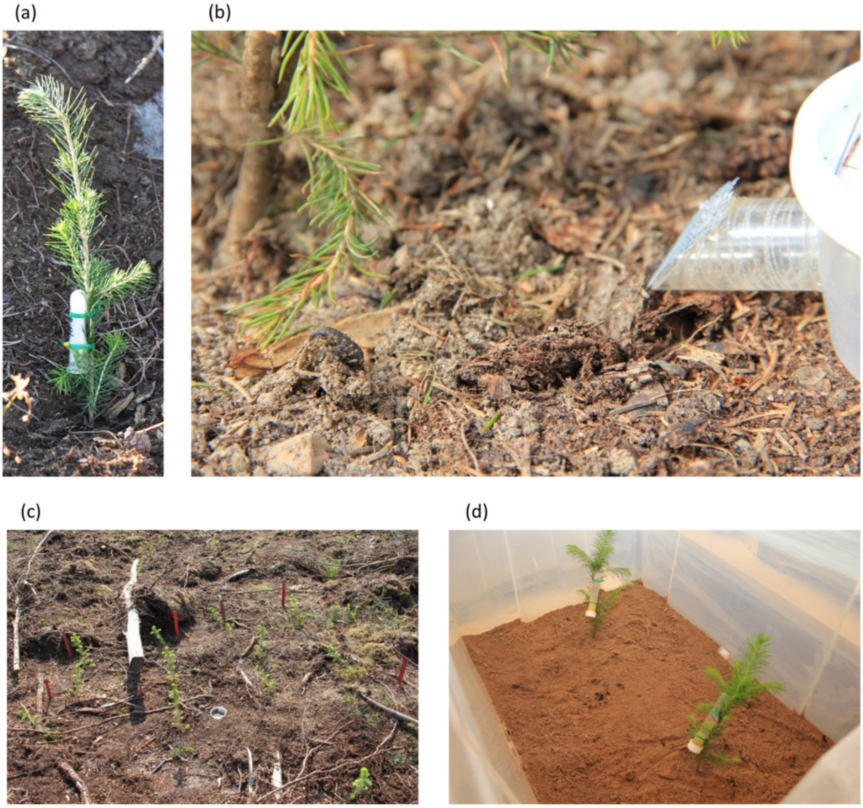

Figure 5. (a) Spruce seedling equipped with sugar bait (Study I), (b) pine weevil released from a jar close to a seedling (Study II), (c) seedling group and a pitfall trap used in Study III and (d) experimental box containing one sugar-baited and one control seedling (Study IV).

Behavioural data were analysed using Multi-state Markov models (Study II). These models are suitable for analysing behavioural sequences that occur over time. We analysed the effect of treatment on ant-weevil interactions and pine weevil behaviours. Further, the effect of aggressive behaviour of ants on movement behaviour of pine weevils was also analysed. The results were interpreted as hazard ratios i.e. how much more or less likely a behavioural transition is under one level of the categorical variable compared to the other.

The analyses were conducted using msm package in R statistical software (Jackson, 2011; R Core Team, 2013).

4 Results and Discussion

We found that baited seedlings attended by ants suffered significantly less damage (by approx. 30%) compared to control seedlings (Study I). The experiment was conducted twice during one summer and feeding-scar area on baited seedlings was significantly lower in both rounds of the experiment (Figure 6). This is an important result, because ants have not been previously considered as a natural enemy of pine weevil (Leather et al., 1999). These results are consistent with the notion that ants attracted to plants can reduce activity of herbivores, and thus benefit the plants (Rosumek et al., 2009). Pine weevils are robust beetles and are probably at low risk of predation by the ants. The decrease in feeding activity on seedlings was therefore ascribed to non-consumptive effects i.e. the presence of, or harassment by, ants distracting pine weevils from feeding.

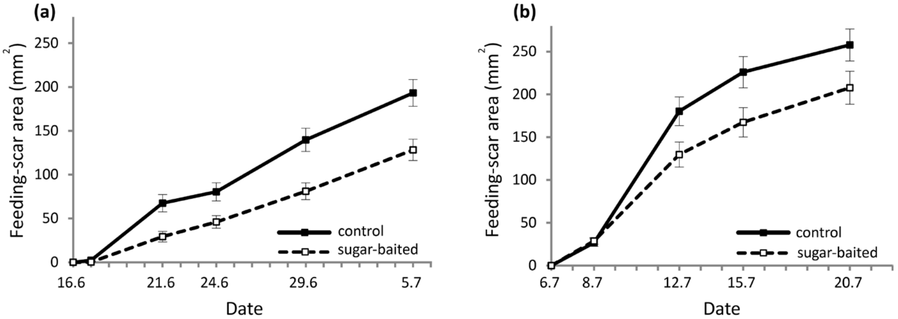

Figure 6. Mean area (±SE) of pine weevil feeding-scars on sugar-baited spruce seedlings (n=160) and control seedlings (n=160) in (a) the first and (b) the second round of the Study I.

Observations of movement behaviour of pine weevils and their interactions with red wood ants supported the hypothesis of non-consumptive effects, because ants were shown to affect the behaviour of pine weevils (Study II). The weevils were significantly (5-fold) more likely to be attacked at ant-attended seedlings and these attacks were much longer (10-fold) compared to control seedlings (Figure 7). Pine weevils were mostly standing still and movement behaviour was recorded in ca. 10% of the time. Locomotion was the most common behaviour, followed by stationary movement and digging. Pine weevil behaviour was only slightly influenced at ant-attended seedlings, as only the length of stationary movement was significantly higher (44%) at ant-attended seedlings compared to controls. During ant attacks, however, pine weevils were less likely to cease locomotion behaviour (60%) and stationary movements (59%).

Figure 7. Pine weevil being attacked by red wood ants at the stem base of a seedling of Norway spruce.

These results suggest that aggressive behaviour of ants can influence locomotion behaviour and the weevils may thus move to other places where the risk of encounters with ants is lower. Increased locomotion behaviour was also observed in lepidopteran larvae on cotton plants visited by ants and it was suggested that these behavioural responses are an important factor influencing the herbivore damage to the plants (Rudgers et al., 2003). Further, Messina (1981) observed that time spent by adult leaf beetles (*Trihabda* sp.) on stems of goldenrod (*Solidago* sp.) was negatively correlated with density of *Formica* ants on these plants. When disturbed by ants, beetles dropped off the plants which is a behaviour that is typical not only for leaf beetles but also other beetle groups (Crowson, 1981).

Low effect of ant presence on weevils' behaviour (while not attacked by ants) is probably due to the low predation risk that pine weevils experience in the presence of ants. Similar observations were done in other systems, where insects that experienced a relatively low predation risk adopted defensive behaviour first after they were attacked by a predator (Sih, 1982; Thaler & Griffin, 2008).

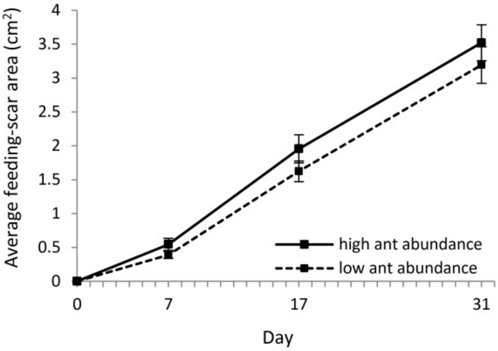

Figure 8. Mean feeding-scar area (±SE) on spruce seedlings in high ant abundance seedling groups (n = 45) and low ant abundance seedling groups (n = 45).

In study III, we found that seedlings planted in areas where red wood ants were abundant (i.e. around ant-hills) suffered similar amount of damage compared to seedlings planted in areas with low abundance of ants (Figure 8). Moreover, pine weevil damage to seedlings in high ant-abundance areas was neither affected by the abundance of red wood ants nor distance from seedling groups to the closest ant-hill or ant-trail. The results suggest that pine weevil feeding activity is not influenced by frequent encounters with red wood ants and that the decrease of damage to the seedlings is probably mainly related to the ants' protection of food sources as observed in studies I and II. The negative effects of red wood ants on abundance and diversity of ground beetles reported from other studies (Hawes et al., 2002; Koivula, 2002; Hawes et al., 2013) may be due to that ground beetles are predators and ants compete with them for same food sources on forest floor. Pine weevils are herbivores, and may thus not be recognized as competitors by red wood ants. Further, pine weevils are relatively slow moving insects compared to ground beetles, which may also affect ants' recognition and aggressive behaviour towards pine weevils.

Several other ant species are present on clear-cuts after harvest and beside red wood ants, *Myrmica* ants were commonly observed on baited seedlings and recorded in pitfall traps. Further, other ant species were observed (e.g., *Lasius* sp., *Leptothorax* sp., *Formica* (*Serviformica*) sp. and *Camponotus* sp.), although in lower numbers (Study I). *Myrmica* ants are less aggressive species compared to red wood ants (Savolainen et al., 1989) but have been shown to be effective in disturbing lepidopteran and beetle herbivores from plants (Koptur & Lawton, 1988). The results of the laboratory experiment with *Lasius* ants (Study IV) suggest that the effects of ant-attendance may be generalized to other ant species, because we found that feeding damage on ant-baited seedlings was significantly lower compared to seedlings where ants were excluded. *Lasius* ants are small species with body size comparable to *Myrmica* ants, and it is therefore plausible that other ant species can deter pine weevils from feeding on conifer seedlings.

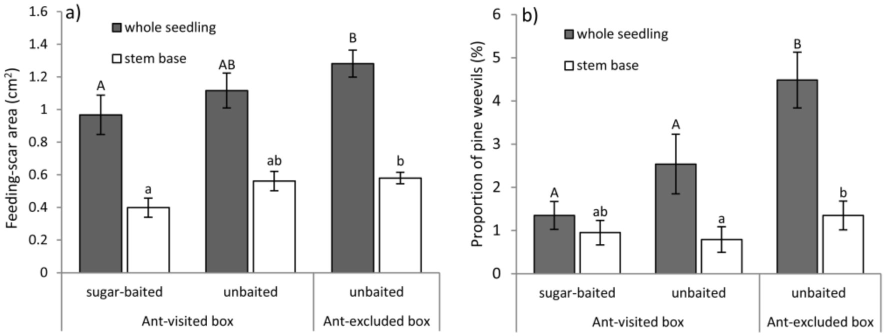

Figure 9. (a) Feeding scar area (cm^2) and (b) mean proportion of pine weevils recorded on sugar-baited (n=42) and unbaited seedlings (n=42) in ant-visited boxes and in seedling pairs in ant-excluded boxes (n=42). Different letters denote significant differences between seedling types.

Seedlings that were planted in the vicinity of ant-attended seedlings (Study IV) did not experience associational resistance, because the feeding damage was not significantly lower compared to ant-excluded seedlings (Figure 9a). Effects of associational resistance through ant-attendance have been observed e.g. in diversified plots in forest regeneration where ant-predation on sawflies and autumnal moths increased when birch seedlings were grown in mixture with conifer seedlings that were attended by ants (Riihimäki et al., 2005; Kaitaniemi et al., 2007). Some evidence of associational effects was observed also in study

IV, because number of weevils recorded on ant-attended and neighbouring seedlings was significantly lower compared to that on ant-excluded seedlings (Figure 9b). These effects, however, did not lead to decreased feeding damage to seedlings at the end of the experiment. This suggests that the strength of non-consumptive effects may not be sufficient for the occurrence of associational resistance in ant-weevil system.

Among other factors, no significant effect of distance of baited seedlings from ant hills was detected (Study I). This may be due to that the ants are highly mobile and can recruit to food sources that are further away from their colony (Evans et al., 2013). Some differences were detected among ant colonies in terms of feeding damage or aggressive behaviour of ants (Study I, II). This may depend on fitness of ant colonies or availability of other food sources in the sites that may in turn influence how ants recruit to seedlings and protect the food sources on them (Katayama & Suzuki, 2003; Mailleux et al., 2010). No relationship was found between sugar consumption and the feeding damage caused by pine weevils (Study IV). This is in contrast to another study, which showed negative relationship between numbers of ants and herbivorous weevil larvae on the plants (Katayama & Suzuki, 2005).

Aphids were mostly observed on the stem base of the seedlings (Study II), so the ant activity on these seedlings was comparable to that in seedlings equipped with sugar baits (Study I and IV). Aphids were, however, also observed on roots of the seedlings and ants were seen to carry soil material from the roots to the surface around seedlings. It has been documented earlier that *Cinara piceicola* moves to the roots of spruces during the summer where they are attended by ants (Heie, 1995). Some pine weevil individuals were observed entering these cavities but it is unclear whether this behaviour constitutes an increased risk for subsequent damage of the seedling or whether ants would prevent pine weevils from feeding on seedlings.

5 Conclusions

The results of this thesis suggest that ants' protection of food sources is the most important factor that can lead to reduction of feeding activity of pine weevils, whereas local abundance of ants has less effect on weevils' feeding. The results also highlight the importance of non-consumptive effects in ant-weevil interactions, because movement behaviour of pine weevils was affected by ants' aggressive behaviour.

A promising area for future research may be to investigate further the possibilities of ant-attendance on conifer seedlings. Recent studies have shown that bottom-up effects, such as different plant genotypes and plant species may influence ant-aphid interactions on plants that affect both plant growth and ants' effects on herbivores (Mooney & Agrawal, 2008; Moreira et al., 2012). Further, chemical cues used by ants have been shown to induce behavioural changes in other arthropods (Mestre et al., 2014). Such effects may be useful in development of antifeedants or repellents applied to conifer seedlings to protect them from pine weevil damage. If such efforts are proven effective, they may become part of integrated pest management programs in the future.

The pine weevil is an important forest pest and the role of weevils' interactions with their natural enemies may be an important aspect in seedling protection in forest regeneration areas. Understanding of the relationships between land use and ecosystem services provided by beneficial species is an important research question in agroecosystems (Bommarco et al., 2013). Enhancing the structural diversity has been recognized as an important measure for increasing biodiversity in managed forests (Fedrowitz et al., 2014), but the ecosystem services that this diversity provides deserve more attention in future studies.

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