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Forest succession and harvesting of hemipteran honeydew by boreal ants

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Ants are important harvesters of plant-derived sugars, but little is known about how anthropogenic disturbances influence this behaviour. We investigated factors related to honeydew harvesting by red wood ants, *Formica aquilonia*, in managed boreal forests. Ant activity was lowest in middle-age stands (30–40 years old), which had the fewest and smallest ant mounds. It was best predicted by a model containing an interaction among tree species, basal diameter and stand age. Individual workers collected similar masses of honeydew from the different aged stands, which suggests that colonies optimise foraging efforts by adjusting the number of active foragers to match resource availability. The rate of honeydew harvesting from recently clear-cut stands during the survey was similar to that in old stands, although significantly faster than in middle-aged stands. This may be a result of high aphid loads on clear-cuts and recent changes in forest management that improve the temporal continuity of forests for red wood ants. Anthropogenic alteration of habitats thus significantly alters energy use by ants, mainly as a result of changes in the abundance and size of ant colonies. This change is likely to have further consequences for ant-driven ecosystem functions.

Introduction

Ant harvesting of plant-derived sugar resources, including nectar, extra-floral nectaries, sap or honeydew from sap-sucking hemiptera, is extensive (Davidson *et al*. 2003). Ants that are behaviourally and numerically dominant often have a mutualistic relationship with honeydew producing hemipterans, which provide a persistent, renewable resource (Davidson 1998). The digestive systems of such ants are highly specialised for the carbohydrate-rich and protein-poor diets obtained from feeding on hemipteran exudates (Cook & Davidson 2006). Specialisation on a persistent and reliable sugar resource allows such species to maintain energetically expensive levels of activity (Way 1958, Room 1975). High activity levels allow them to aggressively defend resources, as well as to increase their use of protein sources through *active* predation (Davidson 1997). Ant–hemipteran interactions may therefore represent “keystone interactions” in many communities (Styrsky & Eubanks 2007).

Anthropogenic disturbances are known to affect many ecosystem processes, but the consequences of disturbances for the rates of honeydew harvesting by ants and broader subsequent flow-on effects are unknown. With only 11.5% of the earth's land protected in national parks or nature reserves (Chape *et al*. 2003), the vast majority of productive landscapes undergo persistent anthropogenic disturbance through agriculture, urbanisation and forestry. In mid-boreal Sweden, forestry has led to a disproportionate area of relatively young and dense stands in the modern forest landscape (Linder & Östlund 1998). The disturbance, habitat loss and change in habitat structure resulting from forestry affects a wide range of species and ecosystem processes (Berg *et al*. 1994, Widen 1997, Thor 1998, Simberloff 2001) and forest management has been shown to affect the composition of ant assemblages in a variety of forest ecosystems worldwide (Puntilla 1996, Vasconcelos *et al*. 2000, Maeto & Sato 2004). In boreal forests, a loss of mutualist aphids from clear-cuts may be responsible for the loss of the dominant red wood ants of the *Formica rufa* group from these areas (Punttila *et al*. 1991, Domisch *et al*. 2005a). However, little is known about the consequences of disturbance-related changes in mutualistic relationships for the harvesting of honeydew by ants. In this study, we investigated factors that affect harvesting of honeydew by the northern red-wood ant, *Formica aquilonia*, in managed forests. In particular, we hypothesised that: (1) The density and volume of ant-nest mounds increases with stand age. These nest mounds provide the source of ants harvesting honeydew and their size and abundance may also be indicative of resource harvesting success; (2) Ant activity on trees is predicted by stand age and tree characteristics; and (3) Worker loads of honeydew are predicted by stand age and tree characteristics. We also determined vegetation composition, to allow us to test the fourth hypothesis: that the volume of honeydew harvested by ants differs between stands of different ages. The quantity of honeydew that is harvested by ants provides an indication of the energy available for ant-driven ecosystem functions as well as for ecosystem functions driven by other organisms.

Material and methods

Study species and sites

Formica aquilonia belongs to the *F. rufa* group, which consists of territorially dominant ant species that have been reported to structure ant communities (Savolainen *et al*. 1989). *Formica aquilonia* is the most common *F. rufa* group species in the central-boreal region of Fennoscandia (Collingwood 1979) and forms polygynous and polydomous colonies throughout its range (Pamilo *et al*. 1992). The mound-building activities of *F. aquilonia* and other members of the *F. rufa* group have been shown to alter soil chemistry (Lenoir *et al*. 2001, Kilpeläinen *et al*. 2007), but their impact on soil invertebrates may be limited (Lenoir *et al*. 2003). In the study area, *F. aquilonia* tends the aphids *Cinara piceae* (Panzer) and *C. piceicola* (Cholodkovsky) and has the numerical dominance typical of heavy exudate feeders that depend on honeydew — Davidson's (1998) "ecological dominants". Previous studies report that *F. aquilonia* is affected by forest succession and is more common in old forests and in larger old-forest fragments (Punttila 1996) This study was conducted in boreal forests of northern Sweden between the latitudes of 63.6°N and 64.5°N and longitudes of 19.7°E and 20.7°E. Sites that supported colonies of the northern red wood ant, *Formica aquilonia*, were the focus of this study. The exception to this was sites used for the nest survey, which was designed to determine overall densities of mound-building ants and mound sizes in stands of different ages. All forests were dominated by Norway spruce, *Picea abies* (70%–100%), although birches, *Betula pubescens* and *Betula pendula*, and Scots pine, *Pinus silvestris* were also common (Appendix 1). The understorey consisted mainly of dwarf shrubs (*Vaccinium* spp.) and soils were moist and of the sandy moraine type. We selected sites that were between 5 and 20 ha in the following age categories: recently clear-cut, middle-aged, and old. Clear-cut and middle-aged stands had been cut 1–4 yrs and 30–40 yrs before the surveys, respectively. Many of the stands in the 'old' age group may never have been clear-cut, but large trees had been selectively removed such that the average tree age in these stands was estimated to be 80–100 years. All sites contained stands of a single age category and were separated by more than 500 m to assure independence. Stands of different ages were geographically interspersed to avoid spatial autocorrelation.

Density of ant mounds

Nest surveys were conducted between May and September 2006, in order to determine if nest density or volume differed between stands of different ages. To assess red wood ant nest density, we surveyed 20 spatially separate and geographically interspersed stands in each of the age classes: clear-cut, middle-aged and old. We had no *a priori* knowledge of whether *F. aquilonia* was found in these stands and our aim here was to determine nest densities and sizes in stands of different ages. Transects began in the centre of each stand to avoid biased selection of transect starting points. Stand centres were determined by GIS data. At five sites in each of the three stand types, we walked four transects that were each 100-m long and 10-m wide and separated by 20 m. This method detected very few ant mounds so, for the remaining fifteen sites within each stand age, transect lengths were between 150 m and 500 m, depending on the size of the stand. We recorded the presence, height and basal circumference of mound nests of *Formica sanguinea* or *F. rufa* or *F. exsecta* group species with mound centres within the transect. Nest volume was calculated using the formula for a dome: $\pi r^2(r - h) - \pi/3(r^3 - h^3)$. Ant samples were collected for identification.

Ant use of trees

We surveyed *F. aquilonia* activity on trees on clear days, i.e., low cloud cover and no rain, in July 2007 at six sites for each stand age to standardise conditions across stand types. Ant activity may have been particularly high on these days. Surveys of all stand types were conducted between 8:30 and 19:00 and temperatures varied between 18 °C and 25 °C. Surveys of sites of different stand ages were temporally interspersed so that approximately equal numbers of sites of each stand age were conducted early and late in the day.

At each of the 18 study sites, we selected a nest of *F. aquilonia*. Nests were greater than 70 m from an edge abutting a stand of another age. We counted ants on trees on 50 m-long transects heading north and south from this nest. We selected one birch, one pine and two spruce trees that were nearest to the 10 m, 20 m, 30 m, 40 m and 50 m marks from the nest. We selected only trees with a basal diameter of at least 1 cm. The maximum number of trees that could have been surveyed was 720 (6 sites × 3 stand types × 2 transect × 5 distances × 4 trees), but only N of 636 trees were surveyed to due to low abundances of pine and birch. In areas with high nest densities, distant sampling points may have been closer to another nest as the average distance between nests is approximately 60 m in densely populated sites (author's own obs.). Observations of ant activity were made for one minute on each side of the trees. The rate of ant activity was determined by recording the number of ants crossing a line 10 cm from the base of the tree. The direction in which ants were travelling was also noted. Basal diameter, time and temperature were recorded and samples of each ant species were collected for identification in the laboratory using Collingwood (1979) and Douwes (1995).

Honeydew harvesting

We determined whether the quantity of honeydew harvested from trees in stands of different ages differed and whether this was related to temperature, basal diameter or distance from the nest. Sampling was performed on clear days in July 2008 in four clear-cut stands, four middle-aged stands and four old stands. Ten spruce trees with *F. aquilonia* activity were selected at each site between 0.5 and 35 m from a central nest. Heloise Gibb (unpubl. data) showed that similar quantities of honeydew were harvested from pine and birch in old forests so interspecific patterns were assumed to be similar in other spruce-dominated stand types. We measured the basal diameter, height and distance of each tree from the nest and recorded temperatures at the time we began sampling. We collected 5 ants ascending and 5 ants descending the trunks of each of the trees. Modified battery-driven vacuum cleaners with aspirators attached were used to minimise the formic acid squirt, which results in weight loss. Ants were collected irrespective of the tasks they were performing so that the data were consistent with the activity surveys. We collected a total of 1200 ants. Ants were placed in a cold box at approximately 5 °C in the field and later frozen for 3 days at –20 °C to ensure that they were killed. Individuals were weighed after needles or prey items were removed. The mean mass of ants was calculated for each tree. The mean mass of the "ascending" ants was subtracted from that of the "descending" ants to determine the mass "gain" per tree.

Aphid surveys

We performed surveys of aphids on clear days in July 2006 to determine whether differences in aphid densities might be responsible for differences in ant activity between stand types. We used eight sites in each age category. Three branches were taken from five different spruce trees or saplings in each of the sites. We used experienced climbers to reach the canopy of spruce trees in old stands and ladders were used to access canopies in middle-aged stands. Branches were collected from the upper canopy, just below the tree crown, in all site types as it was not possible to safely reach the crown in old stands. Branches were cut at the base and bagged at all sites. On the ground, branches were beaten and aphids and other insects were collected from the beating tray using an aspirator. Aphids were counted and identified in the laboratory. Samples were sent to an expert (R. Danielsson, University of Lund) for verification.

Statistical analyses

Generalised linear models (GLMs) in the PROC GLIMMIX add-on in SAS 9.1 (SAS Institute 2002–2003) were used to determine the relationship between stand age, tree species, tree basal area, distance from a nest of *F. aquilonia* and the interactions between these factors on the number of ants descending a tree per minute. The data were overdispersed, due to excessive numbers of zeros, so we tested against the negative binomial distribution (as recommended by Pielou 1969, White & Bennetts 1996). We ran all possible models and then compared the models with the lowest quasi AIC (QAIC) scores (Burnham & Anderson 1998). The QAIC is a modified version of the Akaike Information Criterion (AIC) (Akaike 1974) for generalised linear models with overdispersed data (Burnham & Anderson 1998). A best model was selected by determining which factors occurred most often in these top models and then selecting the simplest model.

A full model ANOVA in JMP (SAS Institute 2003) was used to compare the mean weights of ants on trees and included walking direction (ascending or descending), stand type and their interaction as predictors. We used PROC GLM on SAS to determine the best model describing the relationship between stand type, temperature, basal diameter and distance + height (total distance to the canopy) from the nest on the mean weight gain per ant. A best model was again selected as the simplest model with the lowest AIC index. ANOVA was used to test differences in numbers of aphids between stand types.

Estimation of honeydew harvest by ants

Using the estimated stand composition and density and the parameter estimates from the best model predicting the number of ants descending a tree per minute, we calculated the number of ants descending a tree per hectare within a radius of 50 m from a *F. aquilonia* nest in stands of different ages. In order to determine the mass of honeydew harvested from a hectare, we multiplied the modelled number of ants descending trees by the estimate of honeydew harvested per ant.

Results

Density of ant mounds

Mound nests were located in 45%, 50% and 60% of transects in clear-cut, middle-aged and old stands, respectively. Only 45% of active nests found in middle-aged stands were occupied by *F. aquilonia*, compared with 90% and 100% for clear-cut and old stands. The density of nests of all mound-building species did not differ significantly between stands of different ages ($F_{2,57} = 2.32$, $p = 0.108$). On average, clear-cut and middle-aged stands supported, respectively, only 65% and 39% as many nests as old forests. The lack of significance of this analysis, given the differences in means, is likely due to the high variances for all stand ages.

When examined separately, the abundance of mounds of *F. aquilonia* ($F_{2,57} = 5.74$, $p = 0.005$) and other mounding building ants ($F_{2,57} = 3.52$, $p = 0.036$) differed among stand types (Fig. 1a). Post-hoc Tukey's tests showed that *F. aquilonia* nests were significantly more common in clear-cut and old stands than they were in middle-aged stands. Post-hoc tests for other mound-building ants were not significant, but nest abundances for this group appeared greatest in middle-aged stands. No mound nests belonging to species other than *F. aquilonia* were found in old stands. Middle-aged stands had smaller nests of *F. aquilonia* ($F_{2,30} = 6.22$, $p = 0.006$) and other species ($F_{2,23} = 13.21$, $p < 0.001$). The total volume of nests was also smallest in middle-aged stands ($F_{2,57} = 6.85$, $p = 0.002$), with total volumes in old stands 25× greater than in middle-aged old stands; clear-cut stands were intermediate (Fig. 1a).

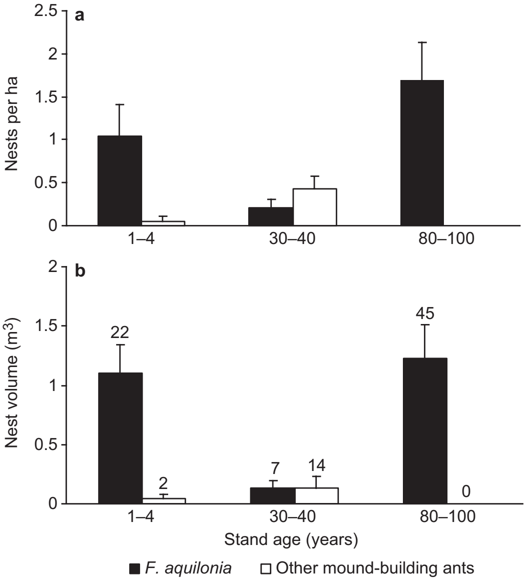

Fig. 1. (**a**) Abundance (mean ± SE) of active mound nests per hectare observed on transects in 1–4, 30–40 and 80–100-year-old stands (n = 20 sites for each age class), and (**b**) volume (mean ± SE) of individual active mound nests on the same transects (n given above the error bars).

Ant use of trees

In total, counts were made on 172 birch, 104 pine and 360 spruce trees. Ants were observed on 49.8% of these trees. Of the 1225 ants observed ascending and descending trees, 96.3% were *F. aquilonia* workers. The remaining 3.7% consisted of *Formica lemani*, *Camponotus herculeanus*, *Myrmica* spp. and *Leptothorax acervorum*. With the exception of the four *C. herculeanus*, these species were small-bodied and rarely observed during the surveys. Thus, these species are unlikely to contribute significantly to honeydew removal in territories of *F. aquilonia*. Although it is possible that species such as *Camponotus herculeanus* dominate this role nocturnally (Klotz & Reid 1993), day length at the time of the study was around 20 hrs, suggesting that nocturnal contributions are unlikely to be significant. Thus, by considering only *F. aquilonia* activity and honeydew removal, we are unlikely to have excluded a significant contribution by other ant species to honeydew harvesting from our analyses.

Using a best model approach to determine which factors were important in determining *F. aquilonia* activity on trees, the best 32 models, which had very similar quasi AIC scores, all included stand age × tree species, basal diameter × distance and stand age × tree species × basal diameter interactions. Hence, the simplest model that included these factors was considered the best descriptor of the system (Table 1 and Fig. 2). The addition of temperature and time of day did not improve the model fit, as changes in temperature during the survey were small. Post-hoc adjusted Tukey's tests showed that spruce and birch trees in middle-age stands supported significantly lower *F. aquilonia* activity than in old stands. Spruce trees in middle-age stands also supported lower activity than clear-cut stands. In clear-cut stands, spruce trees supported significantly higher levels of activity than birch or pine trees (Table 1 and Fig. 2).

Using the Standard Wald Estimates from the generalised linear model, we generated an equation for the number of *F. aquilonia* descending a tree per minute as a function of the significant predictors in the model:

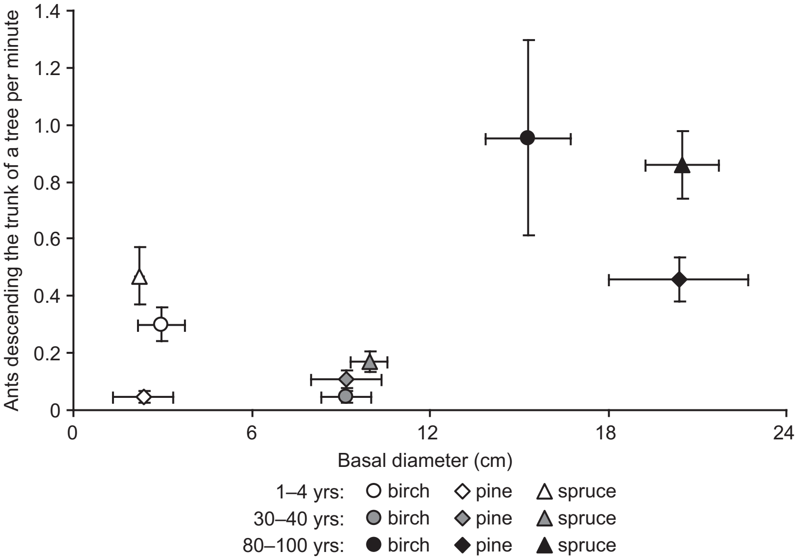

Fig. 2. Ants descending the trunk of a tree per minute (mean ± SE) plotted against basal diameter for the three stand ages and tree species (n = 6 sites for each stand age). A generalised linear model (Table 1) showed a significant 3-way interaction between basal diameter, tree species and stand age.

$$\mathrm{Ln}(F.\ aquilonia\ \mathrm{min}^{-1}\ \mathrm{tree}^{-1}) = 0.6324 + A - 0.0004 \times \mathrm{distance} \times \mathrm{basal\ diameter} + B \times \mathrm{basal\ diameter}$$

where A is the estimate for the stand age × tree species interaction and B is the estimate for the stand age × tree species × basal diameter interaction for each particular stand age and tree species combination (*see* Appendix 2). This model was used to calculate honeydew harvest in stands of different ages (*see* Estimation of honeydew harvest).

Honeydew harvesting

Ants ascending trees weighed significantly less than those descending ($F_{1,229} = 94.56, p < 0.001$). There was no difference in the mass of ants among stand types ($F_{2,229} = 0.90$, $p = 0.407$) nor was there an interaction between stand type and ant walking direction ($F_{2,229} = 0.36$, $p = 0.698$). Foragers descending trees (9.1 ± 0.1 mg) weighed approximately 38% more than foragers ascending trees (6.6 ± 0.1 mg). This is an average load capacity ($\mathrm{Mass}_{\mathrm{ANT}} + \mathrm{Mass}_{\mathrm{LOAD}}/\mathrm{Mass}_{\mathrm{ANT}}$ [Traniello 1989], which was equivalent to the average $\mathrm{Mass}_{\mathrm{DESCENDING}}/\mathrm{Mass}_{\mathrm{ASCENDING}}$ in this study) of 1.38 for honeydew. However, not all workers descending were carrying loads, suggesting that the actual load capacity of this species is higher. Ants descending trees were 2.14 ± 0.40 mg (mean ± SE) heavier than ants ascending trees in clear-cuts, 2.29 ± 0.30 mg heavier in middle-aged stands and 2.36 ± 0.39 mg heavier in old forest stands. These values were not sig-

Table 1. Best generalised linear model (model with lowest QAIC) of factors related to the number of *F. aquilonia* descending the trunk of a tree per minute.* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Effect	df	*F* ratio	*p*
Stand age × Tree species	8,617	4.43	< **0.0001**
Distance × Basal diameter	1,617	2.46	0.1171
Stand age × Tree species × Basal diameter	9,617	4.71	< **0.0001**

Post-hoc Tukey's test of Stand age × Tree species
1–4 yr: spruce > birch**, pine***
Spruce: 30–40 yr < 1–4 yr***, 80–100 yr***: 1–4 yr < 80–100 yr*
Birch: 30–40 yr < 80–100 yr***

nificantly different at $N = 400$ ants per stand type.

We have probably underestimated honeydew load per ant, because ants were collected even if they carried prey, in order to calculate differences between stand types. Using Auclair's (1963) estimate of 84% water for honeydew, we calculated that *F. aquilonia* workers harvested an average of 0.4 mg dry mass of honeydew per trip. Average honeydew loads of *F. aquilonia* workers in this study were thus at the lower end of the 0.4 mg to 2.3 mg dry mass of honeydew per trip reported for the closely related *F. rufa* (Skinner 1980, Wright *et al*. 2000). This is not surprising, given that many of the previous studies targeted ants with obvious honeydew loads, whereas this study did not. Loads have previously been shown to differ between seasons and among ants of different body sizes (Skinner 1980, Wright *et al*. 2000).

The best model explaining the relationship between ant weight difference and temperature, basal diameter, distance of the tree from a nest (added to its height) and stand type consisted solely of basal diameter ($t_{1,114} = 2.33$, $p = 0.022$), but the relationship was weak ($R^2 = 0.045$; Mass gain = 1.988 + 0.032 × basal diameter). The weak role of basal diameter in the best model may reflect a small role of site type, but it was not sufficient to result in different loads being collected in different stand types. This relationship was used in estimating honeydew harvesting rates (below).

Estimation of honeydew harvest

Using the equation derived from surveys of ant use of trees, the stand composition and the relationship between basal diameter and the mass of honeydew collected in stands of each age and the Standard Wald Estimates (Appendix 1), we calculated the mean rate of honeydew harvested by ants within 50 m of a *F. aquilonia* nest in the three stand ages (Table 2). If ants maintain a similar level of activity for 12 hours a day for the whole of July, *F. aquilonia* would be expected to harvest 24 kg ha^{-1} dry mass of honeydew in old stands, 11 kg ha^{-1} in middle-aged stands and 18 kg ha^{-1} in recently clear-cut stands in that month. This may underestimate activity because the sun is under the horizon for just 3 hours at day at 63°N at this time of year. However, surveys were performed on days with unusually warm weather, adding further uncertainty.

These values are clearly specific to the particular year, month and time of day in which we performed the surveys. Other studies have explored the role of season and time of day in honeydew harvesting (e.g., Horstmann 1972, 1974, Skinner 1980), although not across habitat types. Despite this limitation, these values are a good estimate of the changes in honeydew use during succession in managed forests. The amount of honeydew harvested in the different stand types is a strong reflection of activity levels, and the low amounts of honeydew harvested from middle-aged stands indicate low ant activity relative to clear-cut and old stands. Our results also illustrate the importance, in terms of the sheer volume, of *F. aquilonia* honeydew collection in this system.

Aphid surveys

Combined abundances of the mutualist aphids *Cinara piceae* and *C. piceicola* differed significantly between stand types ($F_{2,16} = 22.1$, $p < 0.001$). Post-hoc Tukey's tests showed that clear-cuts (mean ± SE: 275.0 ± 95.1) contained more aphids per upper canopy branch than middle-aged (20.2 ± 6.8) or old (5.5 ± 2.8) stands. It is unclear how this translates to total aphid or honeydew availability at the level of the tree or stand.

Discussion

Our calculations are the first to show differ-

Table 2. Estimated (mean ± SE) rates of honeydew harvesting by ants during the surveys in stands of different ages.

Stand age	Rate of honeydew harvesting (g ha^{-1} hr^{-1})
Clear-cut (1–4 yrs)	315.3 ± 65.2
Middle-aged (30–40 yrs)	195.9 ± 18.9
Old (80–100 yrs)	409.9 ± 31.7

ences in ant harvesting of plant-derived sugar across a managed forest succession and are an important step toward a better understanding of the relationship between forest management and ant-regulated energy flows. We showed that honeydew harvesting is much lower in middle-aged than old stands, reflecting patterns for ant activity and mound density. Despite suggestions that honeydew limitation is responsible for the decline of wood ants after clear-cutting (Rosengren & Pamilo 1978, Punttila *et al*. 1991, Domisch *et al*. 2005a), our results indicate that ants harvest similar quantities of honeydew in clear-cuts and old stands. High densities of saplings with high aphid loads, combined with increased tree retention on clear-cuts, may thus prevent the collapse of *F. aquilonia* populations immediately after clear-cutting.

Density of ant mounds

Mound densities in this study were similar to densities found in earlier studies in European boreal forests (Rosengren *et al*. 1979, Domisch *et al*. 2005b, Kilpeläinen *et al*. 2005). Contrary to predictions, recently clear-cut stands supported numbers and sizes of *F. aquilonia* mounds comparable to old stands, although the mounds appeared less active. This was similar to patterns found by Domisch *et al*. (2005b) in stands where Norway spruce was replaced with Scots pine. In this region, open forests are more suitable for mound-building ants than those created by forestry practices (Kilpeläinen *et al*. 2005). Hence, mid-successional stands may be less favourable to ants because they are densely planted and have not yet been thinned.

Die-offs in formerly healthy mounds after clear-cutting have previously been attributed to changes in microclimate, the loss of orientation cues for foraging (Rosengren 1977, Rosengren & Pamilo 1978), the loss of honeydew-producing aphids (Rosengren & Pamilo 1978, Punttila *et al*. 1991) and increased inter-colonial aggression (Sorvari & Hakkarainen 2004). However, recent conservation-oriented improvements in harvesting in Scandinavia have included the preservation of older living trees in clear-cut forests. Such trees presumably support aphid colonies, so these changes may have resulted in better outcomes for the ant fauna in the years following clear-cutting (Domisch *et al*. 2005b).

The failure of *F. aquilonia* to thrive in middle-aged stands is unlikely to be due to competition with other mound-building species. These stands supported fewer and smaller mound nests as compared with older stands. If resource limitation drives *F. aquilonia* abundance in middle-aged stands, the limitation is unlikely to be a result of competition alone. Gibb and Hochuli (2004) observed a similar failure of the ant assemblage to increase in abundance after removal of a dominant mound-building species.

Ant use of trees

Despite complex interactions in the predictive model, there were clear patterns in ant activity on trees. Middle-aged stands supported the lowest ant activity for most tree species. This directly reflects the patterns for ant mound density discussed above. The higher ant activity on spruce seedlings in clear-cuts relative to seedlings in old stands reflects the greater aphid abundances on these plants. In clear-cuts, aphids reached per-branch abundances approximately 14 and 50 times that in middle-aged and old stands, respectively. Young plants receiving direct sunlight have higher photosynthetic rates (Lof *et al*. 2007). They thus provide a more favourable food source for aphids feeding on new growth. However, substantially larger total amounts of honeydew are produced from 70–80-year-old trees than from 10–15 year old trees (Zwölfer 1952, Zoebelein 1954, Eckloff 1972, Stadler *et al*. 1998). At the whole-tree level, younger trees are thus less productive, but at the stand level, clear-cuts have a greater density of growing trees than older stands. These competing influences may explain why differences in ant activity between clear-cut and old stands are less distinct than those predicted on the basis of tree size alone.

Honeydew harvesting

Despite considerable differences in the size and age of trees, the mass of honeydew collected by individual *F. aquilonia* workers did not differ among stand types. Workers of *F. aquilonia* are thus equally efficient harvesters of honeydew across stand types with varying quantities of available resources. This finding should be considered in the context of optimal foraging theory (MacArthur & Pianka 1966), which is thought to operate at the unit of selection. For ants and other social insects, the unit of selection is the colony, rather than the individual (Hölldobler & Wilson 1990). Colonies in this study may have optimally adjusted for the availability of resources by sending out a subset of foragers when insufficient resources are available, rather than by sending out many foragers to collect sub-optimal loads. Colonies that have survived clear-cutting may thus initially contain more inactive workers due to reductions in food availability. Eventually this may lead to a decrease in colony size through a reduction in resource input.

Although no differences in the quantity of honeydew were detected, it is possible that there are differences in the quality. Honeydew quality and composition depend on both the species of hemipteran and host plant and can even be altered by ant-attendance (Davidson 1997, Fischer & Shingleton 2001, Blüthgen & Fiedler 2004, Fischer *et al.* 2005). It is thus unclear whether the similar masses of honeydew collected in different stand types and on different tree species provide similar nutritional benefits to ants.

Estimation of honeydew harvest and effect of stand age

Ants harvested 77% of the honeydew mass in clear-cuts that they harvest in old stands, contrary to suggestions that honeydew limitation is responsible for the decline of wood ants after clear-cutting (Rosengren & Pamilo 1978, Punttila *et al.* 1991, Domisch *et al.* 2005a). This is likely to be a result of the high abundance of seedlings with high aphid loads in clear-cuts. Most surveys of trees in managed forests ignore seedlings of this size as a food source, but our findings suggest they play a significant role in the extended survival of wood ant colonies. Adherence of forest companies to forest certification requirements that living trees are left standing in clear-cuts also means that more honeydew resources are available to ants in these stands than in the past (Domisch *et al.* 2005).

Our estimate of 196–410 kg ha^{-1} dry mass of honeydew harvested in July is comparable to that of previous studies. *Formica rufa* group nests have previously been estimated to harvest between 10 and 500 kg dry weight annually in old stands (Økland 1930, Wellenstein 1952, Zoebelien 1956, Horstmann 1974, Skinner 1980), with densities usually one to three nests per hectare (Domisch *et al.* 2005). Cinarid aphids can produce 64–112 kg ha^{-1} yr^{-1} dry mass from 70–80 year old trees (Zwölfer 1952, Zoebelein 1954, Eckloff 1972; dry mass calculated using Auclair 1963). Ants may thus remove a large percentage of available honeydew and therefore significantly reduce the through-fall of sugars to the ground. They may also significantly increase the cost of aphid herbivory to plants (Cebrian 2004, Kilpeläinen *et al.* 2009). Broad consequences for ecosystems may thus result from changes in ant harvesting of honeydew and this study is an important first step toward a better understanding of how forest management affects ant-regulated energy flows.

Conclusions

Changes in harvesting of honeydew by ants were clearly associated with the anthropogenic disturbance of forestry, but it is likely that this was primarily through changes in nest densities, rather than in the allocation of activity or in honeydew loads. It is currently unclear whether changes in total honeydew loads are a cause or consequence of differences in ant abundances. Changes in the abundance and activity of *F. aquilonia* and other ants due to forestry will have consequences for ecosystem functions performed by ants beyond those related to ant–aphid mutualisms. Our study did not measure total honeydew availability, but other organisms besides host trees (e.g., microbes: Stadler & Müller 1996, Michelsen *et al.* 1999) are also known to use this energy source and are thus likely to be affected by ant harvesting of honeydew. The broader consequences of anthropogenically driven changes in honeydew harvesting by ants thus emerge as key targets for future research.

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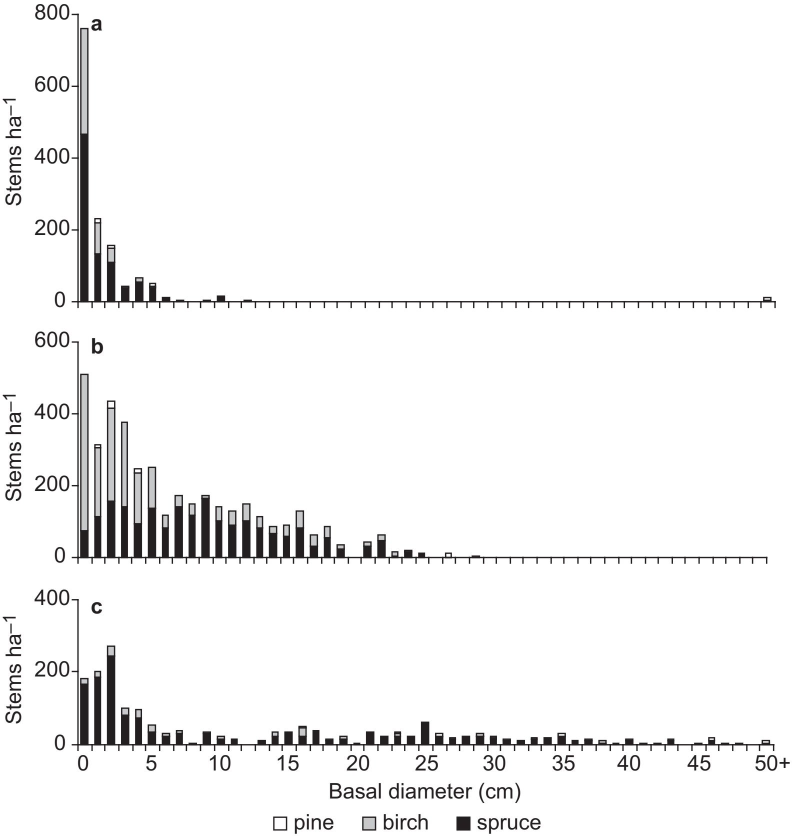

Appendix 1. Frequency histogram of mean stems per ha by stem basal diameter for managed spruce-dominated forests aged (**a**) 1–4 yrs, (**b**) 30–40 yrs and (**c**) 80–100 yrs in northern Sweden. Stand composition and tree density was assessed in June 2007 using transects of 50 m in length and 5 m in width (0.25 ha) in the six sites used for ant activity surveys and in an additional 2 sites in each age class (a total of 8 sites in each age class). Transects headed south from a *F. aquilonia* nest, which was situated at the centre of the study site. Birch, pine and spruce seedlings, seedlings and trees with basal diameter ≥ 1 cm were recorded.

Appendix 2. Standard Wald Estimates for the best model of *F. aquilonia* descending birch, pine and spruce trees per minute.

Parameter	Stand age	Tree species	df	Estimate	Error
Intercept			1	0.6324	0.2746
Stand age × Tree species	1–4 yr	birch	1	–0.3581	0.3742
		pine	1	–2.3454	0.6047
		spruce	1	–0.9619	0.3596
	30–40 yr	birch	1	–3.037	0.7596
		pine	1	–2.2142	0.8327
		spruce	1	–1.027	0.4339
	80–100 yr	birch	1	–0.9905	0.5887
		pine	1	0.1061	0.7991
		spruce	0	0	0
Distance × Basal diameter			1	–0.0004	0.0003
Basal diameter × Stand age × Tree species	1–4 yr	birch	1	–0.0237	0.0551
		pine	1	0.0824	0.0321
		spruce	1	0.336	0.0767
	30–40 yr	birch	1	0.0826	0.0563
		pine	1	0.0863	0.0443
		spruce	1	0.0128	0.0296
	80–100 yr	birch	1	0.101	0.0272
		pine	1	0.0208	0.0236
		spruce	1	0.0396	0.014
Dispersion			1	1.8588	0.1843