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på utbredning och prestationsförmåga hos dominanta myror (*Formica spp.*)

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Abstract

Disturbance regimes caused by fire and wind storms used to be common features in the Swedish boreal forests. However, due to an intense forest management, these events have declined rapidly. Little is known about how natural disturbances affect mound-building ants, even though they are important for ecological processes in their role as ecosystem engineers. Effects on ant communities could thus result in further effects on many other species. Wood ants (*Formica spp.*), a sub-group to mound-building ants, have due to their aggressive behavior and large distribution become the dominant ant species in Swedish forests. The aim of this study was to investigate how restoration of natural disturbances affects the distribution and performance of mound-building ants. Field inventories were conducted during June 2015 in stands subjected to burning and gap creation, with untreated stands used as references. Differences in nest density, ant activity and harvesting of honeydew were measured in the different stand types. My results showed a direct negative affect of fire on nest volume, whilst no effect was found as a result of gap creation. Furthermore, no differences in ant activity among stand types were found, nor did the harvesting rate of honeydew differ. Due to the cold weather for the season, ant activity was in general low, hence resulting in a low honeydew load. My results suggest that ant performance is not affected by the restoration treatments in the short term, but the lack of differences between burned and reference stands might be a result of an adjustment to available resources of the ants. Additionally, the reduced nest volume within burned stands can have further effects on other species interacting with ants. The whole picture of overall effects require a long-term study, and I suggest continued monitoring of *Formica spp.* ant communities over time.

Sammanfattning

Störningsregimer orsakade av bränder och stormar har varit vanligt förekommande i de svenska boreala skogarna, men på grund av det intensiva skogsbruket har dessa störningar minskat kraftigt. Trots stackmyrornas betydelse för ekologiska processer genom sin roll som "ecosystem engineers", finns det väldigt lite kunskap om hur myrorna påverkas av naturliga störningar. Effekter på myrsamhällen kan därför resultera i ytterligare effekter på många andra arter. Skogsmyror (*Formica spp.*), en undergrupp till stackmyror, har genom sitt aggressiva beteende och stora utbredning blivit den dominanta myrgruppen i svenska skogar. Syftet med studien var att undersöka hur restaureringen av naturliga störningar påverkar utbredning och prestationsförmåga hos stackmyror. Fältmätningar genomfördes under juni 2015 i brända och luckhuggna bestånd, med obehandlade bestånd som referensytor. Skillnader i stackdensitet, myraktivitet och insamlandet av honungsdagg mättes i de olika bestånden. Mitt resultat visade en direkt negativ påverkan av brand på stackvolym, medan luckhuggna bestånd inte visade på några skillnader. Vidare hittades inga skillnader i myraktivitet bland bestånden, eller i insamlandet av honungsdagg. Myraktiviteten var generellt låg på grund av det kalla vädret för säsongen, vilket resulterade i en låg mängd insamlad honungsdagg. Mitt resultat tyder på att det inte fanns någon kortsiktig effekt på myrornas prestationsförmåga från restaureringarna, men avsaknaden av skillnader i bränningarna kan tyda på att myrorna anpassat sig till tillgänglig föda. Ytterligare kan den minskade stackvolymen inom de brända ytorna ge vidare effekter på andra arter som integrerar med myror. Helhetsbilden av möjliga effekter från restaureringar kräver en långtidsstudie, och jag föreslår att fortsätta studera myrsamhällen av *Formica spp.* över tid.

Introduction

The boreal forest is one of the largest biomes in the world, accounting for about one-third of the world's forests (Lakehead University, 2014). This region covers large parts of the northern hemisphere, and stretches across Canada, Alaska, Russia and Scandinavia. Within the boreal zone, fire has been recognized as an important disturbance regime (Esseen et al., 1997). Natural burns usually result in large scale impacts, and a single forest fire can cover thousands of hectares (Bergeron et al., 2002). Gap formation is also important in the boreal zone (Kuuluvainen and Aakala, 2011), determining regeneration and stand structure at the local scale (Esseen et al., 1997). Sweden, as a part of Scandinavia, hold the boreal coniferous forest as dominant biome. This forest is an important habitat for many species (Ahti et al., 1968), as well as a resource for timber and renewable products. The forest industry has during the last 150 years developed into one of the most advanced and intensive management system in the world (Linder and Östlund, 1998). Pronounced effects on ecosystem processes have been recognized as a result. For example natural disturbances, which used to be common features in the forests, have declined rapidly due to the forest management (Angelstam et al., 2004).

The traditional view of disturbances as an uncommon, irregular event which cause structural changes in communities at their natural, static condition has been questioned and redefined (Sousa, 1984). Instead of being a single extreme interference, natural disturbances are considered a part of an ongoing interruption in nature which affects organisms. At one hand it causes damage to communities including death and displacement of individuals, but at the other hand disturbances creates opportunities for new colonies or individuals to establish. Angelstam (1998) identifies three main disturbance regimes in Swedish boreal forests: i) gap-phase dynamics in spruce forest; ii) successional development after large-scale disturbances; and iii) multi-cohort *Pinus sylvestris* dynamics. Differences in frequency and intensity of disturbance regimes creates heterogeneity, including patches of different size and distribution, within the forest structure (Bouget and Duelli, 2004). This gives rise to a variation of dead wood resources in benefit for species diversity. However, the Swedish management has resulted in a decline of dead wood within the forest, and many species are endangered as a result of the created homogenous forest structure (Linder and Östlund, 1998, Gärdenfors et al., 2015).

Disturbances function as a condition for selection of species and enable sustainability for species depending on disturbance regimes in order to survive. Conservation models and management plans have developed as a response to the negative effects on biodiversity followed by intense forest management (Bergeron et al., 2002). Consequently, knowledge about ecological processes is required since it can provide information about species' interaction (Angelstam, 1998, Ryan, 2002). Furthermore, the demand from society for a sustainable forest management has increased, as well as the request for recreation of natural habitats (Esseen et al., 1997). Suggestions for conservation management often includes imitation of wild fire or creation of dead wood in the forest (Esseen et al., 1997, Bergeron et al., 2002). The interaction between target species and other species is an important aspect to consider during recreation of disturbance regimes, since a recreation of natural events in the forest affects species differently. Ants for example, are an important taxonomic group with great impact on several organisms in their role as ecosystem engineers (Hölldobler and Wilson, 1990), and restoration effects on ants might impact several other species (Aho et al., 1999, Flatt and Weisser, 2000, Hawes et al., 2002).

Ants as ecosystem engineers

The concept of "ecosystem engineers" was first brought up by Jones et al. (1994). They define ecosystem engineers as organisms which directly or indirectly modify the availability of resources to other species besides themselves. The idea behind the concept is to give a definition to organisms which can modulate, maintain or create new habitats by changing the physical state of materials (biotic or abiotic), and consequently have an important impact on ecosystem processes. The concept is widely discussed and has been accused to be trivialized and misleading (Reichman and Seabloom, 2002). Nevertheless, what Jones et al. (1994) stated has grown into a major research initiative which today has an essential role for conservation and restoration management, and has also been recognized as a new way of trying to explain the complexity of ecological systems (Brown, 1995, Wright and Jones, 2006).

Jones et al. (1994) divide ecosystem engineers into different groups depending on how they affect the environment. The family of ants (*Formicidae*) is categorized under a group called *Allogenic engineers,* which includes organisms who can change the environment by transferring living or non-living materials into a new and different physical state. As ecosystem engineers, ants can change water, nutrients, and energy flow through terrestrial ecosystem (Folgarait, 1998), as well as the local structure and composition of the soil by the redistribution of soil particles and the construction of nests (Jones et al., 1994). Additionally, ants alter above nests vegetation and improve the local diversity of microsite, thus affecting ecosystems at different habitat levels. Not only are ants known for their function as ecosystem engineers, but also as providers of ecosystem services (Del Toro et al., 2012). Several services have been noticed to be supplied or mediated by ants, for example animal community regulation, biological control, and biological indicators. Wood ants of the *Formica rufa*-group have for example been recognized as forest protectors, as they have been seen to control forest pests in European countries (Hölldobler and Wilson, 1990). It is clear that ants are important in ecosystem processes and have a distinctive impact on other organisms, yet there is a lack of information about how ants are affected by strucural changes in their habitat and how that in turn effects other organisms. The need for further research about ant communities and their role as ecosystem engineers has been stressed, and ants have also been suggested to be in the focus of research initiatives consernig conservation efforts (Stadler and Dixon, 2005, Del Toro et al., 2012).

Ecology of mound-building ants

Around 10 000 species of ants have been identified around the world, but the true number could be twice as much (Douwes et al., 2012). Still, only 81 species are found within the Nordic countries, while the majority of species exists in the tropics. The boreal forests of Sweden are dominated by wood ants (the *F. rufa*-group), which is a sub-group to the mound-building ants within the genus *Formica* (Douwes et al., 2012). Wood ants consists of four species (*F. aquilonia, F. lugubris, F. polyctena,* and *F. rufa*), where the most prevalent species is *F. aquilonia* (Hölldobler and Wilson, 1990). The dominant behavior of wood ants is mainly due to their ability to create absolute territories, a definition used for ants which very aggressively defend their established territory. The reason for combining wood ants into their own sub-group is the similarity in their behavior and appearance, which makes it hard to separate the species from one another (Douwes et al., 2012). The mounds, which are the nests, are similar between the species. They are all made out of organic material such as needles, small twigs, and smaller parts of bark, but can have a

pronounced differences in size (Douwes et al., 2012). The shape of the mounds are either cone or dome like. When the mounds are exposed to the sun their shape can be more flat.

The structure and dynamics of boreal forests is a key factor for the distribution and density of mound-building ant species (Punttila, 1996), where productivity, food availability, light conditions and climate becomes important regulating factors (Kilpeläinen et al., 2005). The colonization patterns of ants are usually determined by the territorial species, who are the top competitors (Punttila, 1996, Hölldobler and Wilson, 1990). Young forests with open tree canopy are often colonized by *F. exsecta, F. sanguinea, F. truncorum* and sometimes also *F. lugubris*. However, as soon as the canopy cover becomes too dense it becomes harder for these species to survive. *F. aquilonia* also colonizes during early successional stages when the tree canopy is still open, but in comparison with earlier mentioned species, *F. quilonia* continues to maintain stable populations during more dense conditions (Punttila, 1996). This characteristic of *F. aquilonia* is one explanation to their commonly occurring status in boreal forests, especially in moist and shaded spruce-dominated forests.

Ant-aphid interaction

Wood ants depend on aphids to get a sufficient amount of carbohydrates required for their high activity level (Cook and Davidson, 2006, Stadler and Dixon, 2005). In addition, a mutualistic interaction between aphids and ants is recognized for a few number of ant taxa, e.g. the subfamily of *Formicinae* (Stadler and Dixon, 2005). In order to keep a high growth rate, aphids consume big amounts of phloem sap from plants. The phloem sap is processed through the aphids and excreted as a liquid commonly known as honeydew (McIver and Yandell, 1998). This is an important energy source for ants, who harvest honeydew directly from the aphids. The foraging activity is regulated by physical factors such as temperature and water stress (Traniello, 1989, Skinner, 1980). The activity generally starts at 6 °C, and then increase as the temperature rises (Domisch et al., 2009). However, the activity does normally not continue to increase at temperatures above 25°C.

The harvesting of honeydew is an organized and well-structured system, where the amount of harvested honeydew gives an indication of potential energy that can be used within an ecosystem driven by ant communities (Gibb and Johansson, 2010). However, it is important to consider the benefits and costs of the interaction between ants and aphids, since it requires behavioral and morphological adaptions by the ants (Stadler and Dixon, 2005). The biggest cost for ants is suggested to be the dependency of aphids, and the main food resource for wood ants is honeydew from aphid colonies in trees (Hölldobler and Wilson, 1990). Ants walk from the nest to the aphids, a distance which varies depending on the condition of the aphid colony. When a tree supports a substantial colony of aphids, ants can travel distances of up to 50 meters from the nest to harvest honeydew (Rosengren, 1977, Wright et al., 2000, Sorvari and Hakkarainen, 2009).

On the other hand, the social behavior of aphids, resulting in energy rich sources located in concentrated spots, is a big advantage for ants (Stadler and Dixon, 2005). Ants actively tend to aphids, and have been known to keep aphids as cattle. In this mutualistic relationship, aphids have the advantage of being protected by the ants against natural enemies, in return rewarding the ants by producing more honeydew. It is discussed whether this interaction is controlled by a top-down effect from the ants protecting the aphids, or a bottom-up effect depending on the quality of the honeydew as a result from the quality of the host plant (Stadler and Dixon, 2005). Though, spatial variability within habitat has a

significant impact on the abundancy and distribution of both ants and aphids (Gotelli and Ellison, 2002, Morris, 1992), and consequently addresses the importance of stand characteristic and habitat quality when determining the viability and activity of ant communities. Mound-building ants are more sensitive to disturbances due to the fact that they build their nests on the soil surface (Jurgensen et al., 2008). Especially fire can cause huge damage since the nests are easily burned down (Bradley, 1972). However, fire will probably not kill an entire colony of ants as nests contain galleries deep down under ground where ants can escape the fire (Jurgensen et al., 2008). Probable long term effects could nevertheless have negative impact on the remaining ant-tended aphid populations and site microclimate, which consequently affects ant activity and viability.

Objective

Few studies have investigated relationships between harvested quantity of honeydew and stand characteristics. Variations in stand characteristics and stand structure, which affect available food resources for ants, can potentially play an important role for the efficiency of ant workers, thus affecting the viability of the ant colony. Studies on ants are important since effects on ant communities can affect several species due to their interaction with ants. My study is one of the first to investigate effects from re-introduction of natural disturbances on the distribution and performance by dominant mound-building ants in boreal forests. In this study, I surveyed nest density and the harvesting of honeydew by mound-building ants to detect effects as a result of burning and gap creation. I asked the following questions:

1. How does burning and gap creation affect nest density of mound-building ants?
2. How does burning and gap creation affect ant activity?
3. Does burning and gap creation affect harvesting efficiency of honeydew by mound-building ants?

Both organic mound nests and trees will be affected by the fire (Bradley, 1972, Angelstam, 2004), and I therefore predicted a direct negative impact on nest density and performance by the ants due to the introduction of fire. Since it is suggested that increased patchiness in forest structure will favor ants (Kilpeläinen, 2005), I predicted a positive response to gap creation. This is more likely to be seen as an increased ant performance, rather than a change within the distribution of nests.

Method

Study site

I surveyed ant-nest density and honeydew collection during June 2015 in 28 forest stands in northern Sweden. All stands belonged to the Swedish forest company Holmen AB. The stands are all voluntary set-asides included as a part of Holmen AB:s FSC certification (FSC Sweden, 2010). Furthermore, all stands are included in a restoration project with the goal to reconstruct natural stand characteristics based on natural disturbances. In this case small scale gap dynamics and fire regimes in boreal forests. The project is a large-scale field experiment in association with Holmen and the Forest Biocore research group at the department of Wildlife, Fish and Environmental Studies at SLU, Umeå, Sweden. Gap creation was conducted in 2011, and burning was conducted between 2011 and 2014.

The study area was located between the latitudes of 63.4°N and 65.2°N and longitudes of 17.5°E and 20.2°E (Figure 1). The 28 set-asides included 8 stands subjected to prescribed burning, 10 stands subjected to gap creation, and 10 stands served as untreated reference areas. Stand characteristics - such as age, size, tree volume, productivity and tree species composition - were set to be as similar as possibly among the different stand types. Tree species composition was mainly a mixture of the dominant species Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies.*), but also included a smaller variation of broad leave species such as Birch (*Betula pubescence* and *Betula pendula*), Aspen (*Populus tremula*) and Rowan (*Sorbus aucuparia*). The sizes of the stands varied from 3.6 ha up to 21 ha, and stand ages varied from 79 years old up to 160 years old. In order to minimize spatial autocorrelation among stand types, stands were separated with at least 500 m and spatially interspersed. The survey was conducted from June 2nd to 18th, between 8:00 and 18:00 for all stands, and the temperature ranged from 8 degrees to 17 degrees during the whole survey period. The weather condition was mostly overcast, with some sunny days and a few days with a little rain.
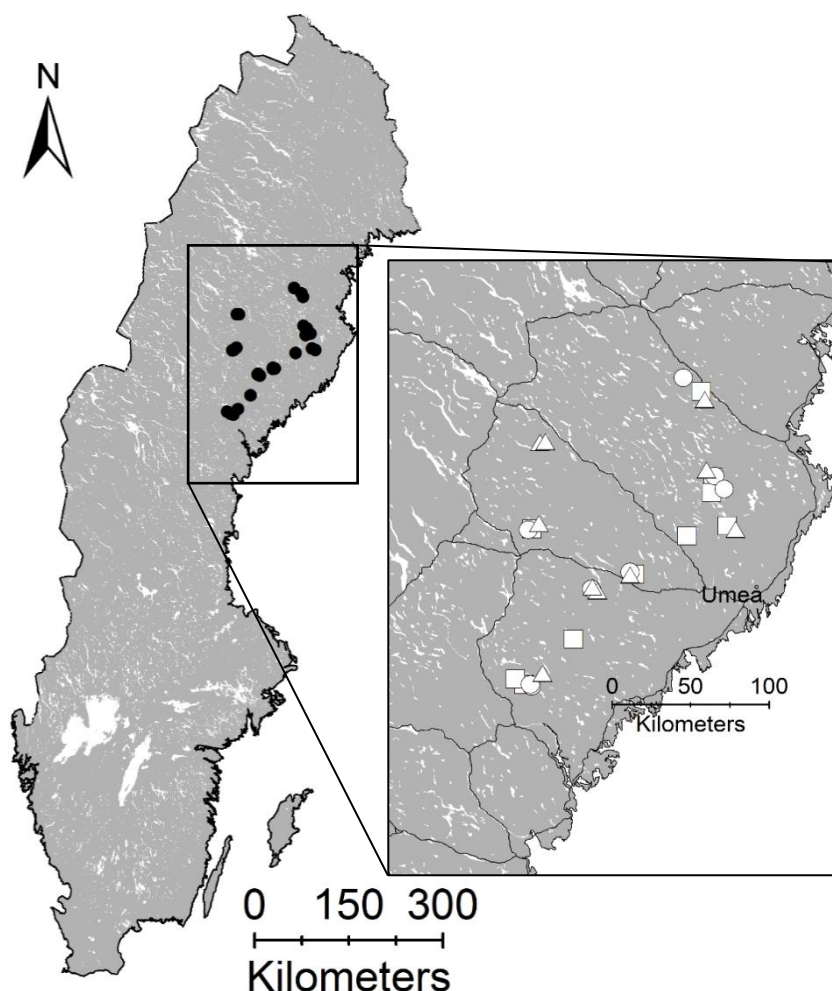
Figure 1. Position of inventoried stands: circle = burned stands (n=8), triangle = gap cut stands (n=10), and square = reference stands (n=10). The main picture shows their locations in relation to the whole country of Sweden, while the enlarged picture shows the distribution of the different stand types. © Lantmäteriet i2014/764.

Nest density

I made inventories of nests to examine if the density of nests differed among stand types, i.e. among burned, gap cut and reference stands. I started by identifying permanent transects stablished in 2010 by GPS data. The total transect length for each stand was 400 m. By walking along the transect, I counted and measured ant nests within 10 meters from the transect, resulting in a total surveyed area of 0.8 ha in each stand. I included both active and non-active nests (abandoned nests) in my study, where I took a sample of minimum 5 large workers from each active nest. Furthermore, I measured height and diameter for all nests. Ants were identified to species in the laboratory, where I used the key of Douwes (1995).

Ant activity on trees

I performed the measurement of ant activity on the trees to examine differences in ant activity among stand types. Activity was measured along transects originating from one central nest in each stand. I used the nest as a starting point, and walked 50 meters north and then later repeated the procedure by walking 50 meters south. For every 10 meters, I chose the tree closest to the transect, with the exception of the first tree, found 1 meter from the nest. If I did not find any tree within 5 meter from the transect, I marked the point as without a tree, and no activity was measured. Since I did not survey differences in ant activity among different tree species, I chose trees along the transect without preference for tree species. On each tree, I counted the number of ants ascending and descending the trunk of a tree per minute. Activity was measured on a line approximately 20 cm above the base of the tree trunk. In total, ant activity was measured in 63% of the burned stands, 100% of the gap cut stands and 80% of the reference stands. A total number of 230 trees were surveyed and circumference in breast height was measured for all chosen trees.

Honeydew harvesting

I surveyed honeydew harvesting to examine differences in harvested amounts of honeydew among stand types. Furthermore, I performed measurements in order to detect eventual relation with distance from nest or circumference in breast height with honeydew harvesting efficiency. The same nest used for survey ant activity was used within each stand for survey honeydew harvesting. I selected 10 trees within each stand between 0 and 30 meters from the nest without any preference for tree species, and collected 5 ascending ants and 5 descending ants from each tree. I identified tree species for each tree, measured the distance from the nest and the circumference in breast height on the trunk. The ants were collected by hand due to generally low activity of the ants as a result from cold weather. Had it been warmer conditions, and therefore a higher activity, I would have used modified battery-driven vacuum cleaners in order to minimize weight loss. It was not possible to collect 10 ants from 10 trees in all stands due to the low activity, and some stands lacked available trees. This was often the case in burned stands.

I surveyed honeydew at 63% of the burned stands, 100% of gap cut stands and 80% of reference stands. The survey resulted in a sample size of 485 ants from burned stands, 940 ants from stands subjected to gap creation, and 731 ants from reference stands, which gave a total number of 2156 collected ants. After collection, I stored the ants in a cool box to minimize weight loss during transport. To ensure that ants were dead before laboratory measurements they were stored in a freezer for at least 48 hours. I measured harvested

honeydew by comparing the weight of ascending and descending ants, where weight was measured after small items, such as needles or bark, had been removed from the ants. Width of the head, length of the gaster, and total length were then measured in order to examine any relation between weight and size of the ants. I used the key of Douwes (1995) for identification of ant species.

Statistical analyses and calculations

To test if nest density differed among burned, gap cut and reference stands, I used an ANOVA procedure in the statistical computer software JMP pro 11 (hereafter 'JMP') (SAS Institute, 2013). I analyzed nest density in terms of volume per hectare. Nest volume was calculated by using the formula for a cone according to equation 1.

$$Equation\ 1. \qquad\qquad V = \frac{\pi h^2}{3}(3r - h)$$

h = height of mound
r = radius of mound

Since the distribution of nest volume did not meet the assumption of parametrical tests, I used a Wilcoxon/Kruskal-Wallis test (rank sums test). When there was a significant difference between the tested groups, I used a non-parametric comparison with pair-wise Wilcoxon test in order to determine which groups were significantly different from each other. I performed the same test in order to analyze number of nests per hectare.

I used JMP (SAS Institute, 2013) to test for differences in ant activity on trees among stand types. In an earlier study on ant activity of *F. aquilonia* (Gibb and Johansson, 2010), tree species, basal diameter and distance from nest was shown to be important factors determining ant activity. Although the stands included in the study were selected to be as similar as possible, I tested for differences in tree species composition between the sampled trees in this study. For this analysis I used a Chi-Square test for two-way table since I had categorical data for both "stand type" and "tree species". Furthermore, I used a generalized linear model (hereafter 'GLM') with normal distribution to test for differences in temperature among stand types during the survey period. Total ant activity (both ascending and descending ants) among stand types were the response variable in my analysis, testing the effect of forest restoration. Circumference of tree in breast height and distance from nest were included as covariates. The distribution of ant activity did not meet the assumption of parametrical test since the data included excessive numbers of zeros. I used GLM's for the analysis of ant activity, and run the models with Poisson distribution (Sall et al., 2005). Furthermore, due to the excessive numbers of zeros, I tested my data for over-dispersion. When over-dispersion occurred, p-values were adjusted accordingly in the model (Schwarz, 2015). If I found a significant interaction between included covariates (circumference of tree and distance from nests) and ant activity, I made separate tests for each stand type as factor.

To evaluate harvesting efficiency of honeydew I used a one-way ANOVA model in JMP (SAS Institute, 2013), where I compared the weight of ascending and descending ants among stand types. I also analyzed the size of ants (width of the head, length of the gaster, and total length) in order to investigate the relation weight/size among stand types. I used student's t-test for comparing each pair. A GLM with normal distribution in JMP was used

to test the interaction of distance from nest and circumference in breast height against total body mass (both ascending and descending ants) among stand types. Identified species were *F. aquilonia* and *F. lugubris*, and I decided to analyze honeydew harvesting efficiency on *F. aquilonia* workers only. The reason for this was the absence of *F. lugubris* workers in burned stands (Table 2), and the rather low number of *F. lugubris* workers in the other stand types.

To estimate the amount of honeydew "gained" per treatment type, I estimated mass gain per ant, by first subtracting the mean weight of ascending ants from the mean weight of descending ants per tree achieving an estimation of honeydew gain per tree. Since there was 5 descending ants per tree, I divided achieved estimation of honeydew gain per tree with 5 to achieve mass gain per ant. I used the mass gain per ant to create an index of harvested honeydew rate (mg/min), with the formula:

$$Index = descending\ ants\ per\ minute \times mass\ gain\ per\ ant$$

Result

Nest density

Ant mounds were found in 63% of the stands subjected to burning, 100% of the stands subjected to gap creation and 90% of the control stands (Table 1). However, only 38% of the burned stands included active nests, whilst 90% and 80% of the gap cut and reference stands had active nests, respectively. Species identified from active nests were *F. aquilonia*, *F. lugubris*, and *F. uralensis* (Table 1).

Table 1. Proportion (%) of total number (active and non-active) nests, proportion (%) of active nests, and nest density for all nests (volume m^3/ha and no. of nests/ha) in stands subjected to burning (n=8), gap creation (n=10) and reference stands (n=10). Identified ant species (*F. aquilonia, F. lugubris, F. uralensis*) in each treatment type are presented in proportion (%) of stands including given species.

Treatment	Burning	Reference	Gap creation
Stands including nests	63%	90%	100%
Stands including active nests	38%	80%	90%
Species in active nests			
Formica aquilonia	100%	63%	78%
Formica lugubris	0%	25%	22%
Formica uralensis	0%	13%	0%
Total nest density			
Volume (m^3) per ha	0.40	0.99	1.48
Nests per ha	2.97	4.38	4.17

Total nest volume per ha (both active and non-active nests) differed significantly among stand types (Wilcoxon test: p<0.0001) (Table 1). Burned stands had the lowest nest volume (Wilcoxon test: p=0.038), while stand subjected to gap creation had the highest (Wilcoxon test: p=0.003). Volume of *F. aquiloina* nests was also lower in burned stands compared to both gap cut stands and reference stands (Wilcoxon test: p=0.0003) (Figure 2). However, I did not find any difference in nest volume of *F. aquilonia* between gap cut stands and reference stands. Other species than *F. aquilonia* were absent in burned stands (Table 1). Gap cut stands on the other hand, had a higher nest volume of other species compared to

reference stands (Wilcoxon test: p=0.032) (Figure 2). I did not find any clear difference in nest volume of non-active nests among stand types (Wilcoxon test: p=0.076), but the low p-value indicates a potential smaller volume of non-active nests in burned stands. Furthermore, I did not find any differences in number of nests among stand types (Wilcoxon test: p=0.42) (Table 1).
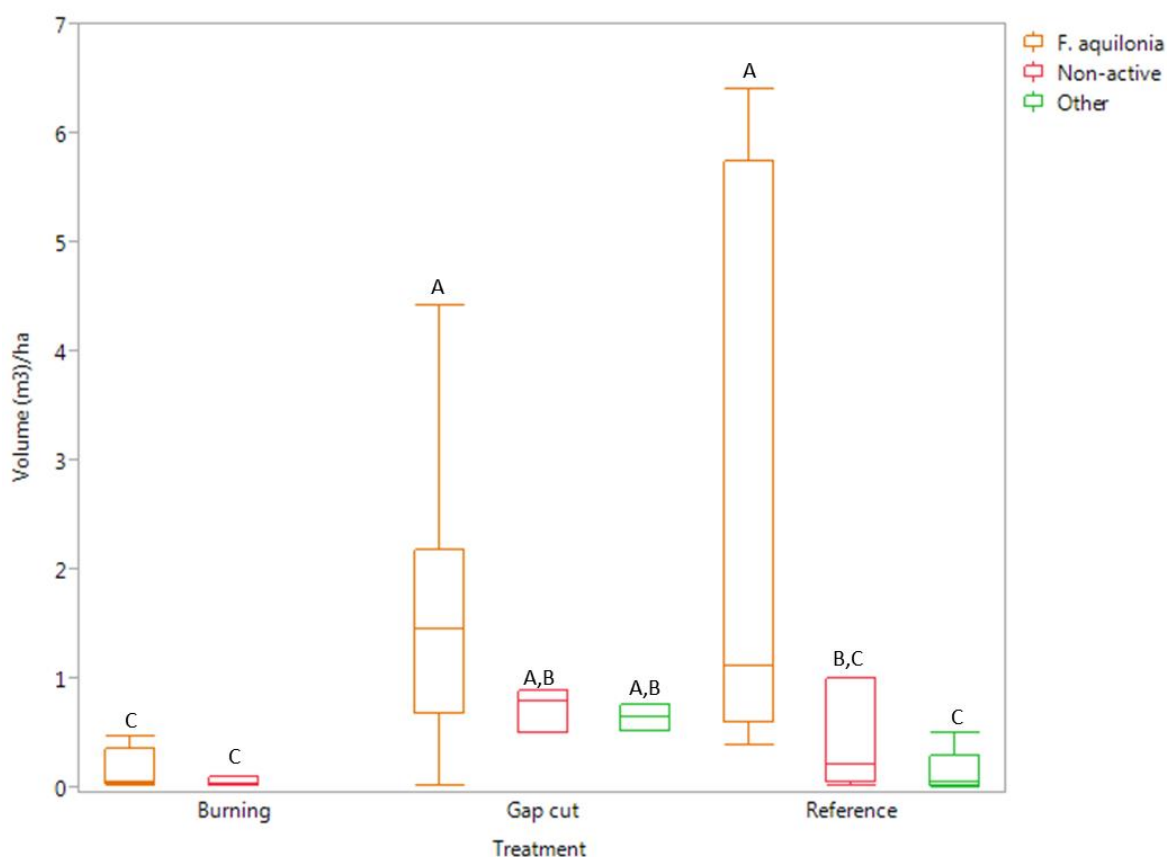


Figure 2. Volume of mound nests per ha of *F. aquilonia*, other mound-building species (*F. lugubris, F. uralensis*) and non-active nests in stands subjected to burning (n=8), gap creation (n=10) and reference stands (n=10). The box plots illustrate the median value inside the box, the 25th and 75th percentiles by the box, and the interquartile range by the whiskers. Boxplots not connected by the same letter are significantly different (Wilcoxon test: p<0.0001).
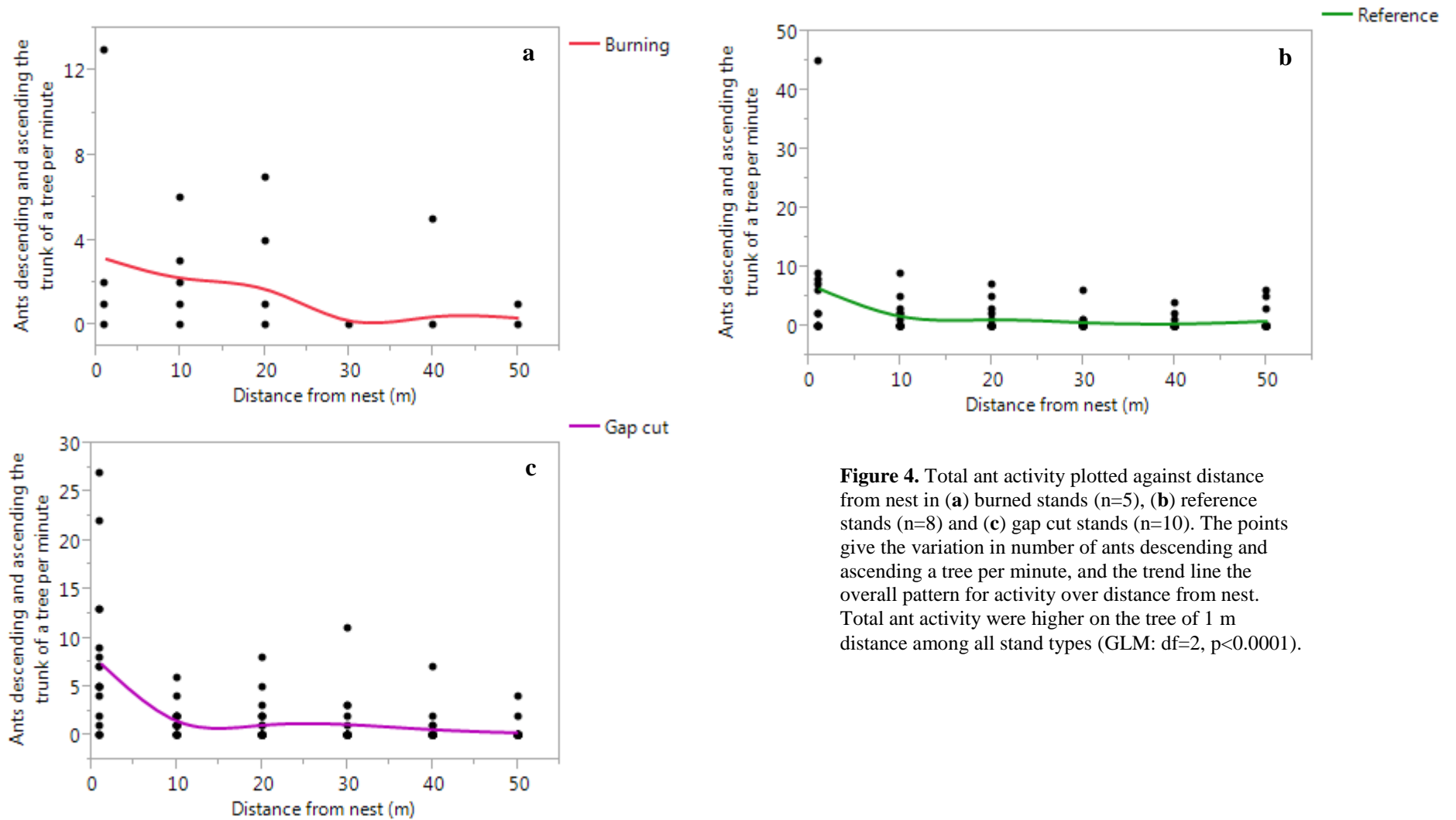
Ant activity on trees

In total, I observed ants on 38.3% of the 230 studied trees among all stands, and measured ant activity on 78 Scots pines (*Pinus sylvestris*), 115 Norway spruces (*Picea abies*) and 37 birches (*Betula spp.*). The total ant activity (descending and ascending ants) did not differ among stand types (GLM: df=2, p=0.633) (Figure 3), but the activity was significantly higher on trees with bigger circumference for all stand types (GLM: df=2, p<0.0001). I did not find any significant differences in circumference in breast height among stand types (GLM: df=2, p=0.210), but my result indicates that sampled trees in gap cut stands could be smaller (Figure 3). My analysis of sampled tree species and temperature was used to control for tree species composition and temperature during the survey period. Since I did

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not find any differences in tree species composition or temperature among stand types, I found that these factors were well controlled for.
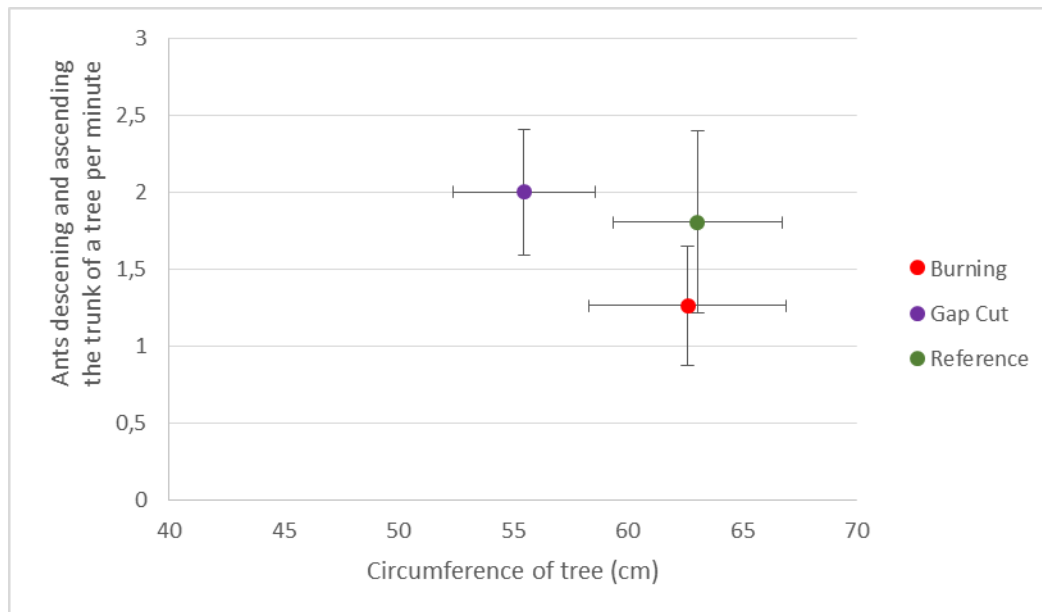
Figure 3. Total ant activity (mean ± SE) plotted against average circumference of the trunk in breast height (mean ± SE) for stands subjected to burning (n=5), gap creation (n=10) and reference stands (n=8). Total ant activity were higher on larger trees (GLM: df=2, p<0.0001). No differences in total ant activity and circumference of tree were found among stand types.

I found an interaction between total ant activity and distance from nest (GLM: df=2, p<0.0001). The activity was significantly higher on trees closest to the nests (1m) among all stand types, and decreased with distance from nest. Each stand type showed slightly different results (Figure 4). Stands subjected to gap creation and control stands followed the same pattern with high activity on the closest tree, followed by a rapid decrease in activity to the second tree, and a continuous decrease in activity further away from the nest. Burned stands had a more even activity level at the three closest distances, before decreasing further away from the nest.

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Figure 4. Total ant activity plotted against distance from nest in (**a**) burned stands (n=5), (**b**) reference stands (n=8) and (**c**) gap cut stands (n=10). The points give the variation in number of ants descending and ascending a tree per minute, and the trend line the overall pattern for activity over distance from nest. Total ant activity were higher on the tree of 1 m distance among all stand types (GLM: df=2, p<0.0001).

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Honeydew harvesting

I preformed ant collection for estimation of honeydew harvesting efficiency in 5 stands subjected to burning, 10 stands subjected to gap creation and 8 reference stands. Of the 2156 ants analyzed during this part of the study 1816 workers were *F. aquilonia* workers and 340 were *F. lugubris* workers (Table 2). *F. aquilonia* was the most common species for all stand types.
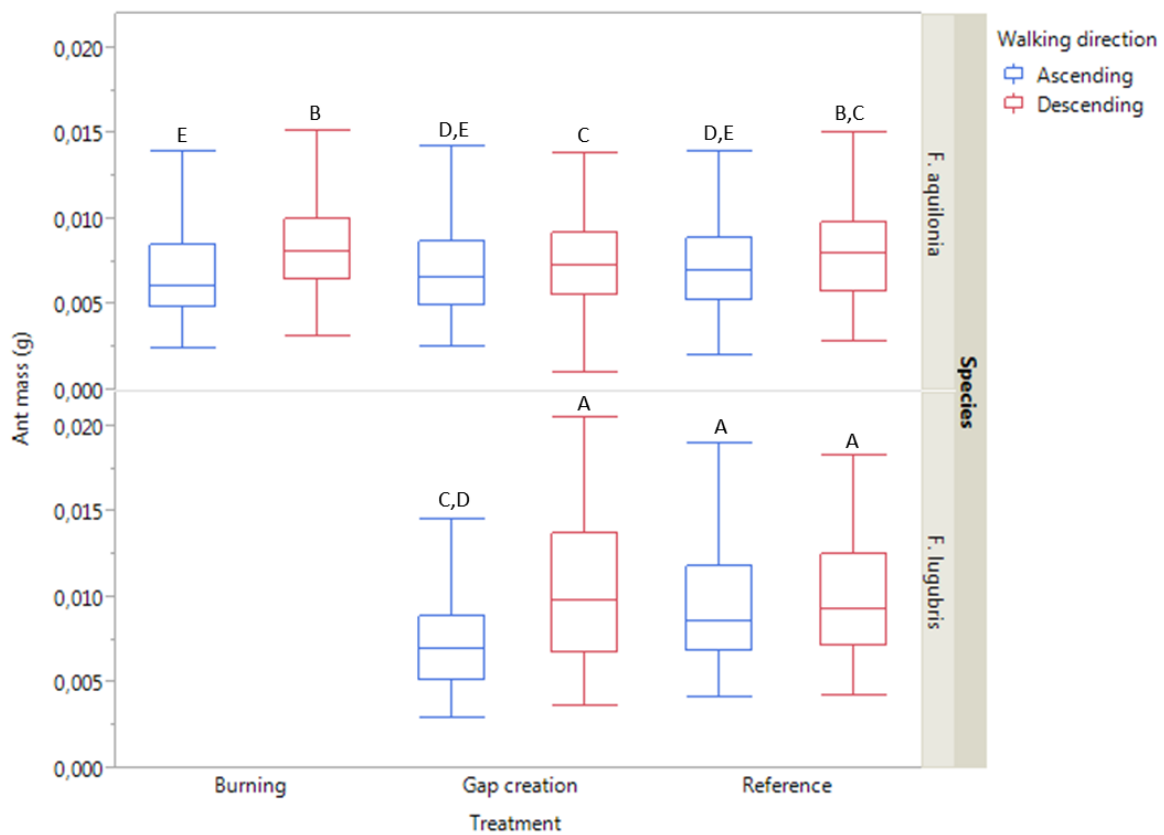
Table 2. Proportion (%) and number of *F. aquilonia* and *F. lugubris* workers in stands subjected to burning (n=5), gap creation (n=10) and reference stands (n=8).

Treatment Species	Burning	Reference	Gap Creation
F. aquilonia	100% (485)	77% (562)	82% (769)
F. lugubris	0% (0)	23% (169)	18% (171)

I found that distance from nest correlated with total body mass (both descending and ascending ants) pooled for both species, were ant weight increased with an increasing distance from nest (GLM: df=2, p<0.0001). The result showed the same pattern when I plotted descending and ascending ants separately. Though, circumference in breast height on trees did not interact with total body mass among stand types. Furthermore, I found that descending ants were heavier than ascending ants of *F. aquilonia* worker among stand types (ANOVA: F_2=3.48, p=0.033) (Figure 5). I also found that descending workers from burned stands were significantly heavier than descending workers from gap cut stands (ANOVA: F_2=5.83, p=0.0031). On the other hand, I could only find weight differences between ascending and descending *F. lugubris* workers in gap cut stands (Figure 5), and not between ascending and descending workers in reference stands. Further survey on weight in relation to body size (mass per length, mass per length of gaster and mass per head width) did not give a different result compared with using only body mass as a factor (data not presented).

The total body mass of descending workers (7.9 ± 0.001 mg) of F. aquilonia were around 14% more than of ascending workers (6.9 ± 0.001 mg). Following the formula: MassANT + MassLOAD / MassANT (Traniello, 1989) I got an average load capacity of 1.14. My index resulted in an average harvest rate per stand of 0.35 mg/min in burned stands, 0.24 mg/min in gap cut stands and 0.29 mg/min in reference stands. I did not find any differences between estimated harvest rate among stand types (Wilcoxon test: p=0.552).

Figure 5. Mass of descending and ascending workers of *F aquilonia* and *F. lugubris* in stands subjected to burning (n=5), gap creation (n=10) and reference stands (n=8). The box plots illustrate the median value inside the box, the 25th and 75th percentiles by the box, and the interquartile range by the whiskers. Boxplots not connected by the same letter are significantly different (ANOVA: F_9=22.19, p<0.0001). Letter A indicates groups with biggest mean weight, and letter E groups with smallest mean weight.

Discussion

Nest density

Number of nest per ha did not differ among stand types. My results (Table 1) are comparable with an earlier study on nest density, were the average number of nests was 4.25 mounds per ha (Punttila and Kilpelainen, 2009). The differences in nest density among stand types in this study is therefore a result of differences in nest volume, and not number of nests. Burned stands resulted in lowest nest volume (Table 1), which was according to my prediction on possible effects on mound nests caused by fire. This is a direct negative effect on nest volume, where the nests were burned down. Another direct negative effect is the low number of available live trees within burned stands (pers. obs.). The low number of live trees was caused by a high tree mortality following the fire. Further consequences, such as reduced condition of mound nests, could thus be expected since limitation of food resources is one important factor regulating mound density (Kilpeläinen et al., 2005). Another possible effect of fire could be reduced viability in the mound nests due to reduced vegetation cover after a fire (Angelstam, 1998). Clear-cuts have been seen to negatively affect the condition of ant mounds (Sorvari and Hakkarainen, 2009). In clear-cut areas, the temperature dropped low during nights, and the mound nests became very dry and hard due

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to dryer conditions on the clear-cuts. The reduced vegetation cover after a fire could possibly cause the same situation as after a clear-cutting, and thus have a negative impact on the condition and viability of the mound nests. I only measured height and diameter of the mounds, and noted if they were active or abandoned. For further studies, I would suggest to also include survey on condition of the nests and microhabitats to evaluate possible direct impact on the mound nests caused by fire.

Nest volume in stands subjected to gap creation and reference stands (Table 1) was similar to earlier findings in mature forests, were the volume was found to be around 1.2 m^3/ha (Domisch et al., 2005, Gibb and Johansson, 2010). Furthermore, total nest volume was higher in gap cut stands than in burned and reference stands. This is most likely not a result of the treatment itself, since the process of building large mounds takes between 10 and 20 years (Hölldobler, 1990). It is more likely that the result reflects previous conditions for nest volume in gap cut stands before the treatment was conducted. However, openness in the canopy cover is hypothesized to benefit monogynous species, such as *F. lugubris* (Punttila, 1996). Windstorms create open patches in the forest cover, and good conditions for ant communities with increased income of solar radiation (Punttila and Kilpeläinen, 2009). Monogynous species could thus be favored by gap creation in forest stands, and be able to remain within the stand during a longer period of time. Patterns for improved condition for mound-building ants due to increased patchiness in the forest cover have been seen in an earlier study (Punttila and Kilpeläinen, 2009). This support my hypothesis that gap creation could improve the condition for mound-building ants, even though it was too early to find effects on nest density by gap creation in my study. Therefore, I would like to stress the need for a long-term study.

Ant activity on trees

Even though total ant activity did not differ among stand types, trees within burned stands supported an even activity level on distances up to 20 meters away from the nest (Figure 4) compared to the other stand types. One explanation could be the higher tree mortality in burned stands, which forced ants to walk further away from the nest to find a suitable aphid colony. Ants have been seen to monitor surrounding trees and react directly to changes in aphid population or migration patterns (Domisch et al., 2009). Higher tree mortality can thus have caused that resources are more scattered within burned stands, and the ants would have to allocate their workers to available trees. Workers of *F. aquilonia* have been seen to keep a higher activity on larger trees (Gibb and Johansson, 2010), and my result showed the same patter for all stand types. This is probably a result of higher abundancy of aphids on larger trees, since ant activity on trees is related to their interaction with aphids (Stadler, 2005). However, the total ant activity in my study was low as a result of the cold weather. The activity can thus be expected to be higher during warmer conditions (Domisch et al., 2009), and my result can be seen as a lower limit for total ant activity.

Honeydew harvesting

On the contrary of my predictions, I did not find any differences in harvested honeydew by individual *F. aquilonia* workers among stand types. However, the load capacity of 1.14 from my study was lower compared to an estimated load capacity of 1.38 from previous studies on *F. aquilonia* (Gibb and Johansson, 2010). The generally low temperature during the survey period has probably affected the foraging efficiency of honeydew, since temperature is an important factor regulating available amount of honeydew produced by

aphids (Skinner, 1980, Stadler et al., 1998). Differences in stand characteristics which can arise from fire or small gap dynamics can further affect the availability of resources for mound-building ants (Bouget and Duelli, 2004, Stadler and Dixon, 2005). However, there was neither a difference in tree species composition nor a pronounced difference in size of trees among sampled trees (Figure 3) in my study. The lack of differences in harvested honeydew can thus be explained by the fact that available resources within the stands did not differ among stand types. Another explanation could be that ants have adjusted to available resources, as I found ants walking further away from the nest within burned stands (Figure 4). An adjustment to available resources can be considered as an optimal use of resources (Macarthur and Pianka, 1966), where ant colonies can be seen as working units, rather than colonies which contains ants working individually. Instead of finding a difference in harvesting rate of honeydew between stand types, it might in fact be that ant colonies in burned stands contain more inactive workers compared to the other stand types in order to regulate for available live trees. Ant colonies of *F. aquilonia* have been suggested to react in the same way to changed availability of resources among stands of different ages (Gibb and Johansson, 2010). Further affects by fire could thus reduce colony sizes due to insufficient resources.

Even though the harvesting efficiency did not differ among stand types, I made further survey on body-mass of ant workers to evaluate if the treatments had other effects on the ants. Harvesting of trees by clear-cutting has been shown to reduce the size of ant workers (Sorvari and Hakkarainen, 2009). Despite these findings, I could not find that ant workers became smaller due to gap creation or burning. In fact, the descending *F. aquilonia* workers in burned stands were heavier than those from gap cut stands. Further effects due to clear-cutting has been shown to be reduced quality of honeydew (Johansson and Gibb, 2012). Fire could possibly result in similar effects on honeydew quality, since the fire is affecting the trees hosting the aphids. However, since honeydew quality is not investigated in my study, I suggest for further surveys on ant performance to include this aspect after restoration of fire. Moreover, I found that differences in body-mass was depending on distance between nest and tree. Ants walking to a more distant tree from the nest were heavier than those walking to closer trees. This pattern has also been seen for the related *F. rufa* species (Wright et al., 2000), were both a size-distance and a load-distance relationship were found. One explanation to this interaction is the cost of transporting load, which is decreasing with increased body size (Traniello, 1989). Furthermore, this could also be an example of ants adjusting to available resources in order to optimize the harvesting of honeydew.

Implications for conservation management

Due to the fact that ants have been recognized as ecosystem engineers (Jones et al., 1994), changed stand characteristics affecting ant populations can have considerable ecosystem consequences. For example litter-dwelling earthworms benefits from the dominant behavior of wood ants (Laakso and Setälä, 1997), and soil heterogeneity in terms of organic matter and nutrients are improved around the mound nest (Risch et al., 2005, Jurgensen et al., 2008). The decreased nest volume after fire can thus have direct negative effects on other organisms such as earthworms, and affect microsite conditions regarding soil heterogeneity. On the other hand, the fire could break the influence of the dominant behavior of wood ants, which will allow suppressed species to increase in numbers. A decline of wood ants is suggested to increase the number of predatory invertebrates (Laakso and Setälä, 2000), creating an abundance of ground beetles (Hawes et al., 2002), and increase the number of

other less competitive ant species (Jurgensen et al., 2008). A re-introduction of fire disturbance will therefore probably have both negative and positive impacts among organisms interacting with ants. On the contrary to fire disturbance, I suggest that gap creation will not break the dominant behavior of wood ants. The interaction between other organisms benefiting from wood ants will thus not be affected by the restoration of small gap dynamics. In regard of conservation management, introduction of gap dynamics can be used for preserving wood ant colonies, and thus preserve the interaction between ants and other organisms. Furthermore, I suggest that endangered species, in bigger need of conservation efforts, can be given more consideration compared to dominant ants when conducting gap creation within boreal forests. However, only a long-term study can give the whole picture of overall effect, and one cannot neglect possible impact which only will be shown over time due to changed stand structure (Vanha-Majamaa et al., 2007). For conservation efforts, it is important to consider species interactions and the possible consequences of conducting restoration treatments, together with the main goal of conservation management.

Limitation of the study

Firstly, no baseline inventory was conducted prior to restoration and this would have provided important information about nest distribution and condition before the treatments were conducted. Such information would have made the evaluation of restoration effects more straight forward. Secondly, the analysis of ant activity in this study was performed with GLM's, using Poisson distribution adjusted for over-dispersion. This is one possible model to use for regulating the kind of data I had in my study, which is a well-known and commonly used method among the literature (Ver Hoef and Frost, 2003, Potts and Elith, 2006, Hoef and Boveng, 2007). Another possibility would have been to perform GLM's with the negative binomial distribution (White and Bennetts, 1996). I chose to use the Poisson distribution due to the limited timeframe of my study, since an analysis with negative binominal would have required the use of a different statistical computer software. The second analysis might have resulted in a more accurate estimation of ant activity, since biological data are suggested to be distributed as negative binominal more often than Poisson (White and Bennetts, 1996). Furthermore, a typical error for Poisson is to exceed the expected 5%, even if the data is regulated for over-dispersion. However, Hoef and Boveng (2007) argue that there is no general answer to choice of method, as they point out that "…an important way to choose an appropriate model is based on sound scientific reasoning rather than a data-driven method.".

Conclusion and future studies

This study is one of the first to investigate the effect of burning and small scale gap dynamics on dominant ants in boreal forests. My main conclusion is that both burning and gap creation are needed as conservation methods on different organism groups due to the differences in resulted stand structure after conducting the treatments. An introduction of fire regimes can break the dominant advantaged of wood ants, and allow species suppressed by the ants to increase. Introducing gap dynamics could on the other hand preserve the condition of mound-building ants, and thus help to conserve ant interactions and services provided by the ants. I stress the importance of considering species interaction when setting goal for conservation management. Furthermore, my results can be used as a foundation for further studies on ant communities of *Formica spp.* and the effects of the implementation of natural disturbances.

To increase our knowledge on long-term restoration effects, I suggest that ant communities within this study area should continue to be monitored over time. Including condition and viability of nests, and quality of honeydew, in future studies could help to estimate possible impact on ant communities. Including effects on stand characteristics while monitoring ants could reveal possible impact due to intensity of fire or increased income of solar radiation. This could furthermore improve the evaluation of overall impact on ant communities of the restoration of fire regimes and gap creation in boreal forests.

Acknowledgements

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