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ABSTRACT

Red wood ants (*Formica rufa* group) impact forest ecosystems in a multitude of ways and can thus be considered as ecosystem engineers. Although they are highly efficacious predators of many arthropods, their nests host a diverse community of other arthropods. In this thesis, I wanted to highlight the diversity of red wood ant associated guest fauna in order to emphasize the role of red wood ants in the maintenance and conservation of forest biodiversity. I examined the underlying factors shaping the community composition and species richness of associates. Particularly, I studied the factors determining the occurrence of the globally vulnerable shining guest ant (*Formicoxenus nitidulus*), an obligate social parasite of mound-building wood ants. I also studied the effects of clear felling on ant nest mounds as well as on the ant-associated beetle community.

A total of 85 different taxa (mostly beetles), including 26 myrmecophiles (species dependent on ants), were identified in the course of this thesis. One unexpected discovery was the sawtoothed grain beetle (*Oryzaephilus surinamensis*), which has so far only been recorded as an indoor pest species in Finland. Overall, I found that species richness and occurrence of associates were negatively associated with isolation of the nest mounds. The occurring probability of the guest ant *F. nitidulus* increased with decreasing isolation and increasing nest mound size. The guest ant was more likely to occur in the nests of the polydomous (multi-nest colonies) *Formica polyctena* than the monodomous (single nest colonies) *Formica rufa*. Also, local spreading along the connecting trails between nests in polydomous host colonies seems to be important to *F. nitidulus*.

I found that *Formica aquilonia* nest mounds in clear fells had significantly lower surface layer moisture content than nests in forests, which reduces the nests' thermal capacity. Though species richness and community composition of beetles did not greatly differ between clearings and forests, total abundance was lower in clear fell nests. Furthermore, total species richness and abundance as well as myrmecophile abundance decreased with decreasing moisture content. I investigated only the short-term effects of clear felling in active nest mounds. However, nests in clear fells have a high tendency of being abandoned, which will inevitably be detrimental to myrmecophiles. How the associate community develops in the long-term in the nests surviving clear felling needs further study.

This thesis reinforces the status of red wood ants as hosts of a highly diverse associate community. This needs to be taken into consideration in the maintenance and conservation of arthropod diversity in temperate and boreal forests. If the whole habitat cannot be protected, forest management practices preserving dense red wood ant populations should be used. Also, colonization chances for the wood ants as well as nest density could be increased by creating small open areas in managed forests, which would also benefit many other forest-dwelling species. Thus, maintaining a varied forest structure could help maintain and even increase the forest biodiversity.

TIIVISTELMÄ

Kekomuurahaisten (*Formica rufa* ryhmä) vaikutukset metsäekosysteemeihin ovat moninaiset ja niinpä niitä voidaankin pitää ekosysteemi-insinööreinä. Vaikka ne ovat hyvin tehokkaita niveljalkaisten petoja, niiden pesät pitävät sisällään monimuotoisen yhteisön muita niveljalkaisia. Tässä väitöskirjassa halusin korostaa kekomuurahaispesien vieraslajiston monimuotoisuutta painottaakseni kekomuurahaisten roolia metsien monimuotoisuuden ylläpidossa ja suojelussa. Tarkastelin pesävieraslajistoa ja -lajimäärää muokkaavia tekijöitä. Erityisesti tutkin maailmanlaajuisesti vaarantuneen norkomuurahaisen (*Formicoxenus nitidulus*), kekomuurahaispesissä elävän sosiaalisen loisen, esiintymistä sääteleviä tekijöitä. Tutkin myös metsähakkuiden vaikutuksia kekoihin sekä niissä pesävieraina eläviin kovakuoriaisiin.

Kaiken kaikkiaan tämän väitöskirjan aikana määritettiin 85 eri taksonia (enimmäkseen kovakuoriaisia), mukaan lukien 26 myrmekofiiliä eli muurahaisista riippuvaista lajia. Eräs odottamaton löytö oli riisihärö (*Oryzaephilus surinamensis*), kovakuoriaislaji, joka on tähän mennessä tavattu Suomessa ainoastaan elintarviketuholaisena. Yleisesti ottaen havaitsin, että pesävieraiden lajirunsaudella ja esiintymisellä oli negatiivinen yhteys kekojen eristyneisyyteen. Norkomuurahaisen esiintymistodennäköisyys kasvoi kekojen eristyneisyyden pienentyessä sekä keon koon kasvaessa. Norkomuurahainen esiintyi todennäköisemmin monipesäisiä yhdyskuntia muodostavan kaljukekomuurahaisen (*Formica polyctena*) kuin yksipesäisiä yhdyskuntia muodostavan punakekomuurahaisen (*Formica rufa*) pesissä. Paikallinen leviäminen monipesäisten yhdyskuntien pesiä yhdistäviä polkuja pitkin vaikuttaisi olevan tärkeää norkomuurahaiselle.

Havaitsin, että tupsukekomuurahaisten (*Formica aquilonia*) pesissä oli merkittävästi kuivempi pintakerros hakkuualueilla kuin metsissä, mikä heikentää kekojen lämpökapasiteettia. Vaikka pesävieraskovakuoriaisten lajirunsaus tai lajisto ei eronnut merkittävästi hakkuualueiden ja metsien välillä, kokonaisyksilömäärä oli alhaisempi hakkuukeoissa. Lisäksi kokonaislaji- ja yksilömäärä sekä myrmekofiilien yksilömäärä pienenivät kosteuspitoisuuden pienentyessä. Tutkin ainoastaan hakkuiden lyhytaikaisia vaikutuksia aktiivisissa keoissa. Hakkuualueiden keoilla on kuitenkin suuri todennäköisyys tulla hylätyiksi, mikä on väistämättä haitallista myrmekofiileille. Sitä, kuinka pesävierasyhteisö kehittyy pitkällä aikavälillä hakkuista selviytyvissä keoissa, tulee tutkia lisää.

Tämä väitöskirja korostaa kekomuurahaisten asemaa erittäin monimuotoisen pesävierasyhteisön isäntinä. Tämä tulee ottaa huomioon niveljalkaisten monimuotoisuuden ylläpidossa ja suojelussa lauhkean ja boreaalisen vyöhykkeen metsissä. Mikäli koko elinympäristöä ei voida suojella, metsätaloudessa tulisi pyrkiä käyttämään menetelmiä, jotka ylläpitävät kekomuurahaisten korkeaa pesätiheyttä. Lisäksi kekomuurahaisten kolonisaatiomahdollisuuksia voitaisiin lisätä luomalla talousmetsiin pieniä aukkoja, mikä hyödyttäisi myös monia muita metsälajeja. Vaihtelevalla metsärakenteella voitaisiin siten auttaa ylläpitämään ja jopa lisäämään metsien monimuotoisuutta.

LIST OF ORIGINAL PUBLICATIONS

This thesis consists of the following publications and manuscript, which are referred to in the text by their Roman numerals:

I   Härkönen, S. K. & Sorvari, J. (2014) Species richness of associates of ants in the nests of red wood ant *Formica polyctena* (Hymenoptera, Formicidae). *Insect Conservation and Diversity* 7: 485–495.

II   Sorvari, J., Härkönen, S.K. & Vesterinen, E.J. (2012) First record of an indoor pest sawtoothed grain beetle *Oryzaephilus surinamensis* (Coleoptera: Silvanidae) from wild outdoor wood ant nest. *Entomologica Fennica* 23: 69–71.

III   Härkönen, S. K. & Sorvari, J. (2017) Effect of host species, host nest density and nest size on the occurrence of the shining guest ant *Formicoxenus nitidulus* (Hymenoptera: Formicidae) *Journal of Insect Conservation* 21: 477–485.

IV   Sorvari, J., Elo, R.A. & Härkönen, S.K. (2016) Forest-built nest mounds of red wood ant *Formica aquilonia* are no good in clear fells. *Applied Soil Ecology* 101: 101–106.

V   Härkönen, S. K. & Sorvari, J. Comparison of ant-associated beetle communities inhabiting mounds of forest-dwelling ants in forests and forest clearings. *Manuscript.*

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Contributions to the individual publications:

	I	II	III	IV	V
Original idea	JS	JS	JS, SKH	JS, RAE, SKH	JS, SKH
Field work	SKH	SKH	SKH	JS	JS
Identification	SKH, others	SKH, TC	-	-	SKH
DNA Barcoding	-	EJV	-	-	-
Statistics	SKH, JS	-	SKH	JS	SKH
Writing	SKH, JS	JS, SKH, EJV	SKH, JS	JS, RAE, SKH	SKH, JS
Commenting	IES	NW	IES	DB	RAE

SKH = Salla K. Härkönen, JS = Jouni Sorvari, EJV = Eero J. Vesterinen, RAE = Riikka A. Elo, IES = Ilari E. Sääksjärvi, TC = Tom Clayhills, NW = Niklas Wahlberg, DB = Daniel Blande, others = Jari Haimi, Veikko Rinne, Seppo Koponen, Kaj Winqvist, Tom Clayhills, Lubomír Masner

1 INTRODUCTION

1.1 Ants and their importance in nature

Jones et al. (1994) defines ecosystem engineers as organisms that directly or indirectly modulate the availability of resources to other species, by causing physical state changes in biotic or abiotic materials. Through the modification, maintenance and/or creation of habitats for other organisms they can significantly impact ecosystem dynamics. Social insects, particularly ants, are among the most successful organisms on Earth, and the key to their success lies in their social organisation. Ants, just like all termites, and some bees and wasps, are eusocial, i.e. truly social, insects (Wilson 1971). Their societies are divided into reproductive and worker castes, where overlapping generations of the more or less sterile workers cooperate in taking care of the brood of the reproductive caste. These insect colonies are often referred to as superorganisms, because the functions collectively performed by the individuals in the colony resemble the physiological properties of different organs and tissues (Wheeler 1928; Wilson 1971; Hölldobler & Wilson 1990).

Currently, there are around 14 000 known ant species, and more are described all the time (Agosti & Johnson 2017). The diversity of ants is vast especially in the tropics where a single tree may hold dozens of ant species (e.g. Longino et al. 2002). In Finland, around 60 ant species can be found (Finnish Biodiversity Info Facility, FinBIF 2017). Over their more the 100 million years of existence, ants have risen to occupy key roles in many environments and have had a major influence in the shaping of present-day terrestrial ecosystems (Hölldobler & Wilson 1990; Wilson & Hölldobler 2005). Apart from Antarctica and some distant islands, ants can be found nearly everywhere, and in most parts, they are among the main predators of other invertebrates (Wilson 1971; Hölldobler & Wilson 1990). In most terrestrial habitats, they even exceed vertebrates in biomass and energy consumption (Wilson 1971).

1.1.1 Red wood ants

Red wood ants of the *Formica rufa* group are dominant species in the boreal and temperate forests of Eurasia, where they build large perennial mound nests consisting of forest litter, resin and soil particles. The above ground nest mound may reach over 2 metres in height and have a volume of several cubic metres. The six species in the group are genetically closely related and morphologically very similar (Collingwood

1979; Goropashnaya et al. 2004). Despite their large populations, the effective population sizes (i.e. the number of reproductive individuals) of red wood ants are relatively small and, thus, the conservation needs of the species may be easily underestimated (Sorvari 2016). Red wood ants are globally classed as Near Threatened species according to the World Conservation Union (IUCN 2015), and they are protected by law in many European countries (Sorvari 2016).

In Finland, there are five red wood ant species (*F. rufa*, *F. polyctena*, *F. aquilonia*, *F. pratensis*, and *F. lugubris*). The number of queens and nests in a colony varies considerably within and between species (Ellis & Robinson 2014). Most Finnish populations of *F. rufa, F. lugubris* and *F. pratensis* are monogynous and monodomous, i.e., the colonies have only queen and they are contained within a single independent nest mound. On the other hand, *F. polyctena* and *F. aquilonia* are polygynous and polydomous, i.e., there are multiple queens per colony and the colonies may consist of several inter-connected nest mounds (Rosengren & Pamilo 1983). The species differ also in their habitat requirements and dispersal abilities. The monogynous and monodomous species prefer forest edges and open forests, whereas the polygynous and polydomous species prefer forest interiors. Monogynous species establish new colonies through temporarily parasitizing the nests of the *Formica* subgenus *Serviformica* ants such as *Formica fusca*. While polygynous species can also use this method, they mainly spread through colony budding, in which a group of workers and queens split from the mother colony to establish a new nest in the neighbourhood. Polygynous species thrive in large continuous forests, while monogynous species are better at dispersing to small and isolated forest patches and are, thus, better adapted to habitat fragmentation (Rosengren et al. 1993; Punttila 1996; Sundström et al. 2005; Mabelis and Korczynska 2016; Sorvari 2017, in press).

Wood ants impact their physical surroundings and other organisms in a multitude of ways. Thus, changes in their populations can have wide ranging effects on both local and global ecosystems. Through predation as well as resource and interference competition they affect the species composition of other arthropods (Adlung 1966; Niemelä et al. 1992; Punttila et al. 2004) and also the breeding success of some insectivorous birds (Aho et al. 1999). By their competitive superiority they affect the distribution and abundance of other ant species (Savolainen & Vepsäläinen 1988, 1989; Savolainen et al. 1989). Furthermore, wood ants also have a role as seed dispersers of many plants (Gorb et al. 2000) and may enhance the growth of trees and shrubs by preventing folivory (Mahdi & Whittaker 1993; Atlegrim 2005). On the other hand, as most of their food consists of honeydew they may also hinder the growth of

some trees due to aphid tending (Rosengren & Sundström 1991; Kilpeläinen et al. 2009). The constant input of organic material and prey into their nests strongly impacts the chemical, physical and biological properties of the soil and creates hotspots for mineralization (Lenoir et al. 2001; Frouz & Jílková 2008). They offer also a food source for other animals, such as bears (e.g. Swenson et al. 1999). Finally, their nests are home to a wide variety of other arthropods as well as earthworms (Donisthorpe 1927; Laakso & Setälä 1997, 1998; Parmentier et al. 2014; Robinson et al. 2016).

1.2   Myrmecophiles and other associates of ants

Concomitantly with ants, a considerable number of other organisms, comprising of at least 17 orders, over 120 families and hundreds of genera, have evolved to exploit their colonies (Donisthorpe 1927; Kistner 1982; Hölldobler & Wilson 1990; Rettenmeyer et al. 2011; Parmentier et al. 2014; Robinson et al. 2016). The earliest known fossil of a morphologically specialized and apparently obligate associate of ants is around 52 million years old (Parker & Grimaldi 2014). Wood ants have a reputation as aggressive predators that actively defend their nests. Apart from ant-tended aphids, the abundance of different invertebrate groups is generally reduced by the ants (Niemelä et al. 1992; Laakso & Setälä 2000; Punttila et al. 2004). Thus, it may seem surprising that ant nests are filled with a multitude of other organisms, apparently living quite unharmed among the ants. However, once the guest species get past the ants' defences, ant nests are like fortresses: well protected against most outside threats and filled with stored resources (Hughes et al. 2008). Wood ant nests are also long-lived and fairly stable environments with controlled temperature and humidity conditions (Rosengren et al. 1987; Laakso & Setälä 1998). These characteristics contribute to make them ideal habitats for various invertebrates.

Species that are dependent on the ants during at least part of their life cycles are referred to as myrmecophiles (Hölldobler & Wilson 1990). The relations they have with ants are varied, ranging from mutualism to parasitism, and include interactions both within the nests and outside of it. Erich Wasmann (1894) placed myrmecophiles into five categories based on their degree of specialization and integration into the host colony:

1. Persecuted guests (Synechthrans): These are mostly scavengers and predators that are treated with hostility. They survive by their agility and swiftness or by

    defensive mechanisms such as retracting under protective cuticular shields and the use of repelling secretions.

2. Indifferently tolerated guests (Synoeketes): These species are mainly scavengers and predators. They are mostly ignored by the ants because they are too small or sluggish to be noticed, too swift to get a hold on, or have no differentiating odour to distinguish them from the nest surroundings.

3. True guests (Symphiles): These species are treated amiably and as members of the colony, i.e., they are groomed and fed by the ants.

4. Ecto- and Endoparasites: These are typical parasites living either on or in the hosts body.

5. Trofobionts: These include herbivorous insects such as aphids and lycaenid butterflies that offer honeydew and other nutritious secretions to the ants and are in turn protected against predators and parasites.

However, many myrmecophiles can have multiple roles within the colony, and thus, do not fit into a single category (Hölldobler & Wilson 1990). A simpler categorization by Kistner (1979) distinguishes two classes: integrated species that are incorporated into the hosts' social life, and non-integrated species, that are not incorporated into the social life but are otherwise adapted to the nest as an ecological niche.

Typically, the highest diversity of myrmecophiles can be found among species with large colonies such as those formed by wood ants (Hölldobler & Wilson 1990). There are 125 myrmecophilous species known to be associated with red wood ants (Parmentier et al. 2014). However, in addition to the myrmecophiles, there is much greater diversity of other associates that enjoy and benefit from the warm nest environment and accumulated resources (Donisthorpe 1927; Laakso & Setälä 1997, 1998; Päivinen et al. 2002; Stoev & Lapeva-Gjonova 2005; Robinson & Robinson 2013). Some of these species are regularly found in the nests (e.g. Päivinen et al. 2002), where they maintain healthy populations, and might be termed as facultative myrmecophiles (Stoev & Lapeva-Gjonova 2005). The relationships range from weakly opportunistic nest commensals and occasional predators to species with some adaptations to life with ants and possibly even mutualistic associations. One example of a possibly mutualistic association can be found between ants and earthworms. Laakso & Setälä (1997) found earthworms to be more abundant in ant nest mounds than the surrounding soil. The earthworms are able to mostly avoid predation due to repelling mucus, suggesting a chemical defence against the ants (Laakso & Setälä 1997). They may benefit the ants by preventing nest mounds from becoming overgrown with mould and fungi, thus increasing the longevity of the colony (Laakso

& Setälä 1997). Another non-myrmecophilous but regular associate species, the pseudoscorpion *Pselaphocernes scorpioides*, also seems to have a repelling mechanism against ants. Donisthorpe (1927) observed that if they were grasped by ants, they were immediately dropped.

1.3 Social parasitism among ants

In social parasitism, a social insect species takes advantage of the colonies of another social insect. Though these interactions may be found among groups such as wasps and bees, they are especially diverse in ants (Buschiger 2009). There are different ways to classify the various associations occurring between different species of ants. Wasmann (1891) distinguished between *compound nests* and *mixed colonies*. In *compound nests*, two or more species live very close to each other, sometimes sharing nest galleries but always keeping their brood separated. The associations range from accidental to truly parasitic and comprise of casual nesting in close vicinity (plesiobiosis), food stealing (cleptobiosis), brood predation (lestobiosis), nest and trail sharing (parabiosis), and guest ant relations (xenobiosis). In *mixed colonies*, which include temporary parasitism, permanent parasitism with slavery (dulosis), and permanent parasitism without slavery (inquilinism), the brood of the parasite is at least temporarily cared for by the host workers. The mixed colonies as well as xenobiosis comprise the four basic types of obligate parasitism in ants (Hölldobler & Wilson 1990; Buschiger 2009):

1. Temporary parasitism: the parasitic species depends on the host species only during colony foundation. The parasitic queen tries to secure adoption into the host colony, where she then replaces the original queen. The first parasitic brood develops with the help of the host workers. Eventually, the host worker force dies out and the colony consists purely of the parasitic species.

2. Slave-makers, dulosis: the slave-maker workers go on raids attacking the colonies of their host (slave) species and bringing the brood back into their own nest. The slave brood then develop into fully functional members of the slave-maker colony performing ordinary chores such as foraging, nest building, and brood care, which the slave-makers are usually unable to do.

3. Inquilinism: the parasitic species spends its entire life cycle in the nests of the host species, where the parasitic queen usually coexists with the host queen. The parasitic species often has no workers of its own, focusing only on the

production of sexual offspring. The parasite brood is taken care of by the host workers along with their own larvae.

4. Xenobiosis, guest ants: one species lives freely within the nests of another species, rearing their own brood and obtaining food from the host in one way or another, often by soliciting regurgitation. Xenobiotic ants are generally only distantly related to their hosts, and may even belong to a different subfamily.

1.3.1   *Formicoxenus nitidulus*

Ants of the genus *Formicoxenus* (Hymenoptera, Formicidae, Myrmicinae) are social parasites with a xenobiotic lifestyle. They have their own nests where their brood is kept separate from the host ants. Many parasitic species, like the so called 'shampoo ants' (*Formicoxenus provancheri* Emery, 1895 and *F. quebecensis* Francoeur, Loiselle & Buschinger, 1985), rely on chemical mimicry to remain unmolested among their host species, and are also highly host specific (Errard et al. 1997; Lenoir et al. 1997). However, the shining guest ant *Formicoxenus nitidulus* (Nylander, 1846), which is the only *Formicoxenus* species in Europe (Francoeur et al. 1985), employs an entirely different strategy. It has chemical deterrents in its cuticle, making it unpalatable for the host ants (Martin et al., 2007). Thus, the guest ant is largely ignored by its host and in the rare occasion it is grabbed, it is immediately dropped (Robinson 2005a; Martin et al. 2007).

This generalist strategy allows *F. nitidulus* to invade the nests of at least nine different host ant species of the genus *Formica* (*F. rufa* Linnaeus, 1761, *F. polyctena* Förster, 1850, *F. aquilonia* Yarrow, 1955, *F. pratensis* Retzius, 1783, *F. lugubris* Zetterstedt, 1838, *F. truncorum* Fabricius, 1804, *F. uralensis* Ruzsky, 1895, *F. exsecta* Nylander, 1846, and *F. pressilabris* Nylander, 1846) (Francoeur et al. 1985; Busch 2001; Czechowski et al. 2002). *Polyergus rufescens* and *Tetramorium caespitum* have also been reported as hosts (Wilson 1971). With such a variety of hosts, the guest ant is more widespread than any particular host. The distribution of *F. nitidulus* ranges from Spain, Italy and Greece to latitude 70°N in Northern Europe and from UK to Eastern Siberia (Collingwood 1979; Agosti & Collingwood 1987; Czechowski et al. 2002). Globally, the species has been classified as vulnerable according to the IUCN Red List (IUCN 2015). However, it is quite common in Finland, and hence the country has been tasked with the international responsibility of preserving the species (Rassi et al. 2010). Thus, the study of this species is especially important in Finland.

1.4   Factors affecting species richness and abundance

Maintaining biodiversity requires understanding of the underlying processes affecting species richness in communities. Hypotheses dealing with different aspects of resource availability such as distribution, size, abundance, and concentration of resources, have been used to explain the species richness of species depending on a certain discrete resource (e.g. Neuvonen & Niemelä 1981; Ricklefs 1987; Marques et al. 2000; Christman & Culver 2001). These have been applied in a variety of situations but mainly in plant-herbivore systems (e.g. Lewis & Waloff 1964; Brändle & Brandl 2001; Sanches & Parmenter 2002) and host animal-parasite systems (e.g. Morand & Poulin 1998; Arneberg 2002; Altizer et al. 2007). Päivinen et al. (2003, 2004) first adapted them to explain the species richness of myrmecophilous beetles in ant nests. According to one of the hypotheses, the resource concentration hypothesis, hosts can support higher species richness when they occur in high densities (e.g. Root 1973; Gonçalves-Alvim & Fernandes 2001; Päivinen et al. 2004). Moreover, following metapopulation theory, populations are more likely to occur in large and well-connected habitat patches (Hanski 1994, 1999). Populations on large patches are less likely to become extinct due to larger carrying capacities, while probability of colonization increases with decreasing isolation (Hanski 1999). In a host ant-associate system, the host ant nest represents a resource or a patch of suitable habitat affecting the distribution of the species that depend on it.

Since insects are ectotherms, they are strongly affected by the physical environment around them. Their growth and reproduction are affected by the temperature of their habitat (Ratte 1985; Atkinson 1994; Chown & Nicolson 2004). Moreover, they are typically small-sized which makes them vulnerable to desiccation (Chown & Nicolson 2004). Moisture and temperature are hence among the most important abiotic factors affecting the distribution, abundance, and life cycles of insects and other soil organisms (e.g. Giller 1996; Chown & Nicolson 2004; Tsiafouli et al. 2005). Consequently, they might determine the quality of ant nest mounds for the associate species as well. In addition to the direct effects trough desiccation, moisture may have indirect effects through changes in food resources and microhabitat modifications (e.g. Setälä et al. 1995; Pflug & Wolters 2001).

1.5   Wood ants and forest clear felling

Forest clear felling has been shown to reduce reproduction and offspring growth of wood ants as well as increase their nest abandonment rate (Sorvari & Hakkarainen

2005, 2007a, 2007b, 2009; Sorvari et al. 2014). These can mainly be explained by the loss of large part of the ants' food resources (especially aphid-containing trees) (Rosengren & Pamilo 1978; Rosengren et al. 1979). However, the drastic changes on abiotic conditions, i.e., increased solar radiation and wind, more extreme temperature conditions, and changed moisture conditions, may also disrupt the inner functions of the nest mounds thus causing additional stress to the ants.

Red wood ants actively regulate the nest temperatures to be optimal for brood development during summer season from April to September (Kadochová & Frouz 2014). Typically, the inner temperature is markedly higher than ambient (Frouz 2000; Frouz & Finér 2007; Sorvari & Hakkarainen 2009; Kadochová & Frouz 2014). Dry nest mounds have more variable temperatures than moist mounds which has been suggested to be due to lower thermal capacity in dry nests (Frouz & Finér 2007). It has been observed that forest nests typically have a moist surface layer and a drier inner core (Laakso & Setälä 1997, 1998; Elo, Penttinen & Sorvari, unpublished). It is thought that as the heat generated by decaying organic material and the ant's activity rises towards the cooler surface, it condenses and thus creates the moist layer (Rosengren et al. 1987; Hölldobler & Wilson 1990). The moist surface layer may function as a barrier preventing cooling wind from penetrating the warm inner layers of the nest. Thus, drying of the surface layer may have adverse effects on the temperature regulation of the nest mound (Sorvari 2016). Indeed, nest mounds in forest clearings have shown greater diurnal variation in the inner temperatures than nests in forest interiors (Rosengren et al. 1979; Sorvari & Hakkarainen 2009). Sorvari and Hakkarainen (2009) suggested that the less stable temperature conditions in clear fells might be caused by drying of the nest mound surface layer. However, the relationship between temperature variations and moisture content remained unconfirmed since they did not measure moisture.

Changes in the nest mound moisture content and thermoregulation may have unknown effects on the diverse associate community within the nest mounds. Less stable temperatures may slow down developmental rates and consequently decrease population growth. Also, due to the temperature and humidity conditions as well as the high organic matter content, nest mounds of red wood ants are hotspots of litter decomposition and nutrient turnover in boreal and temperate forests (Lenoir et al. 2001; Frouz & Jílková 2008; Frouz et al. 2016). Since decomposers are at the basis of multi-level food webs (Laakso & Setälä 1998), changes in the physical conditions of the nest mound could affect not only the decomposer fauna and the rate of

decomposition and nutrient turnover, but also the other associate community higher in the trophic web.

1.6   Aims of the Thesis

The aims of this thesis can be summarized under two main points. First, my aim was to illustrate the diversity of red wood ant associated guest fauna and, through that, emphasize the role of red wood ants in the maintenance and conservation of forest biodiversity. Second, my aim was to examine the underlying factors structuring and determining community composition and diversity of ant nest associates in general, and the occurrence of the shining guest ant *Formicoxenus nitidulus* in particular. In the following, the aims of this thesis are described in more detail chapter by chapter:

I)   In the first chapter, one of my aims was to give an overview of the diversity of the associate fauna found in *Formica polyctena* nests at single study region (12 nests on four sites) in SW Finland. Species accumulation curves were used to give an idea of how successful the sampling was. Another aim was to test how well the resource concentration hypothesis extends to explaining the species richness and abundance of, not just obligate myrmecophiles as in Päivinen et al. (2004), but the entire associate fauna as well as the non-myrmecophiles.

II)   This chapter details the curious discovery of the sawtoothed grain beetle *Oryzaephilus surinamensis*, an indoor pest species, in the nest of *Formica rufa*.

III)   I investigated how host species, isolation and nest size related to the occurrence of the shining guest ant *Formicoxenus nitidulus*. As wood ants that form multi-nest colonies tend to build larger nests and have higher nest density compared to wood ants with single nest colonies (Punttila & Kilpeläinen 2009), I expected the nests of polydomous species to be more likely occupied by the guest ant.

IV)   In this study, the aim was to find out whether clear felling affects the moisture and temperature conditions within ant nest mounds and how the shape and size of the nest mound relates to the physical conditions within them.

V)   My aim in this study was to compare the ant-associated beetle communities between clear fells and forests, and particularly to find out whether nest moisture content was associated with species richness and abundance of the

beetles and whether the species richness and abundance differed between clearings and forests.

2 METHODS

2.1 Study species

Red wood ants of the *Formica rufa* group were the host species in this thesis: *Formica polyctena* (**I**, **III**), *F. rufa* (**II**, **III**), *F. pratensis* (**III**), *F. lugubris* (**III**), and *F. aquilonia* (**III-V**). The level of focus on the associates varied from chapter to chapter in this thesis. In the first study the focus was on almost the entire community. Study **V** focused on a single taxonomic group, the ant-associated beetles. In study **III**, the focus was on the occurrence of the shining guest ant *F. nitidulus*, while study **II** focused on the discovery of a single individual of the sawthoothed grain beetle *O. surinamensis*.

2.1.1 *Formicoxenus nitidulus* (III)

Figure 1. *Formicoxenus nitidulus* (left) and *Formica rufa* (right) (Photo by S. K. Härkönen)

The shining guest ant *F. nitidulus* is a tiny ant of about 3 mm and easily identified by its completely smooth and shiny body (Fig. 1). Unlike in most other ant species, *F. nitidulus* males are wingless and very worker-like in appearance. In addition to regular workers, *F. nitidulus* has several intermediate forms, so called intermorphs, with morphological characters between worker (ergatomorph) and winged female

(gynomorph). The intermorphs may act as either workers or they may create a colony and act as queens (Buschinger and Winter 1976). The guest ants can nest within any given hollows within the host mound: e.g. inside twigs, pine cones, under bark, within small galleries in the wood stump, or chambers formed within the fine material itself. A single host nest mound can have several guest ant nests.

The Red List status of the guest ant is based on the assessment of the IUCN Social Insects Specialist Group from 1996 and requires revision. Recently, intensified ant inventories have resulted in several new records of the species in Belgium and France (Wegnez et al. 2011; Dekoninck et al. 2015), as well as in the UK (UK Biodiversity Group 1999; Green 2009). Due to its elusive lifestyle, *F. nitidulus* is much harder find than many other ant species and may consequently be underrepresented in surveys unless special attention is paid to the habits of the species. The best time for detecting *F. nitidulus* is from late summer to autumn (Robinson 1999; Ölzant 2001; Van Hengel 2011; Wegnez et al. 2011), when males are regularly seen. Instead of dying shortly after mating, which occurs on top of the nest mound, the males continue to come to the nest surface for the rest of the season. Workers, on the other hand, are rarely seen, as they mostly stay hidden within the nest mound.

2.2   Study areas

Field work for the studies included in this thesis was conducted in Turku, SW Finland (60°25'N, 22°09'E) (**I - III**) and Kuopio, central Finland (62°52'N, 27°29'E) (**IV - V**). In order to investigate the diversity of red wood ant-associated invertebrates on Ruissalo Island, which is located very close to mainland, 12 *F. polyctena* nests were sampled in June 2009 (**I**). At the same time, I sampled also four *F. rufa* nests, one of which contained the living *O. surinamensis* individual (**II**). The eastern parts of the Ruissalo Island are covered with extensive herb-rich oak forests and the western parts with coniferous and mixed forests which are more typical in Finnish nature. In study **I**, three *F. polyctena* nests, likely of the same polydomous colony, were chosen from four study sites in different parts of the island (distance between sites was at least 1.2 km). The sites ranged from coniferous to mixed and deciduous type of forest and were mostly dominated by Scotch pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), oak (*Quercus robur*), birch (*Betula pendula*), and Small-leaved Lime (*Tilia cordata*). The *F. rufa* nest from chapter **II** was located in the Kuuva region of Ruissalo Island, where the habitat was dominated by Scots pine, mixed with birch and Norway spruce. To study the occurrence of the guest ant *F. nitidulus* among red wood ants (**III**), 166 nests (120 *F. polyctena*, 25 *F. rufa*, 14 *F. aquilonia*, 5 *F. pratensis*, and 2 *F. lugubris*) in 25

sites were investigated in June-September 2014. The sites were from Ruissalo and also other parts of Turku. Field work for studies **IV** and **V** took place on three sites consisting of clear fell-forest pairs of spruce forest in 2014 near the town of Kuopio. Study **IV** focused on figuring out whether clear felling influences the surface layer moisture content of the nest mound and their temperature conditions, while study **V** focused on the ant-associated beetles inhabiting those nests. The clear felling occurred one to three years prior to sampling.

2.3   Sampling and observation

Overall, sampling of the guest fauna (**I-III** and **V**) was performed in a similar fashion for the different studies, though there were differences in the amount of nest material taken and/or later processing. In each case, the material collected from the nests was first sieved in the field to prevent most wood ants getting into the sample. The coarse material was then carefully returned to the nest after examination to avoid too much disturbance for the ant colony. Fine material was either examined on a tray, from which invertebrates were picked with forceps (**I-III**), or funnelled (**V**). Collected specimens were stored in 70-75 % ethanol.

In each study, nest mound height and basal diameter were measured, and the above ground nest volume calculated with the equation for a half ellipsoid: $V = (4/3\ \pi abc)/2$, where a and b are the radiuses and c the height of the nest. Nest coordinates were recorded. Nearest neighbour distance (**I, III**) and nest density (**III**) were used to describe nest mound isolation. In study **I**, the three nests on each site were chosen so that one of the nests was the closest neighbour to the other two nests. In study **III**, the number of nests within a 100-metre radius of the studied nest was used as a measure of nest density.

In studies **I** and **II**, 3.75 l of nest material, consisting of five sub-samples (0.75 l) taken from different parts of the nest, was collected 3-5 cm beneath the outer layer of the mound and sieved with sieves of 2.5 and 1 mm mesh size (Fig. 2). Invertebrates were picked while still alive to ensure that they were in the nest of their own volition and not brought there as prey. I collected all invertebrates except mites and springtails, for which the collecting method was not suitable.

In study **III**, most of the 166 investigated nests were both sampled and observed (N = 135), while the rest were only observed. Instead of taking an equal amount of nest material from each nest, the sample size was increased with increasing nest size. the amount of space devoid of guest ants is likely to increase the larger the nest mound
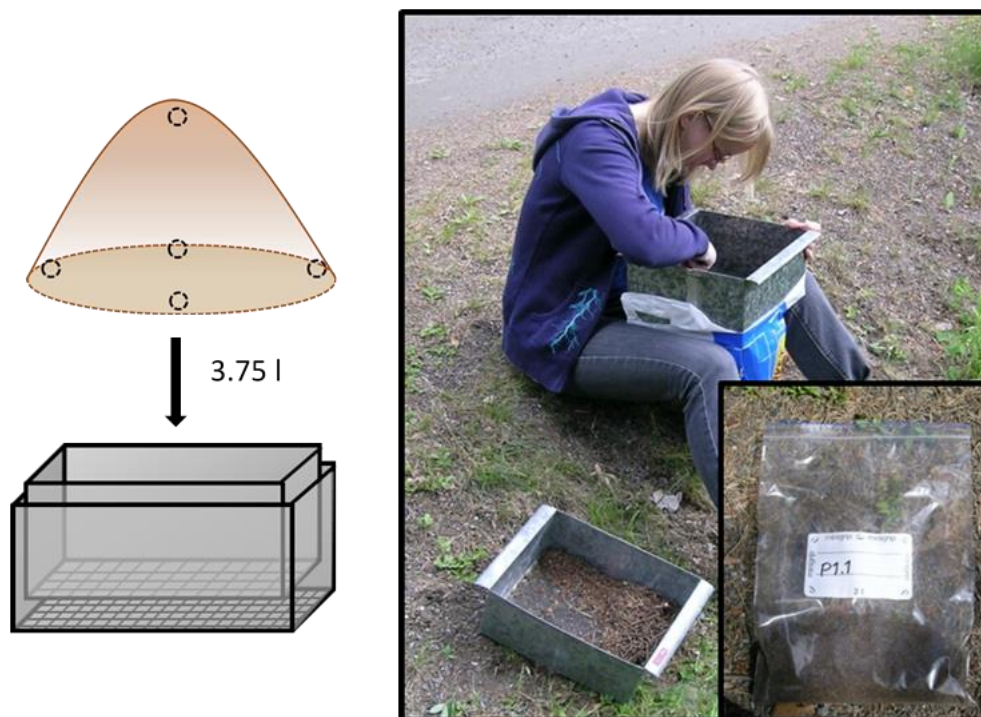
Figure 2. Sampling for studies **I** and **II**; sub-samples were collected from the cardinal points and from the top. Material left on top of the sieve was examined in the field for invertebrates. Fine material was examined later.

is, the likelihood of getting the guest ants in a sample would decrease with increasing nest size. Thus, to counteract this possibility, nests were divided into seven size classes (<250 l, 250–750 l, 750–1,250 l, …, 2,250–2,750 l, 2,750 l <) according to which material was taken 1-7 x 0.5 l (ca. 5 cm beneath the outer layer). Systematic observations of the nests started in August. Each nest was observed a maximum of 10 min, as this has been found to be a sufficient time to detect the guest ant when they are present (Robinson 1998; Green & Westwood 2006). As observation turned out to be much more efficient in detecting the guest ant than sampling, and there were no nests where the guest ants were found only by sampling, I focused only on the observational presence-absence data during analysis. Also, only *F. polyctena* (N = 120) and *F. rufa* (N = 25) nests were included for analyses, since there were so few of the other species' nests in the studied region.

For studies **IV** and **V**, 41 *F. aquilonia* nests were sampled, i.e., seven nests per each clear fell and forest, except in one forest where only six suitable nests were found. Only nests with a minimum basal diameter of 0.70 m were chosen, thus excluding the

young (small) post-harvest nests. Another selection criterion was the presence of a seemingly vital *F. aquilonia* colony, i.e., deserted or semi-deserted nests were not included. Sampling of the nests occurred on during three days in September; one clear fell-forest pair was studied on each day.

Nest inside temperature was measured 20 cm beneath the top of the mound, while ambient temperature was measured 10 cm above ground from a shaded site max 1.5 m away from the mound (**IV**). Temperature measurements were conducted in the afternoons with a digital thermometer (precision ±1°C). The nest surface layer moisture content was measured gravimetrically from a material sample collected from mound surface (0-10 cm depth) near the top of the mound (**IV**). The samples were weighed immediately after field trips, then dried in an oven at 50°C for 48 h, and then weighed again. The weight loss represented the mass of water in the original sample. The percentage of water in the fresh sample was used as the moisture variable in the analysis. For study **V**, beetle samples were collected by taking 0.5 l of nest material 10-15 cm beneath the top of the mound. Sieved (2 mm mesh size) samples were funnelled for five days (Fig. 3).

Figure 3. Funnels and collecting tube filled with ethanol: fine material sample was placed on a large petri-dish which was held at an angle over the funnel allowing beetles and other arthropods to walk over the edge and fall into the collecting tube.
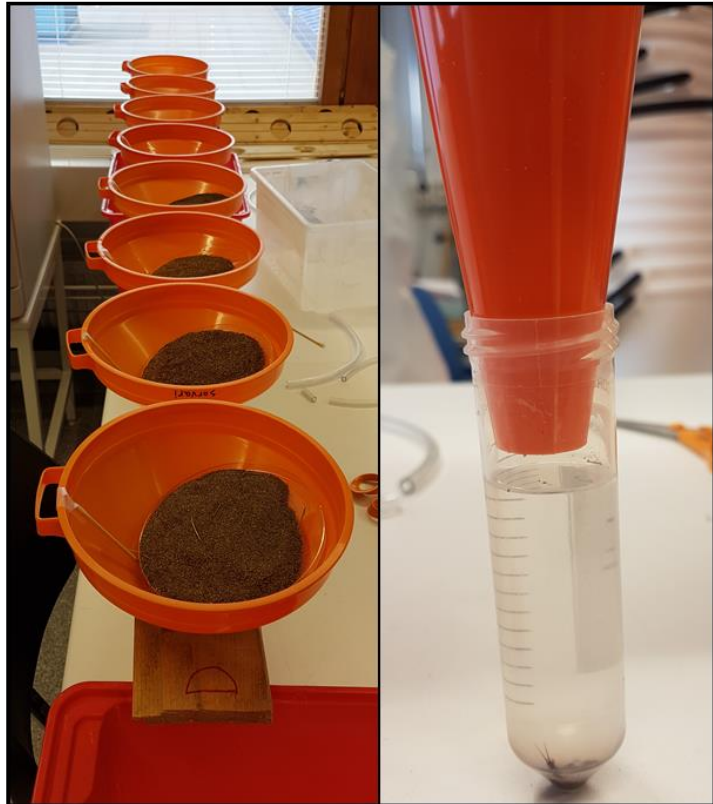
2.4   Species identification

Invertebrates collected during the survey of associates of ants in Ruissalo (**I**) were identified mainly to species level. Some of the less abundant or well-known taxa were not identified to species, but rather morphospecies. Due to difficulties in the identification 29 parasitoid wasp specimens were only identified to the superfamily Chalcidoidea. However, they were treated as one taxon in the analysis even though there could be more than one species. I did the initial sorting and identification of different taxa based on morphology. I identified spiders, pseudoscorpiones and myriapods with the help of identification keys (Locket & Millidge 1968; Gärdenfors & Wilander 1992; Andersson et al. 2005), while beetles were compared to the beetle collection of the Zoological Museum at the University of Turku (ZMUT), Finland. Some groups were given to experts to check and refine the identification. For the identification of beetles in study **V**, I used both the museum collection and, when necessary, identification keys (Freude et al. 1971, 1974, 2012).

In study **II**, the identification of the sawtoothed grain beetle *Oryzaephilus surinamensis,* which is documented to live only as an indoor pest in northern Europe (Halstead 1980; Robinson 2005b), was confirmed with DNA barcode due to the exceptional site of discovery. The sequence got a 100 % match to *O. surinamensis* in the BOLD Identification System. In DNA barcoding, short DNA fragments, which are sufficiently variable between species but not within species, are used to identify species (Hebert et al. 2003a, 2003b). DNA was extracted with a non-destructive method and QIAgen's DNEasy extraction kit. As a barcode region, we used the ca. 600 bp mtDNA sequence of *cytochrome oxidase subunit I* (COI), which is commonly employed in the species separation of many animal taxa. The COI gene was amplified by PCR using universal animal primers (LCO and HCO). The purification and sequencing of the successful PCR product was conducted by Macrogen Inc. (South Korea). Trimming of the sequence was done using the Geneious Pro 5.3.6 software (Drummond et al. 2011).

2.5   Species richness estimation

To evaluate the sufficiency of sampling effort (**I**), species accumulation curves were calculated by studying the number of observed species as a function of sampling effort using EstimateS 9.1.0 software (Colwell 2013). If a curve reaches an asymptote, it would indicate that the sampling effort had been adequate to collect most of the species of the area (Gotelli & Colwell 2011). However, this is rarely the case when

sampling diverse communities with many rare species. When the total number of species is not known because not all species were sampled, the species richness can still be estimated with non-parametric estimators (Gotelli & Colwell 2011). In EstimateS, estimators ACE, Chao1 and jackknife 1 and 2 (Jack1 and Jack2) are suitable for abundance data, where the number of individuals was recorded for each species in a sample, whereas Chao2 and ICE are for incidence data, i.e., a species was either detected or undetected in a sample (Gotelli & Colwell 2011).

3 RESULTS AND DISCUSSION

3.1 Associates of ants (I, II, III, V)

In this thesis, a total of 85 different taxa, including 26 myrmecophilous species, were identified. The literature on myrmecophiles is extensive, mostly consisting of incidental observations or ecological studies of certain genera and higher taxa. Päivinen et al. (2002) did a comprehensive listing of ant-associated beetles in Northern Europe in a review article and later also studied patterns in their distribution and diversity based on a literature survey and samples collected from *F. aquilonia* nests in Finland (Päivinen et al. 2003, 2004). Before the start of study **I** in 2009, the last broad study on red wood ant associates that was not focusing on just one taxonomic group such as beetles was done by Donisthorpe (1927) nearly 100 years ago. In recent years, however, new publications have emerged giving up-to-date listings of red wood ant associates. Robinson and Robinson (2013) surveyed *F. rufa* nests over a three year period and recorded all myrmecophile and non-mymecophile associates. Parmentier et al. (2015) studied the diversity of myrmecophiles in the nests of *F. rufa* and *F. polyctena*. Also, Parmentier et al. (2014) and Robinson et al. (2016) list all the known myrmecophiles associated with wood ants in their reviews. Together these studies give a clear picture of the highly diverse community to be found associated with red wood ants. The myrmecophiles collected during my studies comprise about 20 % of the known red wood ant associated myrmecophiles listed by Parmentier et al. (2014).

Overall, after mites, beetles are the most common myrmecophiles with the family Staphylinidae being the most common beetle family (Hölldobler & Wilson 1990; Päivinen et al. 2002; Robinson & Robinson 2013; Parmentier et al. 2014; Elo et al. 2016). Altogether, 42 beetle species, of which 21 were myrmecophilous, were found in the course of this thesis (**I**, **II**, **V**). Rove beetles (Family Staphylinidae) dominated the beetle list with 13 obligate myrmecophiles and 12 non-myrmecophiles of facultative or unknown association. In study **I**, rove beetles were also the most abundant, whereas in study **V**, the most abundant were featherwing beetles (Family Ptiliidae), which were mostly represented by two myrmecophilous species.

3.1.1 *Associate community in F. polyctena nests (I)*

The first study shows how diverse associate community could be found by sampling just 12 *F. polyctena* nests. Of the 70 different taxa identified in study **I**, beetles were the most diverse with 17 myrmecophilous and 10 non-myrmecophilous species. Myriapods, spiders, and hymenopterans were also well represented. In addition to the myrmecophilous beetles, there were only five other species with an obligate association to the ants: two spiders (*Mastigusa arietina* and *Thyreostenius biovatus*), one fly (*Glabellula arctica*), one true bug (*Xylocoris formicetorum*), and the shining guest ant *Formicoxenus nitidulus*. There was also another ant species, *Myrmica ruginodis*, found in one of the nests, though this species is not a social parasite. Two species included in the Red List of Finnish species (Rassi et al. 2010) were found: the near threatened (NT) pseudoscorpion *Allochernes wideri* (36 individuals from one nest) and the vulnerable (VU) spider *Cicurina cicur* (two individuals from two nests).

Species richness in the study area was estimated to be higher than what was observed. Many of the species were represented by a single specimen (singletons) or were collected only from a single nest. Species accumulation curves did not show signs of reaching the asymptote. These indicate that increased sampling effort would most likely result in the discovery of plenty new species in the studied nests (see Colwell & Coddington 1994; Magurran 2004). Only a small proportion of the true species richness was uncovered in the study area.

Generally, species composition was most similar in nests that were from the same area, especially in the case of non-myrmecophiles. With myrmecophiles this was less clear. Compositional similarity of the whole community as well as non-myrmecophiles decreased with increasing distance between the nests. Myrmecophile community showed a similar trend only when considering species abundance data. The compositional differences may at least partly reflect the differences in vegetation on the four sites. The surrounding environment (e.g. vegetation) should structure the species composition especially in the case of the species that are not dependent on the ants, since for them the primary habitat is outside of the nest. Myrmecophiles are dependent on the ants and the nest environment they provide, and thus the surrounding environment may not be as important for them as long as the conditions within the nest are good. On the other hand, some myrmecophiles spend only part of their life cycles within the ant nest.

3.1.2   *Sawtoothed grain beetle (II)*

A single female individual of *O. surinamensis* was found in a *F. rufa* nest (Fig. 4). This was surprising, since the species lives only as an indoor pest species in Finland and this was the first time it has been recorded from the wild. The species has a wide tolerance of humidity and it is relatively cold hardy, but it cannot complete its development in below the temperature of 17 °C (Halstead 1980; Robinson 2005b). The optimum temperature for its development is between 30 and 35 °C (Halstead 1980).

However, in a red wood ant nest mound, the abiotic conditions are close to optimum for *O. surinamensis* during summer, when a constant temperature of 26-30 °C is maintained, and even in winter the deeper parts of the nest mound stay above freezing point at around 5 °C (Rosengren et al. 1987; Sorvari & Hakkarainen 2009). If the sawtoothed grain beetle can live in wood ant nests, the mounds may become widespread source habitats for future infestations of this stored product pest. However, so far further sampling efforts in search of the species from ant nests in the area have not been successful. The beetle may have found its way into the nest from a nearby cultivated field of cereal crops where it could have ended up along with the grains being sown.

Figure 4. *Oryzaephilus surinamensis* female found in a red wood ant (*Formica rufa*) nest. Scale bar: 0.5 mm. (Photo by E. J. Vesterinen)

3.2   Isolation and nest volume in relation to species richness and abundance (I, V)

In support of the resource concentration hypothesis (Root 1973; Goncalves-Alvim & Fernandes 2001; Arneberg 2002; Päivinen et al. 2004), species richness of associates

(both myrmecophile and non-myrmecophile) was higher in *F. polyctena* nests with close neighbours than in more isolated nests (**I**). Similar pattern was observed by Päivinen et al. (2004) on myrmecophilous beetle species richness in *F. aquilonia* nest, and later also by Parmentier et al. (2015) on myrmecophile species richness in *F. polyctena* and *F. rufa* nests.

Unlike Päivinen et al. (2004), I found no association between abundance and the distance to the neighbouring nest. Even though colonisation is more difficult when the nest is isolated, after a species has successfully colonised a nest, the inter-nest distance may no longer be a limiting factor for that species. Contrary to other studies, in study **V**, neither species richness nor abundance of beetles was associated with isolation, although nearest neighbour distances varied considerably (11-82 m). Rather than inter-nest distance, the overall nest density surrounding the nests could be important as found with the occurrence of *F. nitidulus* in study **III**. The degree to which a nest mound is effectively isolated depends of course on the dispersal ability of the species in question as well as its location in relation to all the other nests in the area, not just the closest one. In study **V**, the variable conditions in clear fells might also be confounding factors.

How most myrmecophiles locate new nests when dispersing is not well known. However, many myrmecophiles, including *F. nitidulus*, are known to follow the scent trails left by their host species (e.g. Elgert & Rosengren 1977; Cammaerts et al. 1990; Hölldobler & Wilson 1990; Dinter et al. 2002). Thus, trails connecting the nest mounds in the multi-nest coalitions such as formed by *F. polyctena* and *F. aquilonia* may act as easy dispersal routes for these guest species. Yet, even with the ability to follow trails, dispersal becomes riskier the longer the distance between nests is.

My results show that in addition to myrmecophiles, non-myrmecophile richness was also associated with isolation (**I**). Though some species likely end up in the nests accidentally, many of them are frequently encountered with ants (e.g. Päivinen et al. 2002) and might actively seek to enter the nests once in their vicinity. For these facultative myrmecophiles, the nest environment might represent a better-quality habitat patch, where the species are able to maintain larger populations due to the accumulated resources and optimal microclimatic conditions. Laakso and Setälä (1998) reported a ten times more abundant insect fauna from the nests of *F. aquilonia* than the surrounding soil.

Päivinen et al. (2004) reported a higher diversity of myrmecophilous beetles in large nests than small ones. Contrastingly, in studies **I** and **V**, species richness and

abundance of associates were not correlated with nest volume, except in the case of myrmecophilous beetles whose richness decreased with increasing volume. However, since an equal amount of nest material was collected from each nest, this gives an indication of associate density rather than population size. Sampling the whole nest, or adjusting the sampling to be proportional to nest size, would likely reveal that large nests harbour more species. Samples were also taken from the same depth, which could explain the decrease of myrmecophiles in the samples, as they could be more aggregated deeper in the large nests.

3.3   Occurrence of *Formicoxenus nitidulus* (III)

The guest ant *F. nitidulus* was quite common in the study area in SW Finland, with ca. 60 % of the observed nests (N = 166) occupied by the guest ant. When the guest ants were found to be present, they were mostly seen within the first couple minutes of observation. Of the *F. polyctena* nests, 75 % were occupied by the guest ant, whereas the species was found in barely a third of the *F. rufa* nests. The guest was found in three *F. aquilonia* nests, while no guest ants were detected in the nests of *F. pratensis* and *F. lugubris*. Observation was by far the better method of detecting the guest ant, as sampling yielded a positive result in only 23 % of the sampled nests as well as being successful in only 39 % of the cases where the guest ant was found by observation. Also, there were no nests where the guest ant was found only by sampling. Failure to get the guest ant in the sample could be the result of not sampling deep enough beneath the surface. Alternatively, trying to focus on the nest openings could also help, as Busch (2001) found workers lurking just beneath within when looking with a flashlight.

Though inter-nest distance as such did not determine guest ant occurrence, it was more likely to occur in nests surrounded by high nest density (**III**). Also, concurring with previous knowledge, the guest ant occurred more likely in large nests (Dietrich 1997; Ölzant 2001). These results are in line with the predictions of metapopulation theory (Hanski 1994, 1999). Most social parasites are rare and published data on their occurrence are scarce (Buschinger 2009). In a large scale, socially parasitic ants usually occur in more or less isolated patches within the host range, while locally, these sites of occurrence are often characterized with particularly high densities of the host species (Buschinger 2009). Patches have to be sufficiently linked by dispersing individuals to ensure the survival of species within them (Fahrig & Merriam 1985; Adler & Nuernberger 1994; Hanski 1999; Bowne & Bowers 2004). In case of local extinction, recolonization relies on the number of dispersers and how easily they can

move within the landscape (Kindlmann & Burel 2008). A high density of occupied nests in an area will increase the chances of a population being rescued or a new nest being colonized. The risk of extinction also decreases with increasing nest (patch) size, since large nests can support larger populations (Hanski 1999). Large nests can provide the guest species with more resources and are better able to buffer against weather fluctuations (Hölldobler & Wilson 1990). Furthermore, they are usually older, and thus, have been around for longer for the guest species to find.

That *F. nitidulus* was much more likely to occur with the polydomous *F. polyctena* than the monodomous *F. rufa* is not surprising, considering that high nest density and large nests are more often the case among polydomous hosts. Furthermore, the connecting trails between nests in polydomous colonies further ease dispersal. Since single-nest colonies are not similarly connected to other nests, they might be harder to find even when distances between nests are relatively short. *Formicoxenus nitidulus* was rarely found in monodomous colonies even when they were relatively close to several *F. polyctena* nests inhabited by the guest ant. Similarly, Van Hengel (2011) reported that the guest ant occurred in nearly all of the nests of one *F. polyctena* super-colony, but was absent from all but one of the nearby *F. rufa* and *F. pratensis* nests. Together these results suggest that *F. nitidulus* prefers dispersing along the connecting trails, which might be especially true for the wingless intermorphic females. When dispersing to a more isolated nest winged females are likely in a key position. Leaving a nest that is not connected to another might be much riskier for the intermorphs, and for them it could be more prudent to remain in the same nest after mating. However, whether this is the case would require further study.

Since the nests were observed only once during this study, it is possible that the guest ant was not detected in all the nests where it is present. The probability of detecting the species is likely to be affected by their population size in the host nest mound. Possible false-negative observations could thus come from nests with only few guest ant inhabitants.

3.4 Clear felling, nest moisture content and ant-associated beetles (IV & V)

Formica aquilonia nest mounds had significantly lower surface layer moisture content in clear fells than in forests (**IV**). This is assumed to decrease the thermal capacity of the nests, since dry nests generally have more variable temperatures than moist nests

(Frouz & Finér 2007). In a previous study, nest mounds in clear fells had less stable temperature conditions compared to forest nests and were also generally cooler (Sorvari & Hakkarainen 2009). However, we found no significant difference in nest temperature between clear fells and forests. This could be due to the fact that measurements were made late in the season, in early September, when the ants stop the active thermoregulation of the nests initiating a slow cooling of the nests towards winter (Kadochová & Frouz 2014). Temperatures were also measured only once per nest during day time; thus, it was not possible to follow whether the nests in clearings lose the inner temperature during the night.

Especially steep-profiled nests seemed to be vulnerable to drying in clearings suggesting that forest built nest mounds have the wrong shape for the exposed conditions in felled areas. Nest mounds are built slowly over the years to fit their environment. In shaded forest with humid microclimate and shelter from wind, the nests are typically high in relation to diameter (Martin 1975). When these high profiled nests are suddenly exposed to drier and windier conditions their shape poses a high risk for drying of the nest material.

In study **V**, I identified a total of 17 myrmecophilous and 15 non-myrmecophilous beetle species. There was no clear difference in species composition between nests in clearings and forests. Nests with similar nest characteristics, i.e., similar moisture content and size, had a similar community composition, whereas geographic distances had no effect on it. Most species were found in both habitat types, though interestingly, all nine singleton species, which apart from one were all non-myrmecophilous, were found from clear fells. Some of them might be new post-felling colonists to the nests.

Despite the lower surface moisture content of nests in clearings, species richness did not significantly differ between the habitats, although the average number of species was slightly higher in forest nests (**V**). Also, while there was no difference in myrmecophile abundance between habitats, total abundance was higher in forests. Moreover, abundance of beetles as well as total species richness increased with increasing nest surface layer moisture content. This result is in line with the general pattern found in soil assemblages (Giller 1996; Tsiafouli et al. 2005). On the other hand, similar to what was reported by Parmentier et al. (2015) from *F. polyctena* and *F. rufa* nests, myrmecophile species richness was not associated with moisture content. Field work was done within one to three years after clear felling. It might take longer than that for clear felling to have an effect on the beetle assemblage. Moisture was only measured near the top of the nest. However, clear fell nests might

retain more moisture closer to the ground than at the top. Thus, beetles could remain in the nests, particularly if they are not very sensitive to the less stable temperature conditions.

A more detailed inspection of the occurrence of myrmecophiles revealed that beetles in the genus *Monotoma* were more common in forest nests: *M. conicicollis* (Fig. 4) was significantly more common in forest nests, whereas *M. angusticollis* occurred only in forest (though only in four nests). Other species showed no difference in occurrence between the habitats. The abundance of *Monotoma* was also positively associated with moisture content. Interestingly, these two species are wood ant specialists (Päivinen et al. 2002). Apart from one other specialist species, *Spavius glaber* (collected once from both habitats), all the other myrmecophiles in this study are more generalist in their host choice, inhabiting also the nests of *Lasius* ants (Päivinen et al. 2002). This could indicate that the wood ant specialists are more vulnerable to changes occurring to the host colony. In addition to scavenging on the ants' prey items and preying on ant brood, *Monotoma* are thought to be fungivores (Parmentier et al. 2016a, 2016b), which may partly explain their increase with increasing moisture content. Drying of the mounds may decrease the growth of decomposing fungi and bacteria, which create the basis for multi-level food webs (Jílková et al., 2015; Laakso and Setälä, 1998), and hence reduce the food resources of fungivores and bacterivores such as earthworms, springtails, oribatid mites, as well as beetles such as *Monotoma* (Laakso & Setälä 1997, 1998; Elo et al. 2016). Elo, Penttinen, and Sorvari (unpublished) found that the species richness and abundance of ant associated oribatid mites, which predominantly occupy the nest mound surface layer, increased with increasing mound surface moisture content.

Figure 4. *Monotoma conicicollis,* Scale bar: 0.5 mm. (Photo by Veikko Rinne)

4   CONCLUSIONS

This thesis, along with other recent publications (e.g. Parmentier et al. 2014; Robinson et al. 2016), clearly highlights the diversity of the associate community found within red wood ant mounds. Despite the role of wood ants as top predators of many arthropods, their nest mounds support highly abundant and species rich assemblages of associates. This needs to be taken into consideration in the maintenance and conservation of arthropod diversity in temperate and boreal forests.

Overall, I found that isolation of the ant nest mound was negatively associated with species richness and occurrence (**I**, **III**). The resource concentration hypothesis, which has generally been substantiated in plant-herbivore and host-parasite systems, is also suitable in studies of host ants and their associates. Not only is it useful in predicting the species richness of myrmecophiles but also that of non-myrmecophiles (**I**), indicating that many of these non-dependent species may perceive the nest mounds as better-quality habitat patches. Inter-nest distance may not, however, always be an appropriate measure of patch density (**III, V**). The effective isolation of a nest mound depends on the dispersal abilities of the species in question and the location of the nest in relation to the other nest mounds in the area and not just the closest neighbour. For most guest species, the information on dispersal and nest location abilities is lacking. Future studies should focus on remedying this situation to properly understand the dynamics structuring myrmecophile communities within ant nest mounds and to better establish the connections to metapopulation theory. The occurring probability of the guest ant *F. nitidulus* increased with decreasing isolation and increasing nest size (**III**). While inter-nest distance did not determine the guest ant occurrence, *F. nitidulus* was more likely to occur in high nest densities, as those found in the polydomous colonies of *F. polyctena*. Though winged queens may fly to distant locations, the results seemed to indicate that local spreading along the connecting trails is important to *F. nitidulus*. Large nests may support larger populations, but have also been around longer for the guest species to find. For high species richness of associates, forest management practices and conservation efforts should focus on preserving dense red wood ant populations. Also, while large nests may be most optimal, small and medium sized nests ensure the continuum of large nests in a population also in the future.

Nest mounds of *F. aquilonia* were significantly drier in clear fells than forest interiors (**IV**). Species richness and community composition of beetles were not greatly

affected by clear felling and only the total species richness was lower in dry nests (**V**). However, the generally lower abundance (total and myrmecophile) in dry nests, and lower total abundance in clear fells, could affect the long-term survival of populations, as small populations are more likely to become extinct (Hanski 1999). Furthermore, some species may be more vulnerable than others to the changes occurring in the nest mounds. They may be either directly affected through the changed abiotic conditions or indirectly through changes in food availability. This study investigated only the short-term effects of clear felling in active nest mounds. In case of nest abandonment, the myrmecophiles will inevitably suffer. However, more research is needed to uncover the long-term developments in the associate community of nests surviving clear felling.

Red wood ants as well as most of the other host species of *F. nitidulus* are globally near threatened (IUCN 2015) due to the loss of suitable scrub and forest habitats caused by agricultural clearing and inappropriate forest management practices. Wood ants seem to suffer even when modern forest management practices are used, and most nests will be abandoned by the wood ants within a few years of the harvesting (Sorvari & Hakkarainen 2007b). Nest abandonment probability is largely dependent on the distance to the remaining forest (Sorvari 2013). Thus, small sized clearings may not be too harmful.

Polydomous red wood ants may need large territories to maintain healthy populations (Mabelis & Korczyńska 2016; Sorvari 2016). Consequently, small forest fragments caused by agriculture and forestry are better suited to monodomous species, while large woodland areas are more common habitats for polydomous species (Mabelis 1994; Punttila 1996). In Central Europe, there is evidence that agriculture can negatively impact the quality of small adjacent woodland patches, and consequently, also the survival of wood ant populations (Mabelis & Korczyńska 2016). Maintaining an adequate habitat quality is thus important for the preservation of wood ants and their guests. Red wood ants prefer to build their nests in sunny and open areas within forests and along forest edges (Mabelis & Korczyńska 2016). Creating small open areas in managed forests, which are often dense, could help increase the chances of colonization for red wood ants. This may also benefit other forest-dwelling species. A varied forest structure will help maintain or even increase the biodiversity of forests.

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Formicoxenus nitidulus on a pine needle. (Photo by Veikko Rinne)

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