

Ant community structure in successional mosaics of boreal forests

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Cover photo © Pekka Punttila: A wood-ant mound established on the base of a dead pine tree located in the edge of a sun-lit forest opening in the Meri-Rastila Forest, Vuosaari, Helsinki.

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List of thesis chapters

This thesis is based on the following articles, which are referred to in the text by their Roman numerals:

I Punttila, P., Haila, Y., Niemelä, J. & Pajunen, T. 1994. Ant communities in fragments of old-growth taiga and managed surroundings. – *Annales Zoologici Fennici* 31 (1): 131-144.

II Punttila, P., Haila, Y., Pajunen, T. & Tukia, H. 1991. Colonisation of clearcut forests by ants in southern Finland: a quantitative survey. – *Oikos* 61 (2): 250-262.

III Punttila, P. & Haila, Y. 1996. Colonisation of a burned forest by ants in the southern Finnish boreal forest. – *Silva Fennica* 30 (4): 421-435.

IV Punttila, P., Haila, Y. & Tukia, H. 1996. Ant communities in taiga clearcuts: habitat effects and species interactions. – *Ecography* 19 (1): 16-28.

V Punttila, P. 1996. Succession, forest fragmentation, and the distribution of wood ants. – *Oikos* 75 (2): 291-298.

VI Punttila, P. & Kilpeläinen, J. 2009. Distribution of mound-building ant species (*Formica* spp., Hymenoptera) in Finland: preliminary results of a national survey. – *Annales Zoologici Fennici* 46 (1): 1-15.

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Abstract

Background and relevance: A large share of boreal biota has become threatened owing to the utilization of forests and mires for wood production. We need to understand how human impact has changed the natural successional patterns and structural characteristics of forest stands and landscape composition in boreal forests, and how these changes have affected the boreal biota, in order to be able to safeguard the native species and habitats, and to develop ecologically sustainable management regimes for forestry. The ants (Hymenoptera, Formicidae) are relevant study objects in this context because of (1) their often strict habitat requirements are coupled with social mode of life and sedentary lifestyle which make them worthy indicators of habitat conditions, and (2) especially because many of the mound-building territorial species exhibit keystone species characteristics. The distribution and abundance of this group has a great importance for forest ecosystems because of the multitude and magnitude of the ecological interactions of these species both with other forest organisms and with their environment. In this study, I pooled these effects under the term “wood-ant impact”.

Aims: The aim of this thesis is to test hypotheses concerning ant-community succession in a patchwork of forest stands of different age. Especially, I try to assess the effects of old-forest fragmentation and age-class distribution changes caused by forest management by focusing on a group of territorial keystone ant species, the wood ants (*Formica rufa* group), in which two main social strategies (monogyny i.e. single reproducing queen, polygyny, several queens) are found. I developed and tested hypotheses on how the social strategy of the species affects the occurrence and worker density of the species in the successional mosaics and, consequently, the strength of the wood-ant impact on the forest ecosystem.

Material and methods: The data were collected during several research projects in 1984–1996, and further data were gathered in the 10th Finnish National Forest Inventory (NFI10) in 2005. Most of the data sets were collected with pitfall traps and nest-mound mapping and measuring in southern Finland. In the NFI10, the sampling scheme was a systematic grid of permanent sampling plots set up over the whole country.

Results and discussion: The wood-ant dominated system of mature forests was found to disintegrate after clearcutting, and the individual-rich but species-poor community dominated by the wood ants was replaced by a species-rich community whose composition at first hand depended on how completely the wood-ant dominated system disappeared. This, in turn, may have depended on the severity of the disturbance, especially the size of the clearcut area. The subsequent ant-community succession followed rather deterministic pathways. The pioneering species were those that are capable of independent colony founding, and these were followed by species that utilize temporary nest parasitism in the colonies of pioneering species. During this stage of succession, the species composition seemed to be largely determined by species interactions (competition and slave-making). Most notably the competitive relationships

between the dominating territorials and slave-makers indirectly affected the distribution and abundance of several submissive species. When the succession proceeded and the densities of colonies increased, the competition for space seemed to be intensified due to gradually closing tree canopy and thus, nest budding may remain the only possible way of nest founding. This promoted polygyny and gave an advantage to the species capable of turning into polygynous colonies. After the tree-canopy closure, most of the species vanished and, depending on the site type and size of the clearcut area, and the vicinity of colonies of polygynous wood ants, wood ants may colonise the site again when the canopy starts to open again following self-thinning of the ageing forest. If the disturbed area were inhabited by wood ants before the canopy closure, only colonies large enough to be capable of metabolic thermoregulation of the nests should be able to survive the thicket phase following canopy closure. The occurrence of wood ant species matched quite closely to the predictions developed based on the social strategy of the species.

Among the keystone wood-ant species, monogynous ones were more common in younger than older successional stages, in less productive site types than in fertile ones, in smaller than in larger fragments of mature forests, and their colonies were concentrated at sun-lit edge habitats. The polygynous *F. aquilonia* showed quite the opposite pattern by occurring in mature forests, in more productive site types, and in large mature-forest stands, and this species was also able to inhabit shaded forest interiors in addition to edge habitats. The drainage of mires seemed to be detrimental to the mound building ants of mire habitats, while providing new suitable habitat for wood-ant species of mineral soils. Finally, the results suggest that changes in forest-disturbance regime, either natural or anthropogenic, may lead to remarkable changes in wood-ant worker population sizes and, consequently, in the strength of the wood-ant impact on forest ecosystem independently from wood-ant nest densities as such. Wood-ant communities may experience complete species turnover from the dominance of monogynous species to the dominance of polygynous ones, or vice versa, depending on the prevailing disturbance regime, and the accompanied changes in worker-ant densities were shown to be much larger than could be predicted from mere nest densities. Such changes may have remarkable impacts on forest ecosystem processes.

Tiivistelmä

Muurahaisyhteisön rakenne metsän sukkessiomosaikissa

Tausta: Merkittävä osa borealisesta metsä- ja suoluonnon monimuotoisuudesta on kärsinyt metsätaloudesta. Keskeinen kysymys luonnon monimuotoisuuden turvaamisen kannalta on se, kuinka luonnonmetsän sukkessiodynamiikka ja maisemarakenne eroavat metsätalouden määräämästä dynamiikasta ja rakenteesta. Tätä ymmärrystä tarvitaan kehitettäessä ekologisesti kestäviä metsätalouskäytäntöjä. Sosiaalisina hyönteisinä muurahaiset soveltuvat tällaiseen tähtävään tutkimustyön kohteiksi siksi, että monilla lajeilla on suhteellisen tiukat vaatimukset elinympäristönsä suhteen, ne muodostavat paikallaan pysyviä, väkirikkaita, pitkäikäisiä ja voimakkaasti ympäristöönsä vaikuttavia yhteiskuntia, ja erityisesti siksi, että monet kekoja rakentavat territoriaaliset lajit ovat ns. avainlajeja omissa elinympäristöissään. Borealaisen vyöhykkeen metsissä tällaisia ovat erityisesti kusiaiset eli kekomuurahaislajit. Näiden avainlajien esiintymisellä ja runsaudella on suuri vaikutus metsäekosysteemeihin siksi, että nämä ovat merkittävässä ekologissa vuorovaikutussuhteissa sekä muun metsälajiston että elinympäristönsä kanssa. Tässä työssä näitä vuorovaikutussuhteita tarkastellaan yleisellä tasolla ”kekomuurahaisvaikutuksena”.

Tavoitteet: Tämän tutkimuksen tarkoitus on testata muurahaisyhteisöjen rakenteen sukkessioon liittyviä hypoteeseja eri ikäisten metsiköiden muodostamassa sukkessiomosaikissa. Erityisesti tarkoituksena on arvioida metsätalouden vaikutusta vanhojen metsien pirstoutumisen sekä metsien ikärakenteen muutosten kautta havumetsävyöhykkeen avainlajien, territoriaalisten kusiaisten eli kekomuurahaislajien (*Formica rufa* -ryhmä) esiintymiseen. Näillä lajeilla ja niiden populaatioilla tavataan kahta pääasiallista sosiaalista strategiaa, jotka perustuvat kuningatarten lukumäärään (yksi- ja monikuningattarinen eli mono- ja polygyyninen strategia). Tutkimuksessa kehitettiin ja testattiin hypoteeseja siitä, miten sosiaalinen strategia vaikuttaa lajien esiintymiseen, kolonioiden tiheyksiin ja sitä kautta työläistiheyksiin, ja lopulta ekologisten vuorovaikutusten voimakkuuteen metsän sukkessiomosaikissa.

Aineisto ja menetelmät: Tässä työssä käytetyt aineistot on kerätty useissa eri hankkeissa v. 1984–1996, ja lisäaineistoa kerättiin valtakunnan metsien inventoinnin (VMI) yhteydessä v. 2005. Suurin osa aineistoista perustuu kuoppapyynteihin sekä kekopesien kartoituksiin ja mittauksiin eri ikäisissä metsissä Etelä-Suomessa. VMI-aineiston otantana oli systemaattinen pysyvien koealojen verkko koko maassa.

Tulokset ja tulosten tarkastelu: Vanhoissa metsissä vähälajisia muurahaisyhteisöjä dominoivien suurten kekomuurahaiskolonioiden havaittiin usein tuhoutuvan metsien avohakkuiden jälkeen, ja hakkuualoille kehittyi lajirunas muurahaisyhteisö, jonka rakenne näytti riippuvan aluksi (hakkuu)häiriön voimakkuudesta eli siitä, kuinka täydellisesti alueella sijainneet kekomuurahaiskoloniat olivat hävinneet. Muurahaisyhteisön sukkessiossa havaittiin testattujen

hypoteesien mukaisesti deterministisiä piirteitä. Häiriön jälkeisen sukkession pioneerilajit olivat avointen metsien lajeja, joiden kuningattaret pystyvät perustamaan pesänsä itsenäisesti. Näitä seurasivat lajit, jotka perustavat uudet koloniansa väliaikaisen pesäloisinnan kautta alueelle aiemmin asettuneiden lajien pesissä. Yhteisön rakenteeseen näyttivät vaikuttavan erityisesti lajien väliset vuorovaikutussuhteet, kilpailu ja orjuuttaminen. Dominoivien territoriaalisten lajien ja orjuuttajien havaittiin vaikuttavan niiden keskinäisen kilpailun kautta epäsuorasti myös alisteisten ja orjuutettujen lajien esiintymiseen. Sukkession edetessä muurahaiskolonioiden tiheydet kasvoivat ja kilpailu pesäpaikoista kiristyi, jolloin pesien pilkkominen vaikutti olevan lähes ainoa mahdollinen tapa uusien kolonioiden syntymiselle, mikä suosii monikuningattarisuutta. Puuston latvuston sulkeuduttua avointa latvustoa vaativat lajit hävisivät, ja jäljelle jäivät vain varjostusta sietävät lajit. Vanhojen metsien territoriaalisten kekomuurahaisten tiheikkövaiheen jälkeiseen kolonisaation varttuvaan, itseharvenemisvaiheen metsään vaikuttavat todennäköisimmin erityisesti häiriön kokoluokka ja monikuningattaristen kolonioiden läheisyys. Häiriöalueen mahdollisesti aiemmin kolonisoineista kekomuurahaiskolonioista vain ne, jotka ovat ehtineet kasvamaan riittävän väkirikkaiksi tullakseen toimeen oman aineenvaihduntansa tuottaman hukkalämmön avulla, voivat selvittää latvuston sulkeutumista seuraavan tiheikkövaiheen ylitse. Kekomuurahaisryhmän lajien esiintyminen oli pääpiirteissään tutkimuksessa kehitettyjen, lajien sosiaaliseen strategiaan perustuvien hypoteesien mukaista. Monogyyneiset lajit esiintyivät erityisesti metsän nuorissa kehitysvaiheissa, karummilla metsätyypeillä, pienissä vanhan metsän saarekkeissa sekä erilaisissa metsien valoreunoissa. Polygyynisen pohjankusian (*Formica aquilonia*) esiintymiskuva oli kutakuinkin päinvastainen: se esiintyi erityisesti metsän vanhoissa kehitysvaiheissa, tuoreilla metsätyypeillä, suurissa vanhan metsän saarekkeissa, ja se pystyi asuttamaan myös metsäsaarekkeiden sulkeutuneita sisäosia. Soiden ojituksen havaittiin hävittävän soiden kekoja rakentavat territoriaaliset lajit, ja näiden havaittiin korvautuvan kivennäismaiden territoriaalisilla lajeilla. Tulokset viittaavat siihen, että metsien häiriödynamian muutokset – olivat ne sitten luontaisia tai ihmisen aiheuttamia – voivat johtaa huomattaviin muutoksiin kekomuurahaisten työläistiheyksissä ja sitä kautta kekomuurahaisvaikutuksen voimakkuudessa metsäekosysteemeissä riippuen siitä, millaista sosiaalista strategiaa kulloinkin vallitseva häiriödynamikka suosii. Tällaiset suuretkin muutokset jäävät havaitsematta, jos kusiaistiheyksiä seurataan pelkästään kekotiheydessä tapahtuvien muutosten avulla huomioimatta tarkemmin lajeja ja niiden ekologiaa. Näillä muutoksilla voi olla huomattavan suuria vaikutuksia metsäekosysteemin toimintaan.

Summary

1 Introduction

This study focuses on ant community succession in a patchwork of forest stands of different age, and on the effects of fragmentation and forest management on a group of territorial keystone ant species in mature forests, the wood ants (*Formica rufa* group), in southern Finland. Keystone species are defined as species whose effects are large, and disproportionately large relative to their own abundance (Power et al. 1996). Additional important research topics are the macrohabitat associations of mound-building territorial species (altogether 11 different species: five species of the *F. rufa* group, five species of the *F. exsecta* group, and *F. uralensis*), including the effects of mire drainage on the occurrence of these species in Finland. The distribution and abundance of these species' groups are of utmost importance for forest and mire ecosystems because of the multitude and magnitude of the ecological interactions of these species with other forest and mire organisms and their physical environment. In this study, I pooled these effects under the term "wood-ant impact".

1.1 Background: From natural disturbance regimes of the boreal forest to anthropogenic (human-driven) ones – effects on open vs. closed-canopy habitat ant species in general, and territorial wood-ant species in particular

Under natural conditions before increased human impact, the successional cycles of boreal forests of northwestern Europe were driven both by stand-replacing disturbances (e.g. strong wildfires) that were mostly rare, and much more common and variable smaller-scale disturbances leading to variable and complex successional dynamics: cohort, patch and gap dynamics occurring with varying frequency in both pine- and spruce-dominated forests (Kuuluvainen 2009; Kuuluvainen and Aakala 2011). These disturbances included wind-throws, wildfires, floods, insect outbreaks, snowbreaks, fungal diseases etc. Because most of the disturbances occurred on a small scale (especially in mesic spruce-dominated forests with naturally long fire rotation) and large pines often survived the less severe surface fires (in dry pine-dominated forests with higher fire frequency), the pristine landscapes were dominated by old-growth forests. Such disturbance regimes favoured polygynous wood ants (exhibiting short-distance dispersal, see below) on most of the landscape apart from barren forest-site types and smaller isolated forested islands surrounded by water of mires.

Disturbance regimes changed with increasing human impact: human use of fire in, e.g. hunting, pasture burning, slash-and-burn agriculture and tar burning elevated the fire frequency and annually burned proportion of forests – already quite a sparse human population has evidently been able to increase these remarkably (Wallenius 2011). The changed disturbance regime favoured monogynous wood ants (exhibiting long-distance dispersal, see above) that were now able to colonise also forests on more fertile soils and continuous heath forest areas because

frequent and large wildfires probably decimated or weakened large polygynous wood-ant colonies in many areas. Only about one century ago the unnaturally high occurrence of fires declined steeply, and this decline seems to relate to a rapid economic and cultural transition from fire-causing traditional livelihoods to modern agriculture and forestry already before the start of efficient fire suppression (Wallenius 2011). Also the average size of forest-fire areas diminished remarkably at the same time in Finland (Fig. 1; for forest-fire statistics, see Lehmusluoto 1956; Aarne 1992; Sevola 1996; Peltola 2014; Lindberg et al. 2020), favouring again the polygynous strategy. Also the forest-management practices of that time were favourable for the polygynous strategy because saw timber was extracted with selection cuttings (high-grading) until it was condemned publicly by influential forestry authorities in the late 1940s.

The presently dominating forest-management model that is based on clearcutting was adopted after World War II. In this management practice, trees are grown in even-aged, homogenous, clearly delimited stands with rotation length of about 100 yrs or less between clear-cuttings. After the war, management based on clearcutting and artificial regeneration was rapidly spread, and several forest improvement programs were launched to intensify forest management. On landscape scale, this era of modern forestry was at first characterized by large clearcuts decimating polygynous wood-ant colonies and favouring monogynous wood ants, and large-scale ditching of mires to enhance forest growth and favouring forest ant species over mire specialists. Later, the size of clearcuts has gradually diminished from openings of > 100 ha down to a few hectares at present favouring polygynous wood ants (Fig. 2). Further, first-time ditching peaked in the end of the 1960s (300,000 ha yr⁻¹) but the practice gradually ceased by the 2000s, although at the same time the area of ditch cleaning and supplementary ditching have increased to annual 70,000–80,000 ha yr⁻¹ (Peltola 2006).

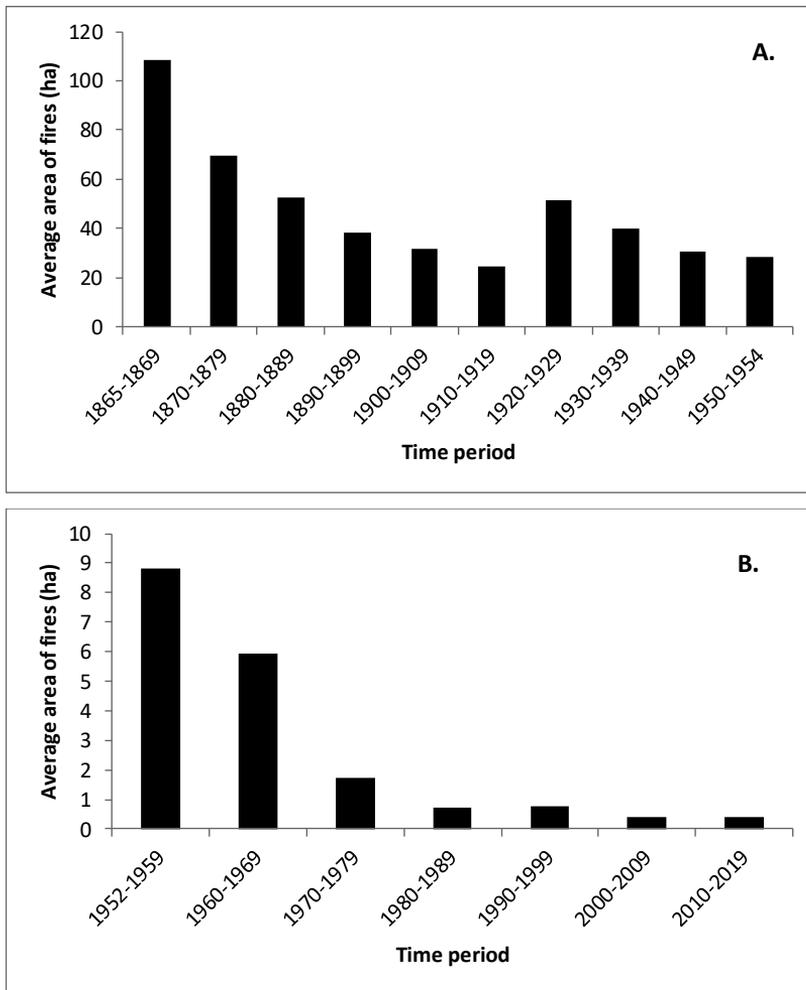


Figure 1. (A) Average area of wildfires (ha) in state forests in 1865–1954 in Finland, and (B) average area of wildfires (ha) in all forests in 1952–2019 in Finland (data from Lehmusluoto 1956; Aarne 1992; Sevola 1996; Peltola 2014; Lindberg et al. 2020). Note that the scales of vertical axes differ between panes A and B.

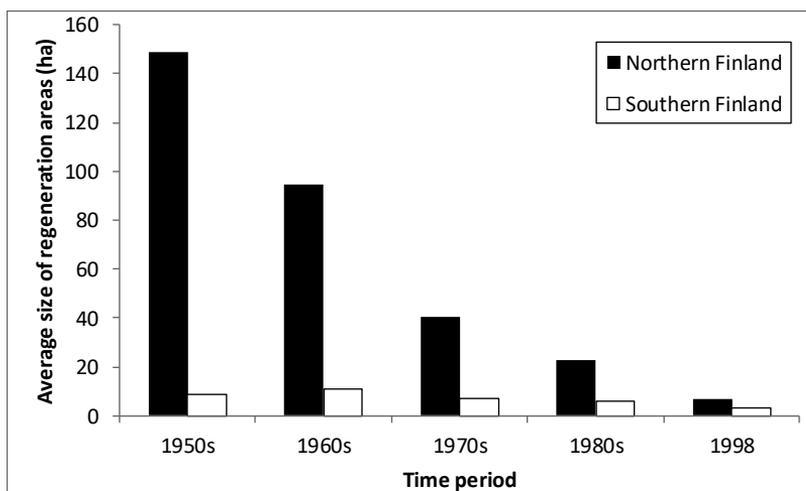


Figure 2. Average size of regeneration areas (ha) in state forests of Finland at different time periods (data from Panu Kuokkanen, Metsähallitus Parks & Wildlife Finland, pers. comm., and Rissanen 1999). At present, size of regeneration areas following clearcutting vary from less than 1 ha to a few hectares (Äijälä et al. 2019), and the average in managed state forests is less than 2 ha or less than 4 ha in southern and northern Finland, respectively (Metsähallitus 2019 <http://www.metsa.fi/uudistushakkuut> accessed 18 December, 2019).

From the early 1990s onwards, the clearcutting-management model has been slightly modified in Fennoscandia such that forest managers try to mitigate the adverse effects of management on the innate diversity of forest ecosystems to some extent. Such means are green-tree retention and safeguarding dead trees, and setting aside various types of valuable woodland key habitats. Further, according to the management recommendations, the size and shape of clearcut openings are to be adjusted to the scenery and topography such that the openings are perceived less extensive, i.e. they have smaller sight distance and, consequently, shorter distances to the neighbouring older stands than was the case with the earlier larger clearcuts. Finally, also the site-preparation methods following regeneration cuttings are lighter than earlier. These changes have favoured polygynous wood ants whose colonies were earlier erased from large clearcuts, which were completely void of trees supporting the vital resources of wood ants, the aphid colonies (II, V, Domisch et al. 2005; Sorvari and Hakkarainen 2005; 2007c; Kilpeläinen et al. 2008; Sorvari and Hakkarainen 2009; Gibb and Johansson 2010; Sorvari 2013; Sorvari et al. 2014).

Recently, however, some further major changes in forest management has taken place. First, the lower age limits for regeneration-cutting age of pine and spruce-dominated forests have been lowered by 10–35 yrs depending on geographic location, site type and tree species in the Finnish management guidelines after the 2000s (Metsätalouden kehittämiskeskus Tapio 2001;

2006; Äijälä et al. 2014) and may further lower remarkably, as in the renewed Finnish Forest Act (implemented in 2014) regeneration-age restrictions were abandoned altogether (Äijälä et al. 2019). Such a development is bound to cause further decline of species dependent on old forests, possibly also of polygynous wood ants. Second, further intensification of management has taken place in the 2000s with rapidly increasing energy-wood harvesting of small-diameter stems, logging residue (i.e. tree tops and branches) and stumps to produce forest chips for heating and power plants in order to cover 38% share of energy consumption with renewable energy sources in Finland (National Energy and Climate Strategy 2013; Peltola 2014). The amount of dead wood may decline further in managed forests because the use of forest chips has increased rapidly and the aim is to increase the annual usage to 13.5 million cubic meters by 2020 and to 15 million cubic meters by 2030 (Maa- ja metsätalousministeriö 2011; 2015; 2019). This is more than an order of magnitude higher level than the present “retention forestry” or “biodiversity-orientated management” has been estimated to produce new dead wood through retention trees in managed forests annually (Hetemäki et al. 2006; Forsius et al. 2016; Korhonen et al. 2016). Also large amounts of dead standing trees and logs have been harvested for energy wood during the logging operations since the beginning of 2010s and, consequently, the so called dead-wood budget (the amount of dead wood produced through green-tree retention minus the amount of dead wood harvested and unintentionally destroyed during logging operations) of managed forests has turned negative (Kuusela and Musta 2015; Forsius et al. 2016; Korhonen et al. 2016; Kuusela and Punttila 2017). Harvesting dead trees, together with their unintentional destruction in forest-management operations (thinning, clearcutting, energy-wood harvesting, site preparation) forms an additional threat for dead-wood dependent biodiversity (Hetemäki et al. 2006; Forsius et al. 2016; Korhonen et al. 2016). Earlier, the logging residues and stumps were left behind to decay in the managed forests which otherwise were suffering from the deprivation of dead wood and thus, these served as man-made substitutive habitat for saproxylic species lacking innate substrates (Forsius et al. 2016). Several ant species – including the wood ants – nest or establish their new colonies in dead wood, e.g. downed logs, snags and tree stumps (III, Oinonen 1957; Oinonen and Wuorenrinne 1976; Franch and Espadaler 1988; Włodarczyk et al. 2009; Persson et al. 2013; Higgins et al. 2017).

Thus, the innately large continuous areas of old forests and virgin mires have been replaced by a small-scale mosaic of small-sized forest stands and ditched mires in younger successional stages, and the proportion of old forests and especially old-growth stands has collapsed (Auvinen et al. 2007; Kaakinen et al. 2019; Kouki et al. 2019). The remaining small old-growth patches have become isolated from each other in the matrix of younger managed stands. At the same time the structure of forest stands has changed throughout and rather uniformly in the managed forest landscape, the most important change being the decreased amount of dead wood (Siitonen 2001; Hyvärinen et al. 2019; Kouki et al. 2019). Similarly, vast areas of mires have been drained to enhance forest growth, especially in southern Finland where nearly 80% mires have been drained (Auvinen et al. 2007), which has benefitted forest-dwelling ant species at the expense of mire species (VI, Vepsäläinen et al. 2000; Punttila et al. 2016). The general

eutrophication of forests and mires resulting from atmospheric deposition of eutrophying substances like nitrogen benefits species of fertile forests at the expense of species of poorer habitats (Kaakinen et al. 2019; Kouki et al. 2019), and in the wood-ant group, the polygynous species may gain advantage over the monogynous ones at least to a certain point – it is possible that the development of dense and tall nitrophilous vegetation may eventually lead to increased probability of colony extinction and decreased probability of colony establishment owing to habitat deterioration (Mabelis and Korczyńska 2016). These changes have affected a large amount of forest- and mire-dwelling organisms dozens of which have become threatened (Rassi et al. 2010; Hyvärinen et al. 2019) while others have benefited even to such an extent that now they are regarded as forest pests.

Further major changes affecting boreal-forest biota are expected because of climate change. Direct model predictions concerning wood ants or boreal ant fauna in general are not available, but major community-level changes are expected because the changes are predicted to be so all encompassing, and temperature has been predicted to increase especially at northern latitudes (see Punttila 2020 and references therein). In Finland, major changes affecting forest biota include e.g. the following: climate has already warmed by 2.5 °C since 1850, and the warming has been the strongest in winter, already 5 °C, reducing ground freezing zone; also yearly precipitation has been estimated to increase by 8–20%, and climate warming will lead to longer thermal growth seasons (see Aapala et al. 2020 and references therein). In forest habitats, spruce is expected to suffer from draught, deciduous tree species are expected to benefit from the increasing temperatures, and xeric and barren habitats are expected to suffer from eutrophication (aerial deposition boosting the effects of warming climate) (Kouki et al. 2019; Punttila 2020 and references therein). Climate change has already increased the annual growth of the forests of Finland (Kauppi et al. 2014; Henttonen et al. 2017) and probably this continues also in the future, although it is not clear that the growing stock should continue to increase because also various large-scale abiotic (wildfires, draught, wind, snow and ice) and biotic (insect pests, pathogens) disturbances are expected to become much more common in the future (Soja et al. 2007; Seidl et al. 2017), and their effect on growing stock is the opposite. The increasing temperature and changes in precipitation and disturbance dynamics are expected to affect forest biota a lot in the future, and these changes are boosted by other simultaneous anthropogenic changes like fragmentation and decline of natural forests, and eutrophication (Milad et al. 2011; Punttila 2020). An important future research topic should be to evaluate how these changes are reflected in the distribution and abundance of the keystone wood-ant species in the boreal zone.

2 Aims of the thesis: testing the hypotheses of ant-community succession, and the predictions based on the variation of social strategies of ant colonies of wood ants in relation to the forest environment, the successional mosaics

The objective of the thesis is to test and develop further hypotheses concerning successional pathways of ant communities and the distribution of species with different social strategies, and to examine how forest management has affected these, and what may the consequences for the forest ecosystem be. The ultimate aim is to answer the important question how natural ant-community successional pathways differ from those driven by forestry. Unfortunately, this question cannot be answered directly owing to the rarity of especially young stands in natural condition and thus, the studies must partly rely on indirect evidence. This study focuses on ant community succession in a patchwork of forest stands of different age, and on the effects of fragmentation to a group of territorial keystone ant species in mature forests, the wood ants (*Formica rufa* group). The distribution and abundance of this group are of utmost importance for forest ecosystems because of the multitude and magnitude of the ecological interactions of these species with other forest organisms. Another aim is to evaluate the effects of mire drainage on mound-building species of mire habitats.

In particular, I test the hypotheses by Vepsäläinen and Pisarski (1982) concerning the successional pathways of ant communities (I–IV). The original hypotheses concerned land uplift islands, but I test them in the context of successional mosaics of mainland forests. These hypotheses state that stochasticity may have a rather limited role after the colonisation of empty or disturbed forest patch. After a successful colonisation several deterministic factors guide the community succession, e.g. the habitat requirements and dispersal capacity of the species, the competitive capacity ultimately determined by the social structure of the colonies, and the dependence of the species on other ant species during the colony founding or throughout the whole colony cycle (Vepsäläinen and Pisarski 1982). I test these hypotheses with several data sets collected mostly with pitfall traps from forest stands of different ages in southern Finland. A short summary of the competitive capacity of the species included in this study is as follows: Savolainen and Vepsäläinen (1988) summarized the factors affecting the social organization of an ant colony and the density of foraging ant workers and further, their competitive ability with other ant colonies, and their table 1 shows the classification of boreal ant species into three-level competitive hierarchy. The lowest-level species are termed submissives with small worker force (often less than 500 individuals) and short foraging ranges (often only a few meters) from the nests – these species defend only their nests against other ants. In this study, submissives include e.g. *Formica fusca*, *F. lemani* of the subgenus *Serviformica* and several species of *Myrmica*. The mid-level species are termed encounterers with somewhat larger worker force and longer foraging distances, and these species defend also valuable food sources in addition to their nests. In this study, encounterers include *Camponotus herculeanus* and *Lasius niger*. Finally, the top-level species are termed territorials with large worker force (hundreds of

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thousands to some millions individuals) and long foraging distances (even more than 100 meters), and these species defend also their foraging area. In this study, territorials include the species of *Formica rufa* group and *Formica exsecta* group.

I also developed further hypotheses for the distribution of wood-ant species with different social strategies (V, see below). These hypotheses were refined by Punttila and Kilpeläinen (VI) who introduced a habitat hypothesis according to which habitat productivity and thus, the amount of resources and related canopy openness as such in addition to the presumed productivity-dependent disturbance frequency favours monogynous strategy. This hypothesis complements the earlier habitat-disturbance hypothesis (V).

The above hypotheses state that monogynous (usually a single reproducing queen in a colony) wood-ant species capable of founding new colonies through long-distance dispersal and temporary nest parasitism in *Serviformica* colonies should be more common in disturbance-prone and less productive open-canopy habitats, in younger successional stages and in edge habitats in smaller and isolated mature-forest fragments than polygynous (many queens per colony) species. Polygynous wood-ant species exhibiting short-distance dispersal (step-by-step dispersal) by colony budding are capable of forming multi-nest colonies where the individual nest mounds are supported by the rest of the colony network. These species should be more common in stable and more productive closed-canopy habitats, in later successional stages, and they are capable of inhabiting forest interiors than monogynous species, and they should dominate well connected larger fragments and continuous areas of mature forests more often than monogynous species. These hypotheses are tested both with comprehensive mound-mapping survey in southern Finland (V, VII) and with a large-scale inventory data set from whole Finland (data collected in the 10th Finnish National Forest Inventory, NFI10) (VI).

I focus on particular methods of forest management that have been practiced on a large scale throughout Finland especially since the 1950s, clearcutting and drainage, both of which have affected a large number of forest- and mire-dwelling organisms. With the NFI10 data, also the knowledge of distribution and habitat associations of the different mound-building *Formica* species encountered in Finland is updated (VI).

Finally, I summarize how forest management has affected the distribution and abundance of the keystone species with different social and ecological strategy, and discuss the potential ecosystem impacts of these changes (VII).

Previous research pertaining to these topics have been reported in detail in the original papers of the current thesis (I–VII), and further studies have increased the understanding of the mechanisms beyond the destruction – and survival – of territorial wood-ant colonies following clearcutting (Sorvari and Hakkarainen 2004; 2005; 2007a; b; c; Sorvari et al. 2008; Sorvari and

Hakkarainen 2009; Gibb and Johansson 2010; Johansson and Gibb 2012). These above studies showed, for instance, that clearcutting affects the aggressiveness, colony size, sexual reproduction, sex ratio, worker size, immune defence and food quality of *F. aquilonia*.

3 Material and methods

The data collection of this study was conducted in two phases: most of the data were collected in several research projects led by Yrjö Haila in 1984–1996, and further data were gathered in the 10th Finnish National Forest Inventory (NFI10) in 2005 in collaboration with a research project led by Leena Finér in 2003–2010.

Most of the data sets dealing with ant-community succession were collected with pitfall traps (I–IV), but also nest-mound mapping and measuring (V–VII), direct nest searching (III) and artificial nest sites (III) were applied. The suitability of pitfall trapping in ant-community studies is discussed in detail in I and IV. Especially in wood ants, heavily biased catches may be obtained by using only a small numbers of pitfall traps because of the unevenness of the distribution of the workers in their territories on their foraging trails and intervening terrain (see e.g. Fig. 2 in Savolainen and Vepsäläinen 1989). Such biases can be alleviated by using larger numbers of traps and avoiding setting the traps on ant trails which, however, is not easy in cases where the trapping season is started very early in the spring before the ants have started foraging. The data dealing with the effects of forest succession and fragmentation on territorial mound-building species were obtained by nest-mound mapping and measuring of all inhabited and abandoned nest mounds in the study stands (V, VII). In NFI10, the sampling scheme was a systematic grid of permanent sampling plots set up over the whole country, and all the inhabited and abandoned mounds on the sample plots were mapped and measured also in this study (VI). For more detailed descriptions of the materials and methods, see the original research papers (I–VII).

In the paper I, the structure of ant communities was studied by sampling with pitfall traps in 24 mixed coniferous old-growth fragments (> 140 yrs old) and their edges, and managed stands of different ages surroundings the fragments in southern Finland, and the study thus comprised separate 48 forests stands and 72 sampling sites. The data comprised 144,048 workers of 17 species and 94 queens of 11 species, and altogether 19 ant species.

In the paper II, the colonisation of clearcut forests by ants was studied by using pitfall-trap data collected from clearcut areas of different age in southern Finland, and mature forests (> 120 yr) were compared with areas that were clearcut 0, 2 and 10 yrs before trapping, and the study comprised 10 separate forest stands and 28 sampling sites. These data comprised a larger midsummer sample with a total 32,205 worker ants of 22 species and a total of 447 queen ants

of 14 species, and a smaller (partly overlapping) whole-season sample where a total of 18,343 worker ants of 16 species and 176 queen ants of 11 species were encountered.

In the paper III, the colonisation of a burned clearcut by ants in southern Finland was monitored for five years using pitfall traps, and for four years using artificial nest sites (altogether 216 nest plates monitored yearly) and direct nest sampling from the ground (altogether 96 sampling plots) and from dead wood (cut stumps, altogether 96 sample stumps), and the succession was compared with a non-burned clearcut of the same age and with mature-forests controls monitored using pitfall traps, and the study comprised 6 separate forest stands and 12 sampling sites. These pitfall-trap data comprised 12,647 worker ants and 278 ant queens belonging to 14 and 12 species (16 species altogether), respectively. The stumps and the artificial nest sites attracted dozens of nest-founding queens of especially two species, but their survival to colony establishment was low.

In the paper IV, the structure of ant communities was surveyed in young forests that were clearcut and planted with conifers 14–20 yrs before the sampling by pitfall trapping in southern Finland. The study comprised 4 separate forest stands (these stands were formed of 1–4 separate forest-management compartments) and 16 sampling sites. These pitfall-trap data comprised 37,479 worker ants and 150 queen ants of 22 and 11 species, respectively.

In the papers V and VII, I mapped and measured the nests of eight territorial mound-building ant species, three of which belonged to the wood-ant group (*Formica rufa* group), in fragmented forests of different age in southern Finland. The total mapped area comprised 12 young forest stands (14 to 25 yrs old; 1.2–11.5 ha in size; 62.0 ha altogether) and 37 old-forest fragments of different size (> 100 yrs old; 0.4–75.8 ha in size; total area 334.6 ha). The data included 1,544 inhabited and 215 abandoned mound nests of four wood-ant species, the mainly (in Finnish populations) monogynous *Formica lugubris* (161 nests), *F. rufa* Linnaeus, 1758 (32) and *F. pratensis* (13), and the highly polygynous *F. aquilonia* (613), and four other territorial mound-building species, the facultatively polygynous *F. truncorum* Fabricius, 1804 (29), *F. uralensis* Ruzsky, 1895 (17), *F. exsecta* Nylander, 1846 (267) and *F. sanguinea* Latreille, 1798 (412). In the paper VII, I compare the use of different wood-ant density indices, and discuss ecosystem-level impacts of management-induced changes in wood-ant distribution and abundance.

In the paper VI, the first year's data of the 10th Finnish National Forest Inventory of mound-building ants (2005–2008) was used and a total of 4,150 sampling plots of little less than 0.05 ha each were covered in the whole country, excluding Åland islands, Kuusamo area and the northernmost Lapland, and altogether 533 active and 178 abandoned ant mounds were encountered, sampled for workers, and measured. These data comprised 11 mound-building ant species.

Statistical methods used in the papers I–VII include redundancy analysis (RDA) to relate the variation in ant community variation to the environmental characteristics of the sampling sites (I, IV), principal component analysis (PCA) and detrended correspondence analysis (DCA) to explore floristic variation and ant-assemblage variation among the sampling sites (I, II, III, IV), two-way indicator species analysis (TWINSPAN) to classify the sampling plots according to their habitat characteristics (II, IV), and log-linear models for contingency tables to explore environmental contingencies in species' interrelations (I, IV). Generally, non-parametric statistics were used throughout the study (I–VII) e.g. to compare the occurrences of species among habitat types and to explore the interrelations of ants and environmental variables (e.g. Kruskal-Wallis tests by ranks, Spearman rank correlations, log-likelihood ratio tests, chi-square tests, and Fisher's exact tests).

4 Main results and discussion

4.1 How forest management has changed the ant communities in general from primeval conditions

The old-forest ant community in my main study area in southern Finland consisted of practically only four common shade-tolerant species, *Formica aquilonia*, *Myrmica ruginodis* Nylander, 1846, *Camponotus herculeanus* and *F. lugubris*, prevailing most likely also in primeval conditions, whereas most of the other ant species inhabited the early stages of forest succession that presumably became more common only with increased human impact (I, II, III, IV, see also Savolainen et al. 1989; Punttila 1994; Niemelä et al. 1996; Punttila 1997). In managed forest landscapes, the changes in age-distribution of the forests from the dominance of old forests to the dominance of young ones, and the fragmentation of old-growth forests resulting in increased proportion of edge habitats as compared with pristine conditions, have provided much more inhabitable area for these open-country species than were available at the times before increased human impact.

Similarly, the relative abundances of the territorial wood-ant species (*Formica rufa* group) exhibiting different social strategies have most likely changed a lot in accordance with the changes in age-class distribution and the average size of disturbances in forest landscapes (V, VII). The multi-nest supercolonies of the polygynous *F. aquilonia* have evidently suffered, and the monogynous species such as *F. lugubris* seem to have benefitted from large-scale and intensive clearcutting under forest-management regimes prevailing from the 1950s to the 1980s. Later, the development in the managed-forest landscapes in Finland from 1990s onwards may have changed the pattern remarkably because of diminished disturbance size which results in higher survival rates of polygynous wood-ant colonies in clearcut areas than earlier (VII and references therein, Punttila 2004). Further, the general eutrophication of barren forest types (Kouki et al. 2019) may have promoted the spread of polygynous wood-ant colonies by providing more inhabitable area not only from the drained mires (VI) but also from xeric and

sub-xeric heath forest types leading to displacement of monogynous, less populous wood-ant colonies there (as discussed in VII).

The drainage of mires seems to be detrimental to the mound building ants of mire habitats (*F. uralensis*, *F. forsslundi* and *F. fennica*) while providing new suitable habitat for wood-ant species of mineral soils (VI, see also Vepsäläinen et al. 2000; Punttila et al. 2013; Punttila et al. 2016). This decimation of the territorial mound-building mire species has happened on a very large scale in southern Finland where nearly 80% mires have been drained (Auvinen et al. 2007). The case of *F. fennica* here is interesting: according to Bernhard Seifert (pers. comm. with the authors of Hakala et al. 2018, and Seifert 2019), these observations represent setae-reduced *rubens*-mutant of *F. exsecta*. Colonies of this type were encountered only on mire habitats in the NFI-data (VI, also Punttila, Kilpeläinen et al., unpublished NFI data 2006–2008), and similarly, also Ødegaard (Ødegaard 2013) reported several colonies of this type inhabiting mires in Hedmark, Norway (see also Hakala et al. 2018 for the lack of genetical differences between these morphs).

4.2 The wood-ant dominated system of mature forests was found to disintegrate after clearcutting

The wood-ant dominated system of mature forests seem commonly to disintegrate after clearcutting, and this has been suggested to be a result of the loss of food resources, especially the aphid colonies of mature trees, and unfavourable microclimatic conditions of clearcut areas (II, Rosengren and Pamilo 1978; Vepsäläinen and Wuorenrinne 1978; Sorvari and Hakkarainen 2007c; Žmihorski 2010; Sorvari et al. 2014). The study by Gibb and Johansson, however, suggested that shortly (1–4 yr) after clearcutting wood ants harvested similar amounts of aphid honey dew in clearcuts and old forest, which may have resulted from large densities of tree saplings with abundant aphid sources and also abundant retention trees in the study clearcuts (Gibb and Johansson 2010). Johansson and Gibb also found that clearcutting seems to affect the quality of the honeydew, and lower food quality may explain the poorer condition of *F. aquilonia* workers in clearcuts than in old forests, the observed smaller size of workers and their reduced abundance in clearcut areas (Johansson and Gibb 2012). It seems, however, that when the disturbance size becomes smaller the polygynous wood-ant colonies show much higher survival rate than when the clearcut openings are larger (I, II, IV, VI, VII, Punttila 2004; Sorvari and Hakkarainen 2005; 2007c; Kilpeläinen et al. 2008; Sorvari et al. 2011; Sorvari 2013).

Clearcutting combined with prescribed burning seemed to have destroyed wood-ant colonies, but additionally also other mature-forest species suffered from fire, although here only one burned area was studied (III). *Myrmica ruginodis* was able to survive only in less severely burned moist sites, whereas in a non-burned clearcut it seemed to have benefitted from the enhanced light conditions (III). At least severe fire seems to result in ant-free disturbed forest

habitats where pioneering species may immigrate freely, although the mortality of dispersing queens appeared to be high (III), before the terrain becomes crowded with ant colonies. Ants presumably survive low-severity fires much better as suggested by the results of a study on the effects of prescribed burning by Gibb and Hjältén in northern Sweden, where the differences in ant fauna between burned and unburned clearcuts seemed to be negligible at least shortly (< 2 yr) after the fire (Gibb and Hjältén 2007). Gibb and Hjältén (2007) observed that burned clearcuts attracted *Leptothorax acervorum* (Fabricius, 1793) queens similarly as found in a study which followed the colonisation of a burned mountain-birch forest for four years following the fire in subarctic Finland (Punntila et al. 1994). More generally, disturbed habitats seem to attract nest-founding queens (II, III, Punntila et al. 2016 and references therein). A field test of removal of territorial wood ants *F. aquilonia* conducted in northern Sweden failed to find any response in the abundances of other old-forest ants, *C. herculeanus* and *M. ruginodis*, in old forests from which the wood ants were removed (Gibb 2011; Gibb and Johansson 2011) – this result can most likely be explained by the lack of canopy-opening and soil-exposing disturbance attracting flying, nest-founding females of these species which seem to establish their new colonies in early-successional disturbed habitats (II, III, Punntila et al. 2016). Further, the nest densities of these species may be very low at late-successional stages, probably both because of unfavourable microclimate and long-term exploitation by the wood ants. Nest densities of ant species with small-sized colonies (in terms of worker population) start to decline following canopy closure in successional boreal forest (II).

4.3 The post-disturbance ant-community succession followed rather deterministic pathways largely as predicted by the hypotheses of Vepsäläinen and Pisarski (1982)

In the colonisation stage after clearcutting, the role of stochasticity may be counter-balanced by several deterministic, species-specific factors in the succession of ant assemblages as suggested by Vepsäläinen and Pisarski (1982). It seemed that the pioneering species were those that are capable of founding colonies independently by single queens, and they were followed by species utilizing temporary parasitism in nest founding (II, III, see also Punntila et al. 2016 for restored mires). The ant-community succession after severe fire on a clearcut treated with prescribed burning differed from that on a non-burned clearcut (III), and there were also remarkable differences in assemblage structure among stands in young 10–20 yr old successional stages suggesting that habitat selection during the colonisation phase and priority effects and competition bring determinism in the successional pathways of boreal ant communities (II, III, IV).

It seems that increasing ant-colony densities and worker populations lead to habitat crowding in young successional stages, and at this point new colonies are evidently established mostly through colony splitting until the closure of tree-canopy cover colonies (see also Seppä et al. 1995), after which only shade-tolerant colonies and species are able to persist (II). Evidently

species interactions are strong and affect a lot to the ant-community succession at this crowded stage, as ecologically similar species pairs tended to show exclusive spatial distributions (II, IV). In crowded conditions of younger (14 yr old) sapling stands, the aggressive slave-making ant *F. sanguinea* seemed to determine the ant-community structure, and in older sapling-stage stands before the tree-canopy closure, ant-community structure seemed largely to be determined by the territorial wood-ants, polygynous *F. aquilonia* and monogynous *F. lugubris* (IV). The competitive status of the species' were reflected in the distribution patterns observed, competition and slave-making being important on larger spatial scales among the forest stands studied (IV). On smaller scales within the stands, variation in moisture and light availability seemed to enable the co-occurrence of certain submissives by mitigating nest-site competition and the effects of slave-making (IV). The species distributions and abundances seemed also to reflect indirect effects of competition and slave-making on submissive species, most notably so in the two common formicines of the subgenus *Serviformica*, *Formica fusca* Linnaeus, 1758 and *F. lemani* Bondroit, 1917, which indirectly benefitted from protection by the territorial wood ants against enslaving by *F. sanguinea* in these data (IV, see also Czechowski 2000; Czechowski and Vepsäläinen 2001; Czechowski and Markó 2006; Väänänen et al. 2010; Peral et al. 2016).

4.4 The hypotheses presented in the papers V and VI on the distribution of wood-ant species exhibiting different social strategies in relation to forest succession, fertility and old-forest fragmentation, were mostly supported by the results

The most common monogynous wood-ant species in my data, *F. lugubris*, seemed to occur more frequently in young than in old forests, and in small than large old-forest stands, whereas the opposite was found in the polygynous *F. aquilonia*, which was more common in old than young forests, and in large than small old-forest fragments (V). Additionally, the monogynous wood-ants seemed to occur more frequently on poor than on fertile forest soils, whereas the opposite was found in the polygynous species (VI). Open-canopy forests were found to be favourable for mound-building territorial species with small colony size, probably because small colonies are dependent on direct sunlight, whereas large colonies with large worker force can rely on metabolic thermoregulation of the nests (Rosengren et al. 1987) and thus, inhabit also shady forest interiors (V, VI, VII). Sun-lit edge habitats of e.g. canopy openings are important for establishing new nests in all mound-building ant species, both for monogynous ones establishing new colonies through temporary nest parasitism in *Serviformica* nests inhabiting such sites, and for polygynous ones spreading through nest-budding into these microclimatically favourable sites (V). Generally, the density of ant mounds was much higher in forest edges than in forest interiors (VI). Further, the monogynous wood ant *F. lugubris* with smaller worker force occurred in edge habitats more commonly than the polygynous *F.*

aquilonia (V). In *F. aquilonia*, the nests in edge habitats were smaller than nests in forest interiors (VII, see also e.g. Kilpeläinen et al. 2008).

4.5 Updated knowledge of the distribution of mound-building territorial ant species

In the paper VI utilizing the NFI10 data, fresh distribution data of altogether 11 mound-building territorial ant species was obtained. Of these species, *F. polycтена*, *F. aquilonia*, *F. lugubris*, *F. exsecta* and *F. uralensis* occurred throughout the country, whereas *Formica rufa*, *F. pratensis* and *F. pressilabris* were more restricted to south. A comparison of the nest densities found in NFI10 data with earlier NFI3 data gathered in the 1950s on general ant-mound densities without species-specific information (Wuorenrinne 1974; Rosengren et al. 1979; Kilpeläinen et al. 2005) suggests that forest fragmentation and increased amount of edge habitats favourable for colony founding have presumably boosted the nest density of mound-building ants (VI). At the same time the drainage of mires has evidently strongly reduced the amount of habitat of three of these mound-building species since the 1950s (VI).

4.6 Changes in disturbance regime are suggested to lead to remarkable changes in the strength of wood-ant impact depending on which social strategy of wood ants is favoured by the regime because of the predicted changes in worker-ant population sizes

My results suggest that changes in forest-disturbance regime, either natural or anthropogenic, may lead to remarkable changes in wood-ant worker population sizes and, consequently, changes in the wood-ant impact independently from mere wood-ant nest densities because of species turnover (VII). Large-scale forestry-induced changes in landscape structure seem to have affected differently the wood-ant species exhibiting different social strategies (the monogynous vs. polygynous strategy, V, VII). Changes owing to large-scale clearcutting and old-forest fragmentation appear to be much more striking when estimated on the basis of worker populations (workers per hectare) than on the basis of more conventional methods of measuring just nest densities or nest volumes per hectare (VII). Large-scale changes in wood-ant worker populations may have far-reaching consequences on ecosystem processes owing to the diverse and significant effects of the wood ants on other forest organisms, the wood-ant impact (VII and references therein, see also Punttila 1998; 2004): in short, wood ants affect the abundance and distribution of many forest-dwelling invertebrates and even vertebrates at all forest layers from the forest soil and floor up to the tree trunks and canopies, they form an important resource for both invertebrates and vertebrates, they affect soil bioturbation, they have an important role in cycling and relocating carbon and nutrients, in plant dispersal and, because they exploit sap-sucking aphids and prey upon leaf-chewing insects, they affect tree growth and plant production. The intensive forest management with large clearcuts and fragmentation of mature forests especially from 1950s to 1980s presumably lowered wood-ant worker densities by

decimating polygynous colonies albeit creating opportunities for monogynous ones (VII), and the wood-ant nest density as such may have remained quite unchanged. It is possible, however, that the present development may lead to the opposite because of diminished clearcut sizes and general eutrophication of barren forests favouring the polygynous strategy (VII). An important future study question is whether wood-ant worker densities can become unnaturally high owing to the dictating polygynous strategy in the absence of large-scale disturbances and with very low densities of the important natural predator of wood ants, the brown bear. A possible scenario is that the wood-ant impact on forest ecosystems may reach dimensions not experienced before – except on small scale within the territories of very large and old polygynous colonies. In forest-conservation areas, such a development might turn out to be a major problem if polygynous wood ants should conquer all available land in great numbers. Such a development should inevitably lead to severe negative consequences for forest biodiversity and to homogenization of forest-species' assemblages (VII, see also Punttila 2011; Frizzi et al. 2018).

5 Conclusions: implications for forest management and nature conservation

The results show that large clearcuts are detrimental to polygynous wood-ant colonies but this effect seems to be mitigated when clearcut size becomes smaller and presumably also when large amounts of living trees potential for aphid colonies are retained in the clearcuts and neighbouring stands close by, which is a direct consequence or by-product of diminished clearcut sizes (V, VII).

Similarly, mire drainage to enhance forest growth is detrimental to mound-building ants (*F. uralensis*, *F. forsslundi* and *F. fennica* [or *rubens*-morph of *F. exsecta*]) of mire habitats. Their habitats cannot be compensated by other means than mire restoration presently practiced mainly on nature conservation areas (VI, Punttila et al. 2013; Similä et al. 2014; Punttila et al. 2016).

The reduced size of clearcut areas may have far-reaching consequences for forest ecosystems because the response of the keystone species, the wood ants, is largely dependent on the spatial extent and the severity of the disturbance and later on, as the succession proceeds to the maturity of the stands, the size distribution of the stands. During the history of modern forest management in Finland, the size of both clearcuts and forest fires has remarkably decreased which has alleviated the negative effects of such disturbances on polygynous wood ants. The results indicate that the densities of mound-building ants may have increased from the 1950s because of increased proportion of edge habitats, a consequence of forest fragmentation and reduced stand size (VI, Kilpeläinen et al. 2005). Before the increased human impact, predation by brown bear most likely controlled the abundance of polygynous wood ants more efficiently than today. This possible effect of brown bear predation on wood ants deserves more research

effort in the future, but in most areas in Fennoscandia the density of the predator is in any case too low for such a control. Thus, there may be no restrictions for polygynous wood ants to spread on all the available forest area at present. At the same time, however, the monogynous wood-ant species and other territorial *Formica* species of young successional stages and mound-building species of mire habitats are losing their potential habitat because they are competitively inferior to the polygynous wood ants (see also Kilpeläinen et al. 2008). These changes may have far-reaching consequences for the forest ecosystems because of the multitude and magnitude of the ecological interactions of wood ants with other forest-dwelling organisms, and because the intensity of these interactions is dependent on the social strategy favoured by forest management practices. When the polygynous strategy is favoured, the much larger worker force in polygynous colonies as compared with monogynous ones may result in extremely high worker densities in the forests when the populations are not controlled neither by severe-enough disturbances nor brown bear (which presumably was the case in primordial conditions). To alleviate such undesirable effects of forest management, management practices should be developed to match more closely to the natural variability in forest disturbance dynamics and landscape structure (see Haila et al. 1994; Kuuluvainen 2002; Jögiste et al. 2007; Kuuluvainen 2009; Kuuluvainen 2016).

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