Dissertationes Forestales 300

Insect and storm disturbance in boreal forests — predisposing site factors and impacts on ecosystem carbon

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Academic dissertation

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Abstract

The importance of forests and soil in carbon (C) sequestration and storage is continually increasing with climate change. Disturbances, such as storms and insect outbreaks, are the drivers of forest functioning, composition and structure, and many of them are predicted to become more common in the future. However, environmental factors that predispose forests to disturbance as well as the diverse effects of disturbances on forest C cycling are not fully known. In this dissertation, stand, site and soil characteristics predisposing forest stands to outbreaks of two common insect species that can cause tree damage and mortality—the common pine sawfly (*Diprion pini* L.) and the European spruce bark beetle (*Ips typographus* L.)—were examined, and the impacts of storm and *I. typographus* disturbance on soil respiration, tree and soil C stocks, and microbial community composition and associated C contents were investigated in forests located in eastern and southern Finland.

The level of tree damage by *D. pini* and *I. typographus* in managed Scots pine (*Pinus sylvestris* L.) and urban Norway spruce (*Picea abies* (L.) Karst.) forests, respectively, were associated with various site and soil characteristics. Defoliation of *P. sylvestris* by *D. pini* was more severe on sites with soil properties indicating greater fertility (e.g. lower soil C/N ratio and finer textured). Highest cumulative probabilities for severe *I. typographus* infestation of *P. abies* were associated with trees growing on sites having an east-facing aspect and the most fertile site types combined with either moderately steep slopes, shallow till soil or high soil C/N ratio.

The effects of storm and *I. typographus* (5–7 years and circa 1–4 years after tree mortality, respectively) disturbance on forest C were studied in *P. abies* dominated forests that had been left unmanaged after disturbance. Soil surface total and heterotrophic CO_2 effluxes, and topsoil C stocks of storm and *I. typographus* disturbed and undisturbed sites differed little, despite the shift in tree C stocks from living to dead after both disturbances and greater litter detritus C stocks on the *I. typographus* disturbed sites. Soil surface autotrophic CO_2 effluxes were mostly lower at the disturbed sites than at undisturbed ones. The most distinct differences in the humus layer microbiology were the lower abundances of tree-symbiotic ectomycorrhizal fungi, and consequently slightly lower microbial and fungal biomasses in the storm and *I. typographus* disturbed sites in comparison to the undisturbed sites. The remaining living trees on or in close proximity to the disturbed sites probably mitigated the belowground response to disturbance to some extent.

This dissertation shows that certain site and soil characteristics predispose trees and forest stands to *D. pini* and *I. typographus* infestations, which could help in identifying sites that are susceptible to insect disturbance. Furthermore, it provides new information about the short-term effects of natural disturbance on boreal forest C cycling and soil microbiology, which is important for improving understanding of the complexity of the possible impacts of climate change on forest C sequestration.

Keywords: insect outbreak, forest soil, site fertility, soil organic matter, tree mortality, windthrow

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LIST OF ORIGINAL RESEARCH ARTICLES

The dissertation is based on the following four articles, which are referred to in the text by their Roman numerals. All papers are reproduced with the permission of the publisher.

I. **Kosunen, M**., Kantola, T., Starr, M., Blomqvist, M., Talvitie, M. & Lyytikäinen-Saarenmaa, P. 2017. Influence of soil and topography on defoliation intensity during an extended outbreak of the common pine sawfly (*Diprion pini* L.). iForest 10: 164–171. https://doi.org/10.3832/ifor2069-009

II. Blomqvist, M., **Kosunen, M**., Starr, M., Kantola, T., Holopainen, M. & Lyytikäinen-Saarenmaa, P. 2018. Modelling the predisposition of Norway spruce to *Ips typographus* L. infestation by means of environmental factors in southern Finland. European Journal of Forest Research 137: 675–691. https://doi.org/10.1007/s10342-018-1133-0

III. **Kosunen, M**., Lyytikäinen-Saarenmaa, P., Ojanen, P., Blomqvist, M. & Starr, M. 2019. Response of soil surface respiration to storm and *Ips typographus* (L.) disturbance in boreal Norway spruce stands. Forests 10(4), 307. https://doi.org/10.3390/f10040307

IV. **Kosunen, M**., Peltoniemi, K., Pennanen, T., Lyytikäinen-Saarenmaa, P., Adamczyk, B., Fritze, H., Zhou, X. & Starr, M. 2020. Effects of storm and *Ips typographus* (L.) disturbance on forest carbon stocks and humus layer carbon fractions in boreal *Picea abies* stands. Soil Biology and Biochemistry 148, 107853. https://doi.org/10.1016/j.soilbio.2020.107853

AUTHOR CONTRIBUTION

Maiju Kosunen (MK) was responsible for writing the summary of this thesis. In papers **I**, **III** and **IV** MK was the corresponding author and was responsible for most of the laboratory work, writing and interpretation of the results. Planning and carrying out the experimental work in all studies was done together with the co-authors and field assistants. In study **IV** Krista Peltoniemi, Taina Pennanen and Hannu Fritze were responsible for the analysis and interpretation of the DNA sequencing results and Bartosz Adamczyk was involved in the ergosterol analyses. In paper **II**, Minna Blomqvist was the corresponding author, MK assisted in carrying out parts of the fieldwork, guiding the laboratory analyses as well as writing sections of the manuscript, and commenting and revising of the manuscript drafts.

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1. INTRODUCTION

1.1 Forest carbon and natural disturbances

Forests are essential carbon (C) sinks as they capture CO_2 from the atmosphere, storing a part of it in plant biomass, dead plant material and soil. The forests of the boreal biome comprise more than 30% of the global forest ecosystem C stocks, the vast majority being in the soil (Pan et al. 2011). The balance between C inputs by gross primary production (GPP, CO_2 fixation via photosynthesis) and C outputs by autotrophic (CO_2 efflux from plant parts and rhizosphere) and heterotrophic respiration (CO_2 efflux from decomposition), and minor fluxes such as dissolved organic C (DOC) leaching mostly determine forest C store changes when there are no harvests or fires. C enters the soil via the fragmentation and incorporation of dead organic material supplied for example from litterfall and the turnover of fine roots and microbes, as well as exudation of C-rich compounds by roots (Deluca and Boisvenue 2012; Jackson et al. 2017). Soil fauna and microbes have a fundamental role in degrading the plant and animal residues and releasing nutrients available for plant use, as well as in the cycling and long-term storage of soil C (Clemmensen et al. 2013; Jackson et al. 2017).

Natural disturbances, such as storms, fires, insect outbreaks and pathogen infestations are the important drivers of the structure, composition and functioning of a forest. These disruptive events lead to the reallocation of vital resources, such as light, water and nutrients, and thereby modify the composition of flora and fauna in the forest ecosystem (Ulanova 2000; Edburg et al. 2012; Mitchell 2013), often having positive effects on biodiversity (Thom and Seidl 2016). Forest disturbances are often considered on a range from single tree death creating gaps, up to landscape scale stand-replacing tree mortality leading to secondary forest succession (Angelstam and Kuuluvainen 2004).

A single disturbance agent does not necessarily lead to tree mortality but can weaken the tree against other disturbances that eventually lead to tree death. Interaction between different disturbance types is common in forest ecosystems. For example, pathogens may increase tree vulnerability to wind disturbance (Honkaniemi et al. 2017), droughts can predispose trees to bark beetle infestation (Netherer et al. 2019), and wind-fallen trees encourage bark beetle gradation (Schroeder 2001). Some of the recent large-scale natural disturbances in the boreal and temperate coniferous forests have been due to wildfires in Sweden and central Europe (San-Miguel-Ayanz et al. 2018), mountain pine beetle (*Dendroctonus ponderosae* Hopkins) and spruce budworm (*Choristoneura fumiferana* Clemens) infestations in North-America (Zhang et al. 2014; Cooke and Carroll 2017), and European spruce bark beetle (*Ips typographus* L.) outbreaks preceded by drought and storms in central Europe (Mezei et al. 2017b).

Besides their ecological importance, natural disturbances can have significant economic consequences (Schelhaas et al. 2003; Grégoire et al. 2015) and effects on forest C sequestration (Lindroth et al. 2009; Ghimire et al. 2015; Williams et al. 2016) and other ecosystem services (Thom and Seidl 2016). Measures for assessing, monitoring and controlling the occurrence and intensity of natural disturbances in forests have thus been widely studied and developed (Kurz et al. 2008; Seidl et al. 2011a; Stadelmann et al. 2013; Mezei et al. 2017a; Junttila et al. 2019). As the susceptibility of a forest to disturbance is often related to its' structure and composition, the risk for tree damage might be diminished by promoting certain forest characteristics and management strategies (Jactel et al. 2009, 2017; Valinger and Fridman 2011).

Climate change can affect forest C sequestration and storage through changes in forest productivity, decomposition and, in the boreal biome, thawing of permafrost (Deluca and Boisvenue 2012; Gauthier et al. 2015). In addition, the occurrence of various disturbances, and their interactions, are predicted to be enhanced or altered, especially in coniferous forests and the boreal biome (Seidl and Rammer 2017; Seidl et al. 2017). Increases in severe forest disturbances could cancel out or reduce the potential increases gained in forest productivity due to climate change or forest management approaches aimed to strengthen forest C sink (Seidl et al. 2014; Reyer et al. 2017). Creating a better balance between C sequestration, biodiversity and resource value of forests under intensified disturbance regimes and a changing climate is thus a great challenge for forest management.

1.2 Storm and insect disturbances in Europe

Storms and other types of wind disturbance are common disturbance agents throughout Europe, which often change the landscape rapidly (Figure 1a). Wind classifies as a storm if the 10 minutes mean wind speed is at least 21 m/s, and is often associated with tree uprooting or stem breakage (Ihalainen and Ahola 2003). During the last decades, some of the most detrimental storms in Europe occurred in 1999 and 2007, causing tree damage to 240 and 66 million m^3 of timber, respectively (Gardiner et al. 2013). In Finland, recent severe storms in 2001 and 2010, resulted in damage to 7 and 8 million m^3 of trees, respectively (Ihalainen and Ahola 2003; Viiri et al. 2011). Tree damage by storms is predicted to increase as a result of climate change (Schelhaas et al. 2003; Gregow et al. 2011; Seidl et al. 2017). Wind speeds in northern Europe may increase in the future (Gregow et al. 2012), but the projected increased tree damage by wind is more associated with changes in precipitation and decreases in the soil frost period leading to lower tree anchorage (Peltola et al. 1999; Gregow et al. 2011; Seidl et al. 2017).

While only a minor proportion of all insect species notably alter tree functioning, under optimal conditions some species can hamper tree growth, reduce wood quality or kill the tree. In comparison to storms, the development of insect disturbances in a forest is much more gradual. In Europe, two common tree damaging insect species are the common pine sawfly (*Diprion pini* L.) (Figure 1b) and *I. typographus* (Figure 1c). *D. pini* is under the leaf-eaters feeding group as a needle defoliator, whose larvae mainly consume all needle age-classes of Scots pine (*Pinus sylvestris* L.) (Figure 1b). This can lead to tree mortality when happening in several consecutive years (Langström et al. 2001). However, although sudden outbreaks of *D. pini* have caused severe defoliation throughout Europe, they more often lead to growth losses rather than tree mortality (Geri 1988). In Finland, *D. pini* had only caused small-scale defoliation prior to an outbreak starting in 1997 (De Somviele et al. 2007). By 2001 the outbreak had resulted in *P. sylvestris* defoliation covering an area ca. 500 000 ha, and was the most widespread insect outbreak in Finland at that time (Lyytikäinen-Saarenmaa and Tomppo 2002).

I. typographus belongs to the phloem borers feeding group, the adults and larvae excavating galleries in the phloem or inner bark of the host tree, usually Norway spruce (*Picea abies* (L.) Karst.). At high population densities, this behavior causes the flow of photosynthates in phloem to cease and potential death of the tree (Figure 1c). The insect is also a vector of various ophiostomatoid fungi that further contribute to tree death (Linnakoski et al. 2012). *I. typographus* is considered as one of the most severe forest damaging insect species in Europe. Bark beetles, mostly *I. typographus*, have caused tree damage losses in

Figure 1a) Landscapes modified by a storm event, **b)** Common pine sawfly (*Diprion pini*) larvae (left), defoliated pine (*Pinus sylvestris*) shoots (middle) and killed trees (right), **c)** an adult European Spruce bark beetle (*Ips typographus*) (left), its' breeding galleries on bark (middle) and killed spruce (*Picea abies*) trees (right). Photos: Minna Blomqvist, Päivi Lyytikäinen-Saarenmaa and Maiju Kosunen.

Europe averaging 2.9 million m^3 each year during the period 1958–2001 (Schelhaas et al. 2003; Seidl et al. 2011b). In Finland, *I. typographus* has not caused such extensive tree mortality as in Central Europe and Scandinavia (Pouttu and Annila 2010; Viiri et al. 2019), but the tree damage caused by the insect has increased during the past decade (Neuvonen and Viiri 2017).

The reproductive potential and dispersal of both, *D. pini and I. typographus* are very dependent on temperature (Geri 1988; Wermelinger 2004). In the northern and mountainous parts of Europe both species generally produce one generation per year, whereas in lowlands of Central and southern Europe they often produce two, or even three (Geri 1988; Økland et al. 2015). However, the warming climate is expected to benefit the voltinism of *I. typographus* and *D. pini* (Haynes et al. 2014; Økland et al. 2015). For example, in the exceptionally warm summer of 2010, *I. typographus* was able to produce two generations for the first time in Finland (Pouttu and Annila 2010). Although also occurring independently, *I.*

typographus outbreaks are often linked to storm disturbance. The insect may reproduce and build up population in fresh wind-fallen trees and then move to standing living trees (Schroeder 2001). Longer-lasting *I. typographus* outbreaks can indeed be triggered by a combination of storms and high temperatures (Mezei et al. 2017b). However, prediction of the overall effects of climate change on tree damage by insects is not simple due to complex interaction between host trees, insects and their natural enemies, as well as abiotic stressors (Jactel et al. 2019). Nevertheless, many bark beetles and defoliating insect species already have greater survival and reproduction at more northern areas and higher elevations than before (Pureswaran et al. 2018).

1.3 Stand, site and soil characteristics predisposing forest sites to storm and insect disturbance

In addition to wind speed and interaction with other disturbances, predisposition to storm damage is related to various stand, site and soil characteristics. For example, tree height, diameter, age and species have been shown to affect susceptibility to wind (Lohmander and Helles 1997; Peltola et al. 2000; Zeng et al. 2004; Valinger and Fridman 2011). Among northern European tree species, shallow-rooted *P. abies* is more prone to storm damage than *P. sylvestris* and birch (*Betula* spp.) (Peltola et al. 2000; Zeng et al. 2004). Mixed-species stands have been shown to be less susceptible to storms, especially in relation to recently thinned pure *P. abies* stands (Valinger and Fridman 2011; Griess and Knoke 2011). Soil and topographical features also affect forest vulnerability to wind damage. Soils provide the anchorage for trees and topography may affect wind speeds at a site. Thus, soil factors, such as soil type, depth and moisture conditions and topographical features, including elevation, slope position and aspect can affect forest susceptibility to storm events (Dobbertin 2002; Schindler et al. 2012; Mitchell 2013; Suvanto et al. 2016).

As with storm disturbance, the performance (e.g. length of larval period, adult body size and survival) and tree damage by bark beetles and defoliating insects can be affected by stand, site and soil characteristics. Stand features would mostly relate to insect outbreaks via host-tree selection. Specialized insects, such as *D. pini* and *I. typographus*, may in addition to a certain tree species, prefer trees and stands of certain size, age, density and basal area (Göthlin et al. 2000; Netherer and Nopp-Mayr 2005; De Somviele et al. 2007; Klutsch et al. 2009; Mezei et al. 2014). Tree damage by the insects can thus be less severe or less likely in forests having more variation in tree species composition and age classes in comparison to even-aged, monoculture stands (Geri 1988; McMillin and Wagner 1993; Jactel et al. 2009, 2017; Griess and Knoke 2011).

Host-tree biochemistry, in addition to climatic factors, have an important direct influence on insect performance. For example, nitrogen (N) and soluble carbohydrates are crucial in the diet of insects and thus even small differences in the N concentrations of nutrition can affect pine sawfly and bark beetle performance (Lyytikäinen 1994; Ayres et al. 2000; Giertych et al. 2007). On the contrary, defensive compounds, such as resin acids (Larsson et al. 1986; Baier 1996), phenolics (Giertych et al. 2007) and some monoterpenes (Barre et al. 2003; Chiu et al. 2017), can have a deterring effect on the insects. In addition to host-tree quality, natural enemies and parasites have an important direct controlling effect on insect populations (Wermelinger 2002; Raffa et al. 2015; Blomqvist et al. 2016).

Site and soil characteristics relate to insect outbreaks usually indirectly. For example, soil affects the biochemistry of the host-trees, and hence their susceptibility and attractiveness to insects. Pine needle (Björkman et al. 1991; Raitio 1998; Tarvainen et al. 2016) and inner bark (Cook et al. 2010) N concentrations as well as needle secondary compounds (Björkman et al. 1991; Holopainen et al. 1995; Kainulainen et al. 1996) have been shown to be related to soil N availability or concentrations. In addition, the availability of soil water can affect resin flow and nutrient contents of trees (Netherer et al. 2015; White 2015). Site fertility and ground vegetation composition could also relate to defoliator performance by affecting levels of insect predation and parasitism (Herz and Heitland 2005; Blomqvist et al. 2016). As *D.pini* and *I. typographus* may overwinter in the forest floor (Økland et al. 2015; Blomqvist et al. 2016), properties of the litter and humus layer may also be expected to affect the insects. Generally, pine sawfly outbreak intensity and attributed yield losses have been seen to be more severe on nutrient poor sites in comparison to more fertile ones (Larsson and Tenow 1984; Geri 1988; Mayfield et al. 2007; Nevalainen et al. 2015). Bark beetle infestations have often been associated with water deficiency and/or shallow soils (Bakke 1983; Seidl et al. 2007; Overbeck and Schmidt 2012; Økland et al. 2015).

Topographical features have both direct and indirect effects on insect outbreaks and their performance. Elevation affects local climatic conditions, such as temperature, precipitation and radiation of a site, factors which can directly influence insect physiology and performance (Hodkinson 2005). As topography also affects soil fertility and water availability (Griffiths et al. 2009), host-tree quality and susceptibility to insects might be altered indirectly. For example, concentrations of pine needle C and N and secondary chemicals have been shown to vary with elevation (Niemelä et al. 1987; Hengxiao et al. 1999; Fan et al. 2019). Elevation and slope have been thus found to relate to the abundance or tree damage by bark beetles and defoliating insects, especially in mountainous conditions (Niemelä et al. 1987; McMillin et al. 1996; Hengxiao et al. 1999; Hodkinson 2005; Netherer and Nopp-Mayr 2005; Kharuk et al. 2007, 2009; Akkuzu et al. 2009). *I. typographus* infestation, for example, has been shown to be positively related to the amount of solar radiation received (Netherer and Nopp-Mayr 2005; Mezei et al. 2014, 2019). Thus, trees on slopes or forest edges facing south have been considered to be more predisposed to bark beetle outbreaks (Kaiser et al. 2013; Kautz et al. 2013).

1.4 Effects of storm and bark beetle disturbance on forests and carbon

The effects of storm and insect disturbances on forest composition, functioning, and carbon balance can vary, and their legacies in a forest last even up to centuries after the event. Although the two disturbance types are different in their nature, both may lead to wide-scale tree mortality. Storm events usually kill trees rather fast by breaking or uprooting them, and thus stand structure is instantly altered (Mitchell 2013), whereas tree mortality by bark beetles is usually slower and the dead trees may remain standing for decades (Edburg et al. 2012). Reductions in living tree biomass due to large-scale storm and bark beetle disturbance can be massive, and possible harvests of the dead trees after the events would lead to further changes is the stand structure and instant decreases of forest C stocks (Pfeifer et al. 2011; Valinger and Fridman 2011; Hicke et al. 2013).

In spite of the differing tree mortality dynamics, the two disturbance types, especially large-scale ones, may affect similar components of forest functioning and composition. The changes in a forest during the first decades are often diverse. The tree mortality and increased light availability can alter the ecosystem water cycling, soil temperature and moisture (Hais and Kučera 2008; Morehouse et al. 2008; Mayer et al. 2014, 2017; Reed et al. 2014, 2018) as well as the composition of the ground vegetation (Fischer et al. 2002; Jonášová and Prach 2008). In addition, the amount and quality of litter inputs to soil are often affected (Sariyildiz et al. 2008; Bradford et al. 2012; Kopáček et al. 2015), and tree mortality would result in the cessation of belowground photosynthate allocation. Such changes can also reflect to forest floor and soil microbial community composition and functioning. For example, abundance and/or diversity of tree-symbiotic ectomycorrhizal (ECM) (Štursová et al. 2014; Mayer et al. 2017; Pec et al. 2017) and saprotrophic decomposer fungi (Štursová et al. 2014; Pec et al. 2017) as well as bacteria (Ferrenberg et al. 2014; Mikkelson et al. 2017) have been indicated to be altered by storm or bark beetle disturbance. Similarly, changes in microbial biomass and DOC concentrations have been observed after bark beetle outbreaks (Štursová et al. 2014; Kaňa et al. 2015; Trahan et al. 2015). The above mentioned changes can further reflect to forest floor and soil decomposition rates as well as nutrient cycling and availability (Sariyildiz et al. 2008; Griffin et al. 2011; Cigan et al. 2015; Mayer et al. 2017). In contrast to bark beetle disturbance, storms can lead to severe soil disturbance if trees are uprooted, and create pit and mound microsites having distinct physical and biochemical soil properties (Mitchell 2013; Kooch et al. 2015).

The tree mortality due to wide-scale storm and bark beetle disturbance and the associated various changes in a forest can significantly impact C cycling of the ecosystem level. GPP and autotrophic respiration would be expected to decrease due to the tree mortality, whereas heterotrophic respiration from decaying tree parts and dead roots could be enhanced (Kurz et al. 2008; Hicke et al. 2012). Forest ecosystems may thus turn into C sources or their functioning as a C sink be at least markedly reduced soon after disturbance, with recovery periods of various decades (Kurz et al. 2008; Lindroth et al. 2009; Hicke et al. 2012; Ghimire et al. 2015). However, it has been observed that if the decreased GPP is accompanied by no clear increases in heterotrophic respiration and total ecosystem respiration is reduced, changes in the forest C balance after bark beetle disturbance can be less severe (Moore et al. 2013). Furthermore, the increase in the availability of light, water and nutrients after disturbance might stimulate growth and C uptake of the surviving vegetation (Brown et al. 2010). The role of surviving mature trees, secondary structure, new seedlings as well as ground vegetation thus is important in determining the magnitude of the change and recovery time of the ecosystem C balance (Brown et al. 2010; Mathys et al. 2013; Kobler et al. 2015; Zehetgruber et al. 2017).

After wide-scaled tree mortality due to disturbance, the role of soil respiration (soil CO_2 efflux) would become increasingly important in determining a forests' C balance (Mayer et al. 2017). Soil respiration is strongly driven by e.g. temperature and moisture conditions as well as the quality of the substrate, C allocation to the roots and rhizosphere, and composition of soil microbial communities (Raich and Tufekciogul 2000; Högberg et al. 2001; Curiel Yuste et al. 2007; Liu et al. 2018), factors that all can be modified by disturbance. Tree mortality after storm or bark beetle disturbance has been shown to decrease soil autotrophic respiration (Kobler et al. 2015; Mayer et al. 2017). On the contrary, for example increased soil temperature or high amounts of needle litter with preferable quality for decomposition (e.g. lower C/N ratio), might enhance litter decomposition and heterotrophic soil respiration some years after the event (Sariyildiz et al. 2008; Mayer et al. 2014, 2017). However, no alteration in soil heterotrophic respiration along with no changes in soil temperature have also been indicated after disturbance (Kobler et al. 2015). Consequently, increases (Mayer et al. 2014), decreases (Moore et al. 2013; Mayer et al. 2014) as well as no change (Morehouse et al. 2008; Köster et al. 2011; Mayer et al. 2014, 2017; Borkhuu et al. 2015) in soil total respiration after storm or bark beetle disturbance could occur. Depending on the balance between inputs of litter and other organic material and rate of decomposition, forest floor C stocks have been indicated to change already within the first decade after a storm event (Bradford et al. 2012; Mayer et al. 2017), whereas changes in mineral soil C stocks seem to be less significant or at least slower (Bradford et al. 2012; Don et al. 2012; Mayer et al. 2017).

Clearly, in addition to disturbance intensity, any differences in the observed changes in the ecosystem after storm or bark beetle disturbance can relate to differences in time since the disturbance, as the magnitude and/or direction of the alterations in a forest often change with time (Edburg et al. 2012; Hicke et al. 2012; Mayer et al. 2014, 2017; Štursová et al. 2014). Furthermore, the recovery of the ecosystem characteristics is also determined by the growth of the remaining and new vegetation. Thus, not only the susceptibility of a forest to disturbance, but also the changes and recovery of a forest after disturbance relate to the pre-disturbance forest composition and structure as well as forest management and operations before and after the event (Knohl et al. 2002; Jonášová and Prach 2008; Seidl et al. 2008; Brown et al. 2010; Jonášová et al. 2010; Taeroe et al. 2019).

2. THESIS AIMS AND OBJECTIVES

The main aims of this study were to identify environmental characteristics predisposing forest stands to insect disturbance, and to elucidate the effects of storm and bark beetle disturbance on C cycling in boreal forest ecosystems. Specific objectives were to:

1) Determine the influence of a range of stand (only in **II**), site and soil characteristics on tree and stand predisposition to outbreaks by *D. pini* (**I**) and *I. typographus* (**II**).
2) Assess and evaluate the effects of storm and *I. typographus* disturbance on tree (living and dead), forest floor and soil C stocks (**IV**), soil surface respiration (**III**) and humus layer microbial community composition and C fractions (**IV**).

The first objective was addressed by examining various stand, site and soil factors across plots and trees covering a wide range of defoliation intensities of *P. sylvestris* due to *D. pini* in managed forests (**I**) and varying levels of *P. abies* infestation by *I. typographus* in urban forests (**II**). The second objective was addressed using replicated plots located in undisturbed, storm disturbed or *I. typographus* disturbed sites over a period of three years (5–7 years after storm and circa 1–4 years after tree mortality by *I. typographus*) in two *P. abies* dominated forest sites that had been left unmanaged after the disturbances (**III** and **IV**). A schematic outline of the studies showing how they are linked is presented in Figure 2.

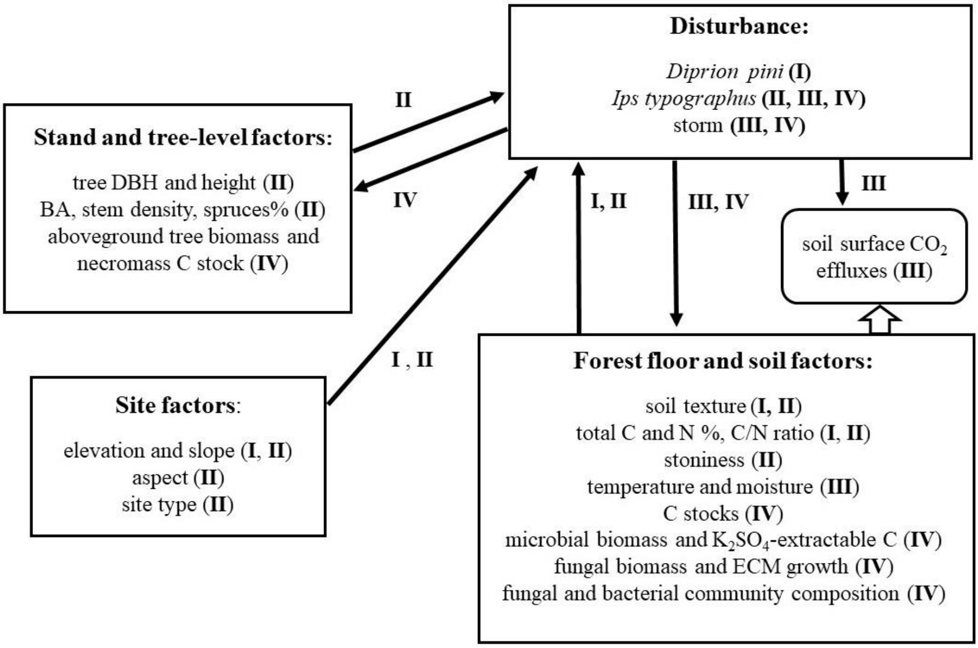

Figure 2. A schematic design of the main contents of each study in the dissertation. Articles are referred to as Roman numerals (**I**, **II**, **III** and **IV**). DBH=diameter at breast height, BA=basal area of trees, spruces%=proportion of spruce, ECM=ectomycorrhizal fungi.

3. MATERIAL AND METHODS

3.1 Studies I and II

3.1.1 Study area, layout and field inventory

The influence of soil and topographical characteristics on defoliation caused by *D. pini* (**I**) was studied in *P. sylvestris* dominated managed forests located in Ilomantsi, eastern Finland (Figure 3). An outbreak of the insect in the area started in 1999 and had developed chronic. Gradation was still going on during field measurements in 2010. Soils in the area are mainly podzols with a low organic matter (OM) content developed in till and glaciofluvial deposits and have a mor type humus layer (Table 1). The forest site types (hereafter referred to as site type) according to the Finnish Cajanderian classification (Cajander 1949; Mikola 1982) were mostly rather poor *Vaccinium* type (VT) and poor *Calluna* type (CT) (Table 1).

Plots (n=28, area=227–531 m^2) representing different *P. sylvestris* defoliation intensities in the study area, which had been established previously for purposes of other studies, were also utilized in this study. In autumn 2009 and May–June 2010, all trees with more than 6 cm diameter at breast height (DBH) in each plot were classified as: dominant, co-dominant and suppressed hierarchy classes. Their DBH and height (only circa every 7th tree) were then measured and level of defoliation visually estimated in 10% defoliation classes (0% being no

Figure 3. Location of study areas: Ilomantsi (**I**), Lahti (**II**) and Ruokolahti (**III** and **IV**). Created using a basemap (sources: National Geographic, Esri, DeLorme, HERE, UNEP-WCMC, USGS, NASA, ESA, METI, NRCAN, GEBCO, NOAA, iPC.) of ArcGIS® software by ESRI ©.

defoliation by the insect, and 100% being a dead tree). Five soil core samples were taken from each plot and thickness of humus layer (O_f+O_h) and each soil horizon ((A_h+)E, B, and C) in each core measured. Horizon samples were then composited by plot and stored (+4 °C) until laboratory analyses.

The effects of stand, site and soil characteristics on infestation by *I. typographus* (**II**) were studied in *P. abies* dominated urban forests in Lahti municipality, southern Finland (Figure 3). An outbreak of *I. typographus* in the area started in 2011, peaked in 2012 after the exceptionally warm summers of 2010 and 2011, and seemed to level off in 2013 and 2014. Soils in the study area are mainly podzols with a high OM content developed in till or sorted glaciofluvial deposits and often have a moder or mull type humus layer on top (Table 1). The site types consist of mesic, relatively fertile *Myrtillus* (MT), herb-rich *Oxalis-Myrtillus* (OMT) as well as some fertile groves *Oxalis-Maianthemum* (OMaT) site types (Table 1).

Plots (n=48, area=314 m^2) were established to the study area in August 2012 and 2013. DBH of each standing tree on plot and height of approximately every 7th tree was measured in 2014. Visible symptoms of *I. typographus* were assessed for each spruce tree on the plots. The symptoms included: entrance and exit holes of *I. typographus* in lowest 2 m of the tree trunk, number of resin flow spots, bark condition (3 classes for each symptom) as well as defoliation and discoloration of the crown (4 classes for both symptoms). Plot stone content was estimated with the rod penetration method (Viro 1952; Tamminen and Starr 1994) by

Table 1. Basic environmental features of the study areas. Annual mean temperature and precipitation sums are for the periods 1981–2010 (Pirinen et al. 2012). Forest site types after Cajanderian classification: CT=poor *Calluna* type, VT=rather poor *Vaccinium* type, MT=relatively fertile *Myrtillus* type, OMT=herb-rich *Oxalis-Myrtillus* and OMaT=fertile groves *Oxalis-Maianthemum.* The stand and soil characteristics are based on measurements from the study plots.

	Ilomantsi study **I**	Lahti study **II**	Ruokolahti studies **III** and **IV**
Coordinates (WGS84)	62° 52′ N, 30° 56′ E	60° 59′ N, 25° 39′ E	61° 17′ N, 28° 49′ E
Mean annual temperature (°C)	2–3	4–5	3–4
Mean annual precipitation sum (mm)	650–700	600–650	600–650
Disturbance type	*Diprion pini*	*Ips typographus*	Storm and *Ips typographus*
Forest site type	CT and VT	MT, OMT and OMaT	MT and OMT
Mean basal area (m^2/ha)	18	29	39
Dominant tree species	*Pinus sylvestris*	*Picea abies*	*Picea abies*
Dominant humus layer type	mor	mull and moder	moder
Dominant soil group	Podzol (low in OM)	Podzol (high in OM)	Podzol (high in OM)
Dominant soil texture	Loamy sand	Loamy sand	Sandy loam

recording rod penetration depth in soil from 41 points in each plot. Soil cores were collected in August 2014 from three points in each plot. Thickness of the humus layer was recorded when it was clearly detectable, and mineral soil divided according to depth (0–5 cm, 5–10 cm and 10–20 cm layers). Humus layer and mineral soil samples of each depth were then composited by plot and stored (+4 °C) until laboratory analyses. Plot center coordinates in **I** and **II** were determined with a Trimble Pro XH-GPS® device (Sunnyvale, CA, USA).

3.1.2 Stand, site and soil characteristics

In **I**, plot mean defoliation (range: 1–77%), consisting of defoliation values of the dominant and co-dominant trees of each plot were used for further analysis, as defoliation of the suppressed trees might have been due to other stressors due to suppression. Since defoliation of more than 20% is often considered harmful for tree growth (Strand 1997; Lyytikäinen-Saarenmaa 1999; Lyytikäinen-Saarenmaa and Tomppo 2002), plots were also classified according to their mean defoliation to *mild,* having less than 20% defoliation intensity (n=21 plots, mean defoliation=10%), or *moderate to severe* defoliation, having more than 20% defoliation (n=7 plots, mean defoliation=54%).

In **II**, the height of the trees that were not measured in the field was estimated using the equation of Näslund (1937). Basal area (BA, m^2/ha), stem density (number of stems/ha), proportion of dead spruce (%) and tree species composition were determined. Defoliation, crown colour and resin flow spots were considered the best indicators of tree infestation level by *I. typographus.* Thus, the sum of the classes to which those symptoms were categorized was used to describe tree-wise insect attack level (i.e. attack level score), resulting in values varying between 3 and 11. The attack level scores were calculated only for trees with a DBH more than 20 cm, as smaller trees might have suffered from other stressors due to suppression. The tree-wise attack level scores were used to classify trees into *infestation index classes*: *no infestation* (class 1, attack level score 3–4, n=116), *moderate infestation* (class 2, attack level score 5–7, n=223), and *severe infestation* (class 3, attack level score 8–11, n=51). Thus, *no infestation index class* represented trees, which at the time of the field assessment experienced lowest level of damage and *severe infestation* ones with greatest level of damage. *Moderate infestation* represented the intermediate level, in which trees might either survive the infestation due to higher herbivore resistance or eventually die under further colonization pressure. *Moderate* and *severe infestation index classes* may have also represented sites with an ongoing and a passed *I. typographus* infestation, respectively. However, the *severe infestation* class identified the most susceptible sites for *I. typographus* in an initial outbreak phase. Trees in the *moderate infestation* did not seem to have a low bark beetle resistance or then colonization was still increasing.

In **I** and **II**, humus layer as well as the mineral soil samples from B-horizon (**I**) and 0–5 cm depth (**II**) were dried, humus layer samples milled and mineral soil samples sieved (2 mm mesh size). Samples were analyzed for total C and N concentrations using a VarioMax CN device (Elementar Analysensysteme GmbH, Hanau, Germany). Mineral soil samples in **I** were also analyzed for particle size distribution (B-horizon only) using laser fractionation (Coulter LS230®, Beckman Coulter Inc., Brea, CA, USA) and pH (humus layer samples only) from a calcium chloride solution using a glass electrode. Volumetric stone content (%) of the soil in **II** was calculated from the stoniness measurements using the equation by Tamminen and Starr (1994). The soil parent material and texture classes in **II** were derived from a 1:20 000 digital map (Hakku open database, Geological Survey of Finland) utilizing ArcGIS (ArcGis v. 9.3, ESRI, Redlands, CA). The following particle size limits were used in **I** and **II**: clay (<0.002 mm), fine silt (0.006–0.002 mm), medium silt (0.02–0.006 mm), coarse silt (0.06–0.02 mm) and sand (2–0.06 mm). In **I**, the sand fraction was further divided into fine (0.06–0.2 mm), medium (0.20–0.6 mm) and coarse sand (0.6–2 mm). In **II**, the glaciofluvial sorted deposits were classified according to the particle size (5 classes) and the glacial till deposits classified into two classes having either sandy till or shallow till (<1 m to bedrock). Those altogether seven classes are from now on referred to as “soil texture class” in **II**.

The following topographical features were derived from a high resolution (1–2 m) Digital Elevation Model (DEM) of the study areas by using ArcGIS: elevation (m above sea level), slope and aspect (only for **II**) of each plot in **I** and **II**. The plot center coordinates and a buffer layer with the size of the plot radius were used to derive pixels covering each plot, and plot mean of pixels used to represent plot elevation and slope. In **II**, the plot mean slope was further classified to five classes: very gently sloping (1.0–1.9%), gently sloping (2.0–4.9%), sloping (5.0–9.9%), strongly sloping (10.0–14.9%), and moderately steep sloping (15.01–

30.5%). In **II**, aspect was based on that of most of the pixels covering each plot and classified according to cardinal and semi-cardinal directions.

3.1.3 Statistical analyses

In **I**, relationships between plot-wise topographic and soil properties and defoliation were viewed with Spearman's rank correlation coefficients. Significant differences in topographical and soil parameters between *mild* and *moderate to severe* defoliation classes were tested with Mann-Whitney U-test. Logistic regression models, including 1–2 predictor variables, were applied to examine plot-wise topographical and soil properties as predictors for the probability of a plot facing *moderate to severe* defoliation. Best models were selected based on classification accuracies, Cohen's Kappa values (Landis and Koch 1977) and p-values.

In **II**, Kruskal-Wallis test followed with a Nemenyi post-hoc test with a Bonferroni correction was used to observe differences in environmental predictor variables (tree, stand, site type, soil and topographical characteristics) between the *infestation index classes*. A cumulative link model (CLM) was used to predict the probability of infestation caused by *I. typographus* with the predictor variables. In the modeling, the tree-wise *infestation index class* was the dependent variable and predictor variables were the tree (tree-wise), stand, site, soil, and topographical characteristics (plot-wise). Various combinations of two to three predictor variables were examined to be used in the final models. Maximum absolute gradient and a condition number of the Hessian matrix were utilized to estimate model convergence, and number of correct decimals and the number of significant digits to determine parameter estimate accuracy (Christensen 2015). Akaike information criterion (AIC), deltaAIC as well as Akaike weights were used to estimate goodness-of-fit of the models (Akaike 1998). Spearman's correlation coefficients were derived between the predictor variables to examine their relationships and suitability for the CLM modeling. Statistical testing in **I** and **II** was done with the R statistical computing environment (R Core Team 2019), and p-values of < 0.05 considered as significant.

3.2 Studies III and IV

3.2.1 Study area, layout and field measurements

The effects of storm and *I. typographus* disturbance on forest ecosystem C (**III** and **IV**) was studied in two *P. abies* dominated forest sites, Paajasensalo and Viitalampi, located in Ruokolahti in southeastern Finland (Figure 3). A large-scale storm occurred on the sites in 2010 and was followed by an outbreak of *I. typographus*. The storm seemed to have occurred partly as a stand-replacing disturbance, but mature living trees had also survived the event inside some of the storm-affected areas. *I. typographus* infestation led to a patchy tree mortality pattern, with groups of a few up to tens of killed *P. abies* trees close to living, lesser colonized ones. Both forests were conserved after the storm event and thus all dead wood was left on site.

Soils in the study sites are mainly podzols with a high OM content, developed in till deposits and mostly have a moder type humus layer (Table 1). Sites types are mainly mesic, relatively fertile *Myrtillus* (MT) and herb-rich *Oxalis-Myrtillus* (OMT) types (Table 1). In 2015 and 2016, three types of plots (n=12, area=400 m^2, hereafter referred to as plot types), describing the state of most of the mature trees on a plot, were established in the sites: undisturbed plots with living trees (LT, n=4), plots with storm-felled trees (SF, n=4), and plots with standing dead trees killed by *I. typographus* (ID, n=4). There was some interaction of storm and *I. typographus* disturbance on some of the SF and ID plots, but the initial cause of tree mortality was the storm in 2010 on the SF plots and *I. typographus* circa during 2013–2014 on the ID plots. Some *P. abies* trees in the LT plots also had visible entrance holes caused by the bark beetle, but all those trees remained living and vigorous throughout the study. DBH of each living and dead, standing or fallen, tree having a DBH > 6 cm was measured. Tree height was measured when possible (74% of trees).

For determination of soil surface respiration (SR_{tot}), a total of 84 measurement points having a plastic collar on top of the forest floor (no vegetation removed), were randomly interspersed in the plots in early summer 2015 (n=60) and 2016 (n=24) (**III**). In the SF plots, the measurement points were further divided to two sub-types of microsite: ground vegetated open (SF_o, i.e. no fallen trees above) or under a fallen tree(s) and detritus covered microsites (SF_d). In July-August 2016, half of the measurement points in each plot that had been established in 2015 (n=30) were trenched to estimate the proportions of autotrophic (SR_a) and heterotrophic (SR_h) soil surface respiration. Trenching was done by cutting the roots around the selected collar to circa. 30 cm depth and inserting a strong fabric into the trenched incision to inhibit root in-growth (Figure 2; **III**). The ground vegetation except for mosses was clipped from inside the trenched collar. Soil respiration measurements were carried out with a closed dark chamber and a CARBOCAP® GMP343 CO_2 probe (Vaisala Ltd., Vantaa, Finland) from top of each collar every week during June–October 2015, May–September 2016, and biweekly during May–October 2017. CO_2 measurements from the intact collars included respiration from the soil and ground vegetation, while those from the trenched collars included that from only the soil and mosses. Immediately after the respiration measurements, soil temperature (°C) and moisture (% vol) were measured around each collar using a S3 11B thermometer (Fluke corp., Everett, WA, USA) probe and a ML3 ThetaKit soil moisture meter (Delta-T devices Ltd., Cambridge, UK).

For the determination of forest floor and topsoil C stocks (**IV**), samples of litter detritus (distinguishable cones, bark and twigs with <1 cm diameter), humus layer and upper mineral soil (0–6 cm) were collected (n=12 per plot) from the 2015 established plots in August 2015 and from the 2016 established plots in August 2016, and placed in separate bags and stored (-20 °C) until laboratory analyses. For determination of C fractions and microbial community composition (**IV**), another set of humus layer samples (n=7 per plot) were collected in August 2017. In-growth bags were inserted vertically under the litter layer through the humus layer and into the top mineral soil at each plot (7 per plot) in June 2017 to estimate ECM fungal mycelial growth (Wallander et al. 2001). The bags were retrieved in late October 2017. The humus layer and in-growth bags were both stored in +4 °C until laboratory analyses.

3.2.2 CO_2 effluxes, C stocks and C fractions and microbial community composition

Soil surface respiration (mg CO_2 m^2/s) was calculated as the slope from the linear fit between CO_2 concentration in the chamber and time. Respiration measurements from the intact measurement points in summers 2015–2017 were counted as SR_{tot} and the respiration measured from the trenched measurement points in 2017 counted as SR_h. As there were some differences in the SR_{tot} measured from the intact and to-be-trenched measurement points before the trenching, a linear equation between the respiration values from the intact and the to-be-trenched measurement points from the time before trenching was derived for each plot and microsite. These equations and measurements from intact points were then used to predict SR_{tot} for the trenched points for the time after trenching, and the difference between predicted SR_{tot} and measured SR_h from the trenched points considered as SR_a. Consequently, SR_a values of each measurement day were means from the plot types and microsites, and SR_h separate values for each measurement point.

The biomass models of Marklund (1988), which use DBH and tree height, were used to estimate aboveground tree dry weight (tree stem, branches and foliage) of dead and living trees. An estimated thickness of bark based on tree height and previous bark thickness measurements from the area (data not shown) was added to the DBH of the dead trees that had lost their bark. A C concentration of 50% was used for calculating tree biomass C (Sandström et al. 2007; Ma et al. 2018). Annual decay rate constants (Krankina and Harmon 1995) were used to roughly correct aboveground necromass (dead trees) C stocks for losses due to decay, assuming that the volumes of the dead trees had not markedly changed yet. The number of years since tree death was estimated to be six years for SF plots and two years for ID plots, and 10 years for the trees that had died prior to the storm in 2010 (7% of all trees). BA (m^2/ha) and stem density of living and dead trees was also determined for each plot.

Litter detritus and soil samples collected in 2015 and 2016 were dried, after which twigs, bark and cones of the litter samples were separated, weighed, and milled. Roots and pieces of litter were separated from the humus layer samples, and samples were weighed and milled. Mineral soil samples were sieved (2 mm mesh size) and >2 mm and <2 mm soil fractions and roots weighed. Total C concentration was measured from the milled litter detritus, humus layer and mineral soil (<2 mm) samples with the VarioMax CN device. Litter detritus sample dry weights and area as well as plot mean C concentration were then used to calculate litter detritus C stocks. The humus layer and topsoil C stocks were calculated with the dry weight bulk density (homogenized humus layer material and roots, and the <2 mm sieved mineral soil fraction and roots) of each sample, sample thickness as well as measured plot mean C concentration for humus and mineral soil and an assumed C concentration of 50% for roots.

The fresh humus layer samples collected in 2017 were homogenized by separating roots and litter from them. Subsamples were then taken from each sample and combined by plot type, but separately for the two study sites, resulting in six samples which were stored at -80 °C for DNA sequencing. Randomly chosen sets of humus layer samples at each plot were then composited, ending up with 3 samples per plot and 36 altogether. A part of those composited samples was used for fumigation-extraction analysis and the rest stored at -20 °C for determination of ergosterol and total C concentrations.

Microbial biomass (C_{MB}) was determined from the fresh humus layer samples using the fumigation-extraction method (Vance et al. 1987). One replicate of each humus layer sample was fumigated in a desiccator with chloroform and another replicate treated without fumigation. Extraction was done with a 0.05 M potassium sulphate (K_2SO_4) and total organic C (TOC) concentrations determined using a TOC analyzer (Shimadzu TOC-V CPH, Shimadzu Corp., Kyoto, Japan). C_{MB} was calculated as the difference between fumigated and non-fumigated C concentrations divided by 0.45 (Vance et al. 1987) and the non-fumigated C concentrations represented K_2SO_4 extractable C (C_{EXT}). The humus layer subsamples retained for total C concentration analysis were dried and total C concentrations were determined using the VarioMax CN device.

The in-growth bags were cut open and mixed, after which the sand in each bag was visually examined under a stereomicroscope and the abundance of ECM hyphae estimated in classes of: 0 = no hyphae, 1 = at least one visible hyphae, 2 = some hyphae easily found and slight aggregation of sand, 3 = several hyphae easily found and clear aggregation of sand.

The humus layer samples collected in 2017 as well as the sand from the ECM in-growth bags were also analyzed for ergosterol concentration, a biomarker indicator of fungal biomass, using high-performance liquid chromatography (HPLC) (Frostegård and Bååth 1996), similarly as in Adamczyk et al., (2019b). Extraction of ergosterol was done with cyclohexane and 10% KOH in methanol. After removing the cyclohexane phase, samples were evaporated and the residue dissolved in methanol. Amount of ergosterol was then measured using HPLC (HP Agilent 1100, Hewlett Packard, USA), with a C18 RP column. Pure ergosterol (Sigma-Aldrich, cat no 45480) was used as a standard. C_{MB}, C_{EXT}, and concentrations of ergosterol were all calculated per sample dry weight. To obtain an index that describes the growth and abundance of ECM fungi (ECM_{growth}), the visual estimates as well as the ergosterol concentrations determined from the in-growth bags were normalized, summed and normalized again (Mayer et al. 2017). In addition to ECM fungi, small proportions of saprotrophic fungi and some amounts of other types of mycorrhizal fungi may have also entered the in-growth bags. However, as ECM fungal mycelium has been shown to dominate in-growth bags in boreal coniferous forests (Wallander et al. 2001), the chosen method was considered appropriate for our comparative (i.e. between plot types) purposes.

DNA was extracted from the composited humus layer samples collected in 2017 using NucleoSpin soil kit (Macherey Nagel, Germany). Nanodrop One (Thermo Scientific) was used to measure DNA concentrations. ITS2 region for fungi and V4 region of 16S SSU rRNA for bacteria were amplified in polymerase chain reaction (PCR) and fragments were then sequenced with MiSeq platform (Illumina) by utilizing MiSeq v3 kit. PipeCraft 1.0 pipeline software (Anslan et al. 2017) was used for quality filtering as well as removal of artifacts, primer-dimers and primers from the raw 16S rRNA and ITS sequence reads. After assembling of paired end reads and a two-step quality filtering, an operational taxonomic unit (OTU) table was created from the sequence reads. OTUs were then annotated taxonomically using BLAST and a reference ITS2 database (sh_genral_release_dynamic_01.12.2018.fasta) from UNITE (Nilsson et al. 2018) and 16S rRNA (SILVA_123_SSURef_Nr99_tax_silva.fasta) from SILVA (Quast et al. 2013; Yilmaz et al. 2014) to find representative fungal and bacterial sequences, respectively. After quality filtering, functional information of fungal guilds of OTUs was derived from FUNGuild (Nguyen et al. 2016).

3.2.3 Statistical analyses

In **III,** SR_{tot} and SR_h values were first adjusted for soil temperature (10 °C) by fitting a nonlinear regression (Lloyd and Taylor 1994) between soil temperature and respiration for each measurement point, and adding the estimated respiration value at 10 °C of each measurement point to the residual of each measurement. Analysis of variance (ANOVA) with a linear mixed effects model structure, followed by Scheffe's post-hoc test was then used to compare estimated marginal means of SR_{tot} and SR_h (measured and soil temperature-adjusted) between plot types and microsites (LT, SF_d, SF_o, ID), separately for the two forest sites (Paajasensalo and Viitalampi). Plot type and microsites was the fixed variable and measurement day (running number over the study period) and measurement point (1–84) crossed random variables in the mixed model. No statistical testing was done to compare differences SR_a as there was only one value for each plot type or microsite for each measurement day. Spearman's rank correlation coefficients were used to evaluate the relationship between plot mean soil surface respiration (measured and soil temperature-adjusted), soil temperature and moisture and BA (living, dead and total). The BA of each SF plot was used for the corresponding SF_d and SF_o microsites.

In **IV,** the two forest sites (Paajasensalo and Viitalampi) were handled mostly together, as most of the studied variables showed similar patterns between the plot types at both sites. ANOVA with a linear mixed-effects model structure followed by Tukey's post-hoc test was used to compare estimated marginal means of litter detritus and soil stocks, humus layer C fractions, ergosterol concentrations and ECM_{growth} between plot types (LT, SF, ID). Plot type was the fixed variable and plot number (1–12) a random variable in the mixed model. Interaction between plot type and forest site was also first set as a fixed variable in the model, but it was removed if it did not show a statistically significant effect, which was the case for all variables except the humus layer ergosterol concentration. Principal component analysis, Venn diagrams and heatmaps (containing proportions of most abundant fungal and bacterial OTUs) were created to describe and visualize the fungal and bacterial community composition between plot types, but no statistical testing was done due to low number of cases. Statistical testing in **III** and **IV** was done using the R-statistical computing environment (R Core Team 2019) and p-values of < 0.05 considered as significant.

4. RESULTS AND DISCUSSION

4.1 How do stand, site and soil characteristics relate to tree damage caused by insects?

Stand, site and soil characteristics that predispose trees to insect damage were studied across plots having a wide range of defoliation caused by *D. pini* (**I**) as well as trees with varying levels of infestation by *I. typographus* (**II**). The *D. pini* outbreak had developed chronic (gradation and post-gradation level for over 10 years) in the studied managed *P. sylvestris* forests (**I**). *I. typographus* infestation in *P. abies* dominated urban forests was studied during/right after peak densities of the gradation phase of the insect (**II**).

4.1.1 Diprion pini

In **I**, the range in the studied environmental variables was rather limited as most of the study plots located on poor (CT) site types and rather flat terrain, with plot mean elevations ranging from 165 to 200 m (above sea level) and plot mean slopes varying between 1 and 14 ° (**I**: Table 2). However, there was more considerable variation in some of the soil properties. For example, plot mean humus layer C/N ratios varied between 27 and 56, and B-horizon contents of soil particles < 0.06 mm (coarse silt and finer) varied between 10.7 and 44.2% (**I**: Table 2).

Contrary to expectations, higher defoliation level caused by *D. pini* was associated with plots having soil properties that indicated greater soil fertility. For example, plot mean defoliation was positively and significantly correlated with plot mean humus layer N concentration and B-horizon content of <0.02 mm (medium silt and finer) soil particles, and negatively with humus layer and B-horizon C/N ratios (**I**: Table 4, Figure 2). In addition, plot mean defoliation had a negative correlation with plot mean slope and a positive one with (A_h+)E-horizon thickness. Variables, or variable combinations, that best predicted the probability of a plot having *moderate to severe* defoliation (>20 % foliage loss) were:

thickness of (A_h+)E-horizon alone (positive association, classification accuracy 88%, Kappa value=0.65), C/N ratio and pH of humus layer (negative associations, classification accuracy 86%, Kappa value=0.58), C/N ratio of B-horizon and slope (negative associations, classification accuracy 85%, Kappa value=0.57) and N concentration and pH of humus layer (positive and negative associations, respectively, classification accuracy 82%, Kappa value=0.50) (**I**: Table 5). Interpretation of the positive relationship between (A_h+)E-horizon thickness and site fertility is, however, not straightforward. While an increasing A_h-horizon thickness could indicate increasing fertility, a thicker E-horizon would indicate greater leaching of OM (i.e. poorer topsoil). Nevertheless, (A_h+)E-horizon had a positive relationship with humus layer N concentration and negative with B-horizon C/N ratio (**I**: Table 3), which would imply an increasing fertility with increasing (A_h+)E-horizon thickness at our plots.

As the insect outbreaks are partly driven by host tree quality, the higher *P. sylvestris* defoliation on the more fertile plots could relate to the nutritional quality of host trees for *D. pini*. For example, the European pine sawfly (*Neodiprion sertifer* Geoffr.) has been observed to actively search and select needles with best nutritive quality, containing more N but less phenolics (Giertych et al. 2007). Increased soil N, whether due to fertilization or natural variation, has been shown to increase *P. sylvestris* needle N concentrations (Björkman et al. 1991; Raitio 1998; Tarvainen et al. 2016). Soil N availability may also affect tree secondary chemistry. Both, increases (Björkman et al. 1991; Kainulainen et al. 1996) and decreases (Holopainen et al. 1995; Kainulainen et al. 1996) of resin acid concentrations as well as decreases in monoterpene and phenolic concentrations (Kainulainen et al. 1996) of mature or seedling *P. sylvestris* needles have been indicated after N additions to the soil. Furthermore, NPK-fertilization and watering of pines has been observed to result in greater pinyon sawfly (*Neodiprion edulicolis* Ross) mass (Mopper and Whitham 1992). Thus, the *P. sylvestris* needles on trees growing on the more nutrient rich plots may have been more nutritious and favorable for *D. pini* consumption.

Some studies have shown that pine sawfly tree damage is greater or more common on nutrient poor soils and sites (Larsson and Tenow 1984; Geri 1988; Mayfield et al. 2007; Nevalainen et al. 2015). The results of **I,** showing that *D. pini* defoliation was greater on plots having more fertile soils, was therefore unexpected. This contradiction might be related to the limited fertility range in **I**. If there had been greater variation in site types and soil fertility, the relationship between soil fertility and *D. pini* defoliation could have shown a different pattern. However, in Finland *P. sylvestris* commonly grows on such low fertility site types as the ones in **I**.

Similarly, the modest variation in elevation and slope in **I** probably explains the lack of clear effect of topography on defoliation. Although there was no significant difference in plot mean slope between the *mild* and *moderate to severe* defoliation classes (**I**: Table 4), and the terrain was generally flat, plot mean defoliation was higher on smoother slopes (i.e. decreasing slope angle). Such sites could have for example a more optimal host-tree quality or soil microclimate for *D. pini,* overwintering. The association of defoliating Siberian silkmoth (*Dendrolimus superans sibiricus* Tschetw.) outbreaks with certain topographical characteristics has been shown to change as the outbreak proceeds (Kharuk et al. 2009). In **I**, the chronic outbreak of *D. pini* could have also resulted in different host-tree preferences and outbreak patterns than those of more recent outbreaks.

4.1.2 Ips typographus

In **II**, the plots were located on the relatively fertile (MT) to herb-rich (OMT) and fertile grove (OMaT) site types, but also as in **I** on a relatively flat terrain. Plot mean elevation varied between 86 and 161 m (above sea level) and slope between 2 and 24 ° (**II**: Table 3). Plot mean spruce DBH ranged between 6 and 66 cm, and height between 6 and 37 m (**II**: Table 3). Plot mean BA of spruce was 29 m^2/ha and plot mean stem density varied between 159 and 955 stems per hectare and proportion of spruce stems between 31 and 100% (**II**: Table 3). Most (21) of the plots were found on sandy till deposits, ten with a shallow till, six with a sandy soil and 11 had finer soil textures. Plot mean volumetric stone content ranged between 0.5 and 63.5%, and mineral soil (0–5cm depth) C/N ratios between 14 and 21 (**II**: Table 3).

The results of **II** indicated that *I. typographus* infestation was related to tree and stand-level factors. Trees having *moderate* and *severe infestation* tended to have a lower DBH, height and BA values than trees in the *no infestation index class* (**II**: Figure 2). However, only the differences between the *no infestation* and *moderate infestation* for DBH and height, and between *no infestation* and *severe infestation* for BA were significant (**II**: Figure 2 and Table 4). Generally, the spruce trees on the plots were very large, and among such variation in tree size, *I. typographus* might have preferred the smaller ones. In comparison to the larger trees, the smaller trees may often have a thinner bark and periderm and lower amount of resin ducts, and thus poorer resistance against *I. typographus* boring efforts (Baier 1996).

Plot elevation, slope, site type, soil stoniness, soil C, N concentrations and C/N ratios did not differ between the *infestation index classes*, but aspect and soil texture class in the *severe infestation index class* were significantly different in comparison to the other *classes* (**II**: Table 4). In the *severe infestation index class,* 71% of the trees were found in the north, northeast or east-facing aspects, whereas in the *moderate* and *no infestation,* the corresponding proportions were 31 and 33%, respectively. Most dominant soil texture class in the *severe infestation index class* was shallow till (57% of trees) and in *moderate* and *no infestation classes* it was sandy till (45 and 49% of trees, respectively). Aspect and site type were shown to be important explanatory variables in the CLM modeling, resulting in high cumulative probabilities when combined with various other variables. Three CLM models were further evaluated (**II**: Tables 5, 6 and 6). Highest cumulative probabilities for *severe infestation* of *P. abies* by *I. typographus* were related to eastern aspect and rich site type fertility (OMaT or OMT) combined with moderate steep slopes, shallow soils or high soil C/N ratio. Those of *no infestation* were mostly related to southern to western-facing aspects and moderate site fertility (MT site types), combined with very gentle slopes, finer soil textures and low soil C/N. Highest probabilities for a *moderate infestation* were mostly associated with similar predisposing factors as *severe infestation*, except for the aspect.

In the best CLM model (*model* 1, AIC=692), aspect, site type and slope were utilized to predict the probability of *I. typographus* infestation. Eastern aspects, moderately steep slopes combined with OMT or OMaT site type had the highest cumulative probabilities (0.73 and 0.72, respectively) for *severe infestation* (Figure 4a). When eastern aspect and the OMT or OMaT site types were combined with very gently sloping sites, the probability (0.11) decreased notably, however. For south-facing aspects, probabilities for *severe infestation* were also low (< 0.16), but some combinations showed relatively high cumulative probabilities for *moderate infestation*, such as south-facing aspect, OMT or OMaT sites types on moderately steep slopes (probability 0.66). Highest probabilities for *no infestation* were associated with very gently sloping sites. Probabilities more than 0.90 for that class were a

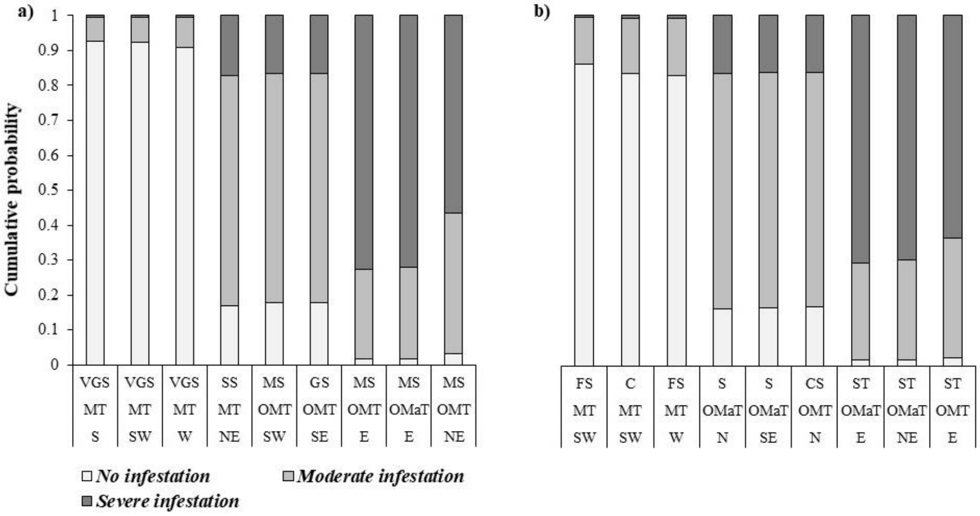

Figure 4a) Three variable combinations with highest probabilities for *no infestation, moderate infestation* and *severe infestation index class* according to *model 1*, including slope, site type and aspect, and **b)** *model 2*, including soil texture class, site type and aspect. VGS=very gently sloping, SS=strongly sloping, MS=moderately steep sloping, GS=gently sloping, MT=relatively fertile *Myrtillus* type, OMT=herb-rich *Oxalis-Myrtillus* and OMaT=fertile groves *Oxalis-Maianthemum,* S=south, SW=southwest, W=west, N=north, NE=northeast, E=east, SE=southeast, FS=fine silt, C=clay, SA=sand, CS=coarse silt, ST=shallow till.

combination of very gently sloping sites with MT site type and southern, southwestern or western aspects (Figure 4a).

In *model* 2 (AIC=707, deltaAIC=14), aspect and site type were combined with soil texture class. The highest cumulative probability (0.71) for *severe infestation* was predicted for OMaT site types growing on shallow till on east-facing aspects (Figure 4b). Also, when combining OMaT or OMT site types with shallow till soil on east or northeast-facing aspects, cumulative probabilities for *severe infestation* were almost as high (0.62–0.70). When combining the OMaT site types on shallow till with southwestern slopes, probability for *severe infestation* decreased to 0.25 (**II**: Figure 4b). Considerable *moderate infestation* probabilities (0.50–0.67) were, however, found with various combinations of aspect, site type and soil texture class (Figure 4b; **II**: Figure 4a and b). Shallow till soils increased the probability for *moderate* and *severe infestation* slightly. Highest probabilities for *no infestation* (0.80–0.86) were given by combinations of MT site type, southwestern or western aspects and finer soil textures (Figure 4b).

Model 3 (AIC=711, deltaAIC=19) combined aspect and site type with mineral soil (0–5cm) C/N ratio. The cumulative probability for *severe infestation* increased with increasing soil C/N ratio, while probability for *no infestation* showed the opposite (**II**: Figures 5a–d). The highest probabilities for *severe infestation* were on OMaT site types having an eastern aspect and high soil C/N ratios (**II**: Figure 5a). When combined with OMaT sites types on southern aspects, or MT site types having either eastern or southern aspects, the probability for *severe infestation* was on a clearly lower level, and increased towards higher C/N rations

(**II**: Figure 5b–d). The probability of *no infestation* was relatively high when combined with MT site type and south-facing aspects and low soil C/N (**II**: Figure 5d).

Based on previous research, we had expected that tree infestation by *I. typographus* would be greater on sites with soil and topographical properties indicating water deficiency, such as shallow soils as well as steep south-west facing slopes. The results were partly according to the expectations, as *severe infestation* was associated with sites having for example shallow till soils, but contrary to the expectations, aspects facing east to north rather than south to west. Water limitation could hamper *P. abies* resistance against *I. typographus* for example as a result of decreased resin flow (Netherer et al. 2015). A limited moisture availability, especially in drought conditions, has also been suggested to lead to increased tree tissue nutrient contents and thus faster development of bark beetle larvae (White 2015).

That east to north-facing aspects were more susceptible to infestation could indicate more preferable habitats for the bark beetle on the aspects that receive less radiation. A preference by mountain pine beetle *D. ponderosae* for unthinned pine stands, which receive less radiation than thinned stands has been shown, and suggested to relate to lower host-tree bark and phloem thermal conditions (Bartos and Amman 1989). In our study, the cooler eastern aspects may have been preferred during the hot summers 2010, 2011 and 2013, before of our field assessment in 2014. As discussed above in the context of *D. pini* outbreaks and topography, the preference for certain type of sites may, however, change due to a lack of their availability or changes in environmental conditions as the outbreak proceeds. For example, *I. typographus* infestation in mountainous central European areas has been shown to start on the sites receiving more radiation but then move to the less sun-exposed ones (Mezei et al. 2019). Possibly, our sites showed a different pattern due to prevailing weather conditions, and the outbreak moved during and after a cooler summer in 2014 from the northern-eastern aspects more towards other aspects as well.

The greater susceptibility of the more fertile (OMT and OMaT) site types (when combined with certain site factors) and slightly, but not significantly, higher mineral soil N concentrations in the *severe infestation* class (**II**: Figure 2) could be a reflection of a more optimal nutritional quality of host trees growing on such sites. Moderate increases in soil N availability have been indicated to relate to increased N concentrations in the inner bark of lodgepole pines (*Pinus contorta* Watson) as well as *D. ponderosae* larvae (Cook et al. 2010). Loblolly pines (*Pinus taeda* L.) with greater N contents have also been shown to produce larger southern pine beetle (*Dendroctonus frontalis* Zimmermann) adults (Ayres et al. 2000). The increasing risk of *severe infestation* with increasing soil C/N ratios (indicating lower nutrient availability) in *model 3* (**II**: Table 5) may suggest interaction between the effect of soil fertility and aspect.

4.2 How do storm and *Ips typographus* disturbance influence forest C?

To estimate effects of storm and bark beetle disturbance on forest ecosystem C, soil surface respiration, tree, litter detritus and soil C stocks, as well as humus layer C fractions and microbial community composition were examined on undisturbed (LT), storm disturbed (SF) and *I. typographus* disturbed (ID) plots in *P. abies* dominated forest sites, Paajasensalo and Viitalampi (**III** and **IV**). At the SF and ID plots, most of the trees had been killed due to the disturbance events (dead to total tree BA ratios: 0.64–1.00), while most of the trees at the undisturbed LT plots were living (dead to total tree BA ratios: 0.01–0.19). Both study forest sites were included into a conservation area after the storm in 2010, so the dead trees were left untouched, which made the sites ideal for examining the disturbance effects. The field work in the study sites was carried out five to seven years after the storm and one to four years after *I. typographus* had caused tree mortality. Due to this difference in the length of time since the disturbance, potential differences in the effects of the two disturbance types on forest and soil C and microbiology could not be directly evaluated.

4.2.1 Soil surface CO_2 effluxes

We expected that soil surface autotrophic respiration (SR_a) would be lower but heterotrophic (SR_h) higher at both of the disturbed plots than at the LT plots due to tree mortality and possible alterations in litter quantity and soil microclimate after the storm and bark beetle disturbances (**III**). Furthermore, we hypothesized that SR_a and SR_h would differ between the storm-disturbed dead tree detritus covered (SF_d) and open-vegetated (SF_o) microsites due to differences in insolation, amounts of litter and coverage of ground vegetation.

Although it was not possible to statistically test if there was a difference in SR_a between the plot types because of the small sample size, SR_a was lower at the disturbed plots than the LT plots at the Paajasensalo site. (Figure 5a). At the Viitalampi site, SR_a values only at the SF_d microsite were lower than at LT; however, the values at SF_d, SF_o and ID at Viitalampi were still lower than those of the LT plot at Paajasensalo (Figure 5a). All of the SR_{tot} and SR_h did not show a consistent difference between the disturbed and undisturbed plots. At Paajasensalo, SR_{tot} and SR_h tended to be lower at the disturbed plots than at the LT plots (Figures 5a and 5b). The mean SR_{tot} (mixed model-adjusted) at SF_d, SF_o and ID were 82, 64 and 79%, respectively, of the LT plot values, but the only significant difference for SR_{tot} and SR_h in Paajasensalo was between SF_o and LT (**III**: Table 2). At Viitalampi, SR_{tot} and SR_h did not significantly differ between the plot types or microsites (Figure 5b; **III**: Table 2). The SR_a/SR_{tot} ratios at the undisturbed LT plots (0.51 in Paajasensalo; 0.31 in Viitalampi) were in the range to what has been observed in boreal forests, when considering the generally large seasonal variation in SR_a (Comstedt et al. 2010; Pumpanen et al. 2015); however, the ratio at the LT plot in Viitalampi was rather low. The SR_a/SR_{tot} ratio for SF_d, SF_o and ID respectively averaged 0.20, 0.36, 0.40 at Paajasensalo and 0.14, 0.45 and 0.36 in Viitalampi.

The high SR_a at the SF_o and ID at Viitalampi was probably due to the inclusion of respiration from ground vegetation and from the roots of remaining living trees inside and outside the plots. The trenched Viitalampi SF and ID plots were located on the edge of a large gap created by the storm and facing southwards, and thus received more radiation than most of the other plots. In 2015, the ID plot at Viitalampi was also affected by another storm which broke half of the standing dead trees leading to a further enhancement in received radiation. These conditions at the plots seemed to have enhanced the development of the ground vegetation in comparison to the other disturbed plots, and possibly offered better growing conditions for the remaining living trees. However, at the other disturbed plot types and microsites, the lower SR_a values in comparison to the LT plots must have been due to the tree mortality and cessation of belowground allocation of photosynthates.

That SR_h was not higher at the disturbed plots may be related to the time since disturbance. The high amounts of more easily decomposable litter, such as needles (Sariyildiz et al. 2008; Kopáček et al. 2015) and fine roots (Kohout et al. 2018) may have increased heterotrophic respiration during or soon after tree mortality (i.e. before the start of our field work). However, an initial peak in the rate of litter and topsoil decomposition processes during and right after an *I. typographus* outbreak have been suggested to decline already during the following couple of years, after the inputs of easily decomposable litter have been

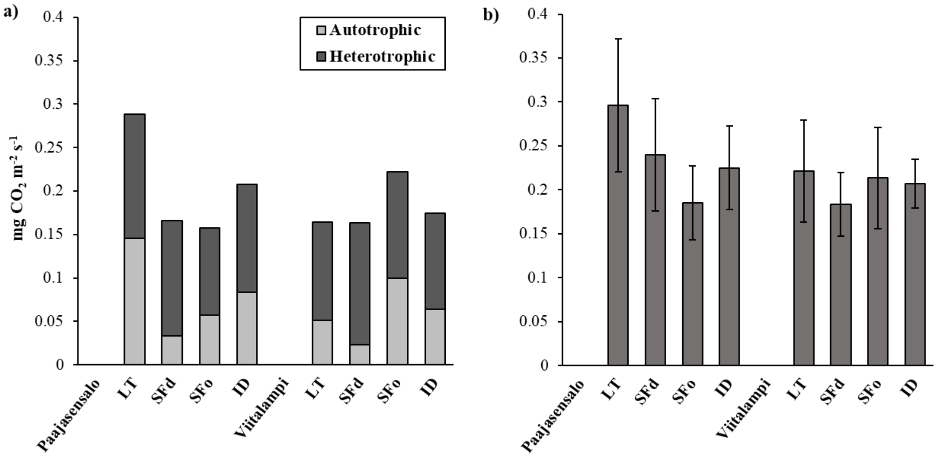

Figure 5a) Plot type and microsite autotrophic (SR_a) and heterotrophic (SR_h) soil surface respiration means measured and estimated from the intact and trenched measurement points (in the plots established in 2015) in summer 2017, and **b)** total soil surface respiration (SR_{tot}) means (± standard deviation, based on mean values of each measurement point) measured from the intact measurement points (in all plots) in summers 2015–2017 at Paajasensalo and Viitalampi forest sites. LT=living trees (undisturbed), SF_d=storm-felled trees-dead tree detritus, SF_o=storm-felled trees-open vegetation, ID=*Ips typographus* killed trees.

utilized (Štursová et al. 2014). Litter from the dead trees and C supply from the remaining living vegetation, as well as the existing soil organic matter at our disturbed plots, however, appeared to keep SR_h at rather similar levels as those at the LT plots, seven (storm) and three-four (beetle) years after the disturbances. Litterfall in an unmanaged forest after *I. typographus* disturbance has indeed been shown to be higher compared to an undisturbed forest throughout a study lasting for almost a decade after the infestation (Kopáček et al. 2015). Although there were no significant differences in SR_{tot} or SR_h between the SF_d and SF_o microsites, SR_a was slightly lower and SR_h slightly higher at the SF_d microsites than at the SF_o microsites (Figure 5a). This likely relates to the greater amount of litter detritus at the SF_d microsites and more living vegetation at the SF_o microsites.

As was expected, soil respiration was positively related to soil temperature (**III**: Supplementary material Table 2), and soil temperature and moisture showed some differences between the disturbed and LT plot types. SF_d and SF_o microsites had significantly lower soil temperatures than the LT plots at Paajasensalo, and the ID plots had significantly higher temperatures than the LT plots and SF microsites at Viitalampi (**III**: Table 2). The differences in soil temperature between the plot types were, however, quite modest and thus adjusting the SR_{tot} or SR_h values for soil temperature did not notably change the respiration differences, or the lack of them, between the plot types and microsites (**III**: Table 2). Some previous studies have shown increased soil temperature after wind and partial harvest disturbance to be a major contributor to increased heterotrophic or total soil respiration after the event (Mayer et al. 2014, 2017). However, these studies were carried out in mountainous areas where steeper slopes would have a greater enhancing effect on insolation in comparison to our flatter sites. In addition, the ground vegetation and dead tree trunks at our disturbed plots may have dampened the potentially increased radiation towards the soil surface.

Soil moisture was higher at the disturbed plots and microsites than at the LT plots at both forest sites, but differences were significant only at Paajasensalo (**III**: Table 2). The tree mortality leads to decreased tree transpiration, and thus often to higher soil moisture (Edburg et al. 2012). In Viitalampi, the lack of significant differences in soil moisture between the plot types and microsites may have been related to the development of the ground vegetation, received insolation and/or enhanced growth of the remaining living trees. The relationship between soil moisture and both, SR_{tot} and SR_h, at the within plot type and microsite-scale were generally weak and non-significant, except for significant negative correlations for SR_h at ID at Paajasensalo and at LT and SF_d at Viitalampi (**III**: Supplementary material Table 2). Plot mean SR_{tot} also had a significant negative correlation with soil moisture (**III**: Table 3). Those can indicate that elevated soil moisture conditions after tree mortality might have a dampening effect on soil respiration.

4.2.2 Forest C stocks, humus layer C fractions and microbial community

In paper **IV**, the effects of storm and *I. typographus* disturbance on forest C stocks as well as humus layer C fractions and microbial community composition were investigated, and the two forest sites (Paajasensalo and Viitalampi) were handled together and the SF plots were not separated to microsites. Aboveground tree C stocks obviously had shifted from living biomass towards necromass at the disturbed plot types. Mean living tree aboveground biomass C stock to total tree aboveground C stock ratios were 0.93, 0.21 and 0.29 for the LT, SF and ID plot types, respectively (Table 2).

As was expected as a result of the tree mortality after disturbance, litter detritus C stocks were higher on both of the disturbed plots than at undisturbed LT plots (Table 2). However, the difference was significant only between ID and the other plot types (Table 2) and was a lot due to a high amount of bark and cone litter at ID (**IV**: Figure 2b). Bark beetles may detach the bark at least from some parts of the host trees quite fast (Lieutier et al. 2016), whereas bark at SF plots seemed to have mostly remained on the dead trees. Furthermore, some of the litter from the dead trees at the SF plots was probably more decomposed than at ID plots as the tree mortality by the storm happened some years earlier than that of *I. typographus*. As discussed earlier, litterfall in an unmanaged forest after an *I. typographus* outbreak can remain relatively high for at least a decade (Kopáček et al. 2015), and could be expected to be considerable also in storm disturbed sites. The humus layer and 0–6 cm mineral soil C stocks did not significantly differ between the plot types, although humus layer stocks were slightly smaller at the disturbed plots than at LT (Table 2), indicating a small impact of disturbance on humus layer and topsoil C stocks at this period of time after the events.

It was expected that cessation of belowground allocation of photosynthates following tree mortality would result in lower K_2SO_4 extractable C concentrations (C_{EXT}) and root-associated ectomycorrhizal mycelial growth (ECM_{growth}), and consequently lower ergosterol (i.e. fungal biomass) and total microbial biomass C (C_{MB}) concentrations at both of the disturbed plots than at the LT plots. Although mean C_{EXT} concentrations were slightly lower at the disturbed plots than at the LT plots, the differences between the plot types were not significant (Table 2). This was probably because of contributions of belowground C allocation by remaining living vegetation as well as litter decomposition to the concentrations of C_{EXT}. As was expected, ECM_{growth}, fungal biomass and C_{MB} concentrations were all lower at both of the disturbed plots (Table 2). Since ECM fungal mycelium accounts for 30–40% of total microbial biomass in coniferous forests (Högberg and Högberg 2002; Högberg et al. 2010), the differences in fungal and total microbial biomass between the plot types were

Table 2. Mean tree and soil C stocks and humus layer (except ECM mycelial growth determined from humus layer and top mineral soil) C fractions and microbial properties by plot type. All values are presented per dry weight. LT=living trees, SF=storm-felled trees, ID=*Ips typographus* killed trees. Different letters indicate a significant difference in the mixed effects model-adjusted marginal means among plot types (ANOVA with mixed-model structure and Tukey's post-hoc). In addition to plot number, interaction between forest site and plot type was included in the model of humus layer ergosterol concentration.

	Plot type		
	LT	**SF**	**ID**
C stocks			
Tree aboveground biomass (Mg C/ha)	108.5	15.6	30.9
Tree aboveground necromass (Mg C/ha)	7.8	62.5	77.2
Litter detritus (Mg C/ha)	0.9 ^{a}	1.2 ^{a}	2.5 ^{b}
Humus layer (Mg C/ha)	23.0 ^{a}	17.7 ^{a}	20.2 ^{a}
Mineral topsoil (0–6 cm depth, (Mg C/ha)	21.8 ^{a}	20.8 ^{a}	22.1 ^{a}
Humus layer C fractions and microbiological properties			
Total C concentration (%)	46.1 ^{a}	42.6 ^{a}	42.9 ^{a}
Microbial biomass C concentration (mg/g)	6.7 ^{a}	5.1 ^{b}	5.1 ^{b}
K_2SO_4 extractable C concentration (mg/g)	1.2 ^{a}	0.7 ^{a}	0.8 ^{a}
Ergosterol concentration (fungal biomass, mg/g)	0.21 ^{a}	0.15 ^{b}	0.14 ^{b}
ECM mycelial growth index	0.45 ^{a}	0.19 ^{b}	0.16 ^{b}

likely mostly due to decreases in ECM fungal biomass. Fungal biomass was the only variable that showed a significant interaction between plot type and forest site in the mixed model. This was because differences between the LT and disturbed plot types were more distinct and patterns between the SF and ID plots opposite at Viitalampi (0.24, 0.11 and 0.14 mg/g, at LT, SF and ID, respectively) in comparison to Paajasensalo (0.19, 0.19 and 0.14 mg/g, at LT, SF and ID, respectively). Such a difference was possibly partly explained by smaller differences between the LT and SF plots at Paajasensalo and Viitalampi in their proportions of living to total tree basal area (**IV**: Table 1) as well as in ECM_{growth} (Paajasensalo, 0.39 and 0.21, at LT and SF, respectively; Viitalampi, 0.52 and 0.17, at LT and SF, respectively).

Although the DNA sequencing results can only be considered directional due to the low sample size, they also indicated a lower ECM fungal abundance and a slightly lower ECM fungal diversity at both of the disturbed plots than at LT. Various OTUs belonging to common ECM fungal genera, such as *Russula*, *Piloderma* and *Cortinarius* were abundant at the LT plots, but nearly absent at the disturbed plot types (Figure 6a; **IV**: Supplementary material 3). LT had more unique OTUs (n=27) than the SF (n=17) and ID (n=12) plots, and

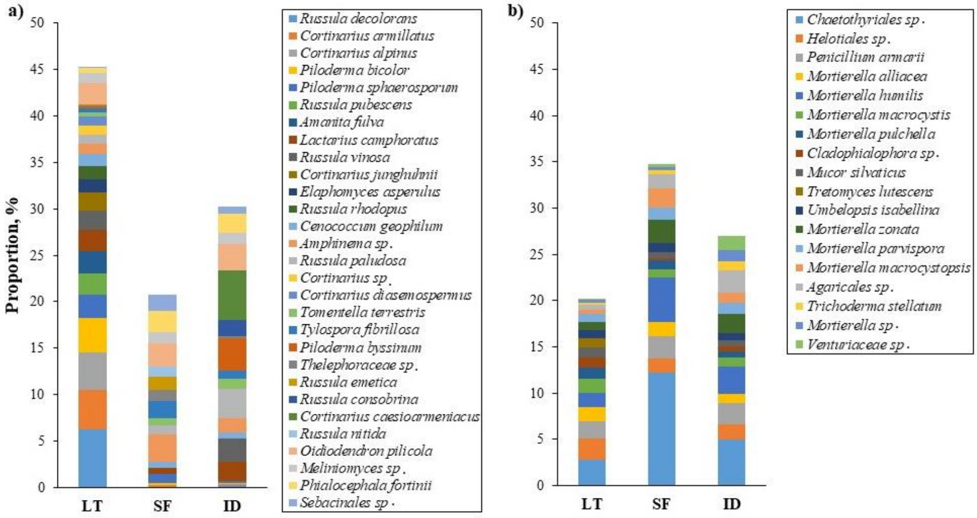

Figure 6. Proportions (read amount of database match from total read amounts in plot type) of the most dominant (proportion of all reads in plot type more than 1%) **a)** tree-symbiotic (all ectomycorrhizal fungi, except *O. pilicola*, *Meliniomyces* sp. and *Sebacinales* sp. are also found as ericoid mycorrhiza and *P. fortinii* endophytic fungi), and **b)** decomposition-associated fungi (mostly saprotrophic, some have also pathogenic or symbiotic putative ecological functions, *Agaricales* sp. include fungi with various ecological functions) representative OTUs (species level) in living trees (LT), storm-felled trees (SF) and *Ips typographus* killed trees (ID) plots.

67% of those were ECM fungi (**IV**: Supplementary material 4a). However, 68% (n=315) of the fungal sequences did exist on all of the plot types (**IV**: Supplementary material 4a).

Fungal residues, especially those of root-associated ones, are essential for the long-term and stable storage of C in soil (Clemmensen et al. 2013; Adamczyk et al. 2019a). Re-establishment of ECM fungi after disturbance would therefore be important for the forest soil C storage potential. Furthermore, ECM fungal recovery would be expected to benefit forest C uptake by benefiting tree and seedling survival and growth. After harvest disturbance, the recovery of ECM fungi can take a few decades (Wallander et al. 2010), but the remaining living trees inside and adjacent to our disturbed plots could be expected to quicken the process.

Although the SR_h results (**III**) indicated no increases in soil organic matter decomposition seven years after the storm and three to four years after tree mortality by *I. typographus*, the DNA sequencing results indicated a slight increase in the abundance of some fungi with saprotrophic and pathogenic ecological putative functions (**IV**). For example, *Chaetothyriales* sp. (common ascomycetous, yeast-like group of fungi), as well as some *Mortierella* sp. were indicated to be relatively more abundant on both of the disturbed plots in comparison to the LT plots (Figure 6b; **IV**: Supplementary material 3). These likely benefited from the greater amounts of litter detritus and decreases in ECM fungi after disturbance. The differences in the abundance of many decomposition-associated fungi between the plot types, however, seemed to be rather modest. Saprotrophic fungi appear to be quite important utilizers also of root exudation (Ballhausen and de Boer 2016). Thus, the tree mortality and likely decreased amount of root exudates might have to some extent dampened possible stimulating effects of increased litter inputs on decomposing humus layer microbes.

The DNA results also indicated a slightly higher bacterial diversity at the SF and ID plots than at LT (**IV**: Supplementary material 4b and 5). However, the abundance of several dominant bacterial genera, such as *Burkholderia*, *Acidothermus*, *Bradyrhizobium* and *Occallatibacter* indicated similar or slightly higher abundance at the LT plots than at the disturbed plot types (**IV**: Supplementary material 5 and 6). The LT plots had less (n=18) unique bacterial OTUs than the SF (n=35) and ID (n=36) plots as well as less shared bacterial OTUs with the disturbed plot types (with SF, n=18; with ID, n=8) than the disturbed plot types had with each other (n=55) (**IV**: Supplementary material 4b). However, 60% (n=260) of all bacterial sequences were found at all of the plot types. As with ECM fungi, the remaining living trees inside and outside the disturbed plots possibly contributed to the magnitude of some of the differences in bacterial abundance and diversity between the disturbed and the LT plots. The proportion of living trees after disturbance has indeed been shown to be related to the stability of the bacterial community (Mikkelson et al. 2017) and diversity of ECM fungi (Sterkenburg et al. 2019).

4.3 Uncertainties and limitations

Ideally, in order to predict sites susceptible to insect caused damage, and to quantify the actual effects of disturbance on a forest, field data should be collected *a priori* to the disturbance. However, predicting where and when a storm or insect disturbance will occur and carrying out field work beforehand is often impossible. Thus, the data generally has to be collected after the initialization of the disturbance, and the potential sources of error recognized when interpreting the results. To some extent such problems may be reduced with a large enough sample size and careful site selection.

In studies **I** and **II**, the soil was sampled some 10 (**I**) and three years (**II**) after the initiation of the insect outbreaks and thus soil properties could have been influenced by the outbreak, contrary to what we were aiming to examine. Defoliator and bark beetle disturbance can have considerable temporary effects on the availability and cycling of N and C in forest floor and soil, lasting at least up to a few years after the events (Lovett and Ruesink 1995; Morehouse et al. 2008; Griffin and Turner 2012; Kaňa et al. 2013; Ferrenberg et al. 2014; Norton et al. 2015; Trahan et al. 2015). However, studies on the effects of defoliators and bark beetles on humus layer and/or mineral soil total C or N concentrations or C/N ratios in coniferous forests have mostly indicated no change during, a few years or decades after an outbreak (Streminska et al. 2006; Morehouse et al. 2008; le Mellec and Michalzik 2008; Griffin et al. 2011; Griffin and Turner 2012), with some exceptions (Kaňa et al. 2013; Mikkelson et al. 2017). Although the possibility of the higher soil N concentrations being due to *D. pini* defoliation (**I**) cannot fully be excluded, the relationships of soil physical soil properties (texture and (A_h+)E-horizon thickness) with defoliation (**I**: Table 4) could be interpreted as causal. Also, as soil N concentrations and C/N ratios were significantly related to those physical soil properties (**I**: Table 3), it can be assumed that they represented the longer term nutrient status of the site rather than a recent effect of the insect outbreak. In study **II**, soil total C and N concentrations or C/N ratio did not differ between the *infestation index classes* (**II**: Table 4), and it is unlikely that those would have been affected by the recent *I. typographus* infestation and they mostly reflected the pre-outbreak soil conditions of the sites.

As no measurements prior to the disturbances were carried out in **III** and **IV**, we were not able to quantify the actual effects of the disturbances, and some of the observed differences between the plot types may have been affected by potential pre-disturbance differences among the plots. However, by grouping the different plot types at carefully selected locations, and by replicating the groups at two separate locations in each of the two forest sites, the risk of pre-disturbance plot type differences in stand, site and soil conditions were considered to be minimized as much as possible in such field studies. Nevertheless, the results in **III** and **IV** represented plot type differences at certain periods of time after the disturbances, when the effects of disturbance on a forest vary over time (Edburg et al. 2012). In addition to possible pre-disturbance differences in site characteristics, uncertainty to comparability of trees, plots and sites in field studies like ours (**I**–**IV**), may be brought for example by physiological differences between tree individuals that affect their susceptibility to insect herbivory, as well as compensatory responses of trees to consumption by herbivores (Strauss and Agrawal 1999; Chen et al. 2001).

Taken that **I, II**, **III** and **IV** were carried out on a relatively limited range of environmental factors, their results may not apply to forests with stand, site and soil features and climatic conditions from outside of those ranges. In addition, as host-tree preferences and site characteristics associated with an insect outbreak may change as the outbreak proceeds (Kharuk et al. 2009; Mezei et al. 2014, 2019), the observed relationships between environmental variables and insect outbreaks of a certain phase, as in **I** and **II**, might not be representative for all phases. Furthermore, outbreaks of an insect species do not always occur and develop under similar conditions, as they are a result of multiple interrelated factors, such as host-tree quality, abiotic stressors and populations of natural enemies.

Studies **III** and **IV** were carried out in forests where the dead trees were left on site, which is unusual among the generally intensively managed Finnish forests. In managed forests, the tree C stocks would obviously rapidly decrease as the disturbance-killed trees, and possibly also living trees among them, would be harvested. Clearing of trees would often lead to more distinct changes in light availability and ground vegetation composition, cause more severe soil disturbance, and reflect to forest regeneration (Fischer et al. 2002; Jonášová and Prach 2008; Jonášová et al. 2010) as well as litterfall dynamics. These alterations would be expected to contribute to soil microbiology and forest C cycling and their recovery after the events.

Over greater spatial scales, disturbance by *I. typographus* might often result in a patchier tree mortality pattern than a heavy storm due to the more selective tree mortality by the insect. The differing environmental conditions created by the rapid change in stand structure and tree uprooting by storms in comparison to the more gradual disturbance by *I. typographus* that leaves most of the dead trees standing, could be expected to reflect also in soil properties and dynamics. Our results, however, showed few significant differences in the examined variables between the two disturbance types (**III** and **IV)**, which might relate to the similar amounts of tree necromass at the SF and ID plots (Table 2) and our sampling strategy. In addition, all of the SF and ID plots located rather close or were surrounded by undisturbed forest, which may have also contributed to similarity between the two disturbed plot types. Furthermore, as the time since the storm and *I. typographus* disturbance was different, the impact of disturbance on the ecosystem was at different stages of development in the SF and ID plots. Thus, direct comparisons between the effects of the two disturbance types cannot be done based on our results. Nevertheless, the results of **III** and **IV** showed that both abiotic storms and biotic *I. typographus* disturbances have a notable impact on forest ecosystem C. While the response of soil surface respiration, humus layer C fractions and composition of the microbial community of the two disturbance types can be similar at the sampling and measurement scale used in this study, differences may be found when examining the two disturbance types at different spatial and temporal scales.

5. CONCLUSIONS

The role of forests and soil in capturing and storing C is continually increasing in importance in the changing climate. Disturbance events are essential for forests and some of them, such as storms and insect outbreaks, are expected to become more common in various parts of the world in the future, with potential implications on forest C sequestration and storage capacity. The various environmental characteristics predisposing forests to disturbance as well as the diverse effects of disturbances on forest ecosystems and their C cycling are, however, not fully understood.

This dissertation identified site, soil and stand factors that predispose trees and forest stands to defoliating *D. pini* and bark beetle *I. typographus* disturbance, and assessed the effects of storm and *I. typographus* disturbance on forest C stocks, soil surface CO_2 effluxes, as well as humus layer C fractions and microbial community composition. Site predisposition to *D. pini* and *I. typographus* were studied in managed *P. sylvestris* and urban *P. abies*-dominated forests, respectively. Effects of storm and *I. typographus* disturbance on forest C were examined in *P. abies*-dominated forests where all the disturbance-killed trees had been left on site after the events.

Although forest stand predisposition to insect outbreaks was studied on a relatively limited environmental range, it was associated with several site and soil characteristics. Higher defoliation of *P. Sylvestris* caused by *D. pini* was found to be related to soil properties indicating greater fertility (e.g. lower C/N and finer texture). Highest cumulative probabilities for severe *I. typographus* infestation of *P. abies* were found for trees growing on sites with east-facing aspect and rich site type fertility combined with moderately steep slopes, shallow till soils or high soil C/N ratio. In contrast, lowest probability for infestation was associated with southern to western-facing aspects and moderate site fertility, combined with very gentle slopes, finer soil textures and low soil C/N. Susceptibility of sites with these environmental characteristics to *D. pini* and *I. typographus* disturbance possibly related to a more favourable tree nutrition and secondary compound chemistry for the insects.

The studied forest C and soil microbiological characteristics were rather similar on the storm (5–7 years after) and *I. typographus* (1–4 years after tree mortality) disturbed sites. Soil surface total and heterotrophic CO_2 effluxes, humus layer and mineral topsoil C stocks and humus layer K_2SO_4 extractable C concentrations of storm and *I. typographus* disturbed as well as undisturbed plots differed little, despite the shift of tree C stocks from biomass to necromass after both disturbances and much greater litter detritus C stocks on the *I. typographus* disturbed plots. Soil surface autotrophic CO_2 effluxes were mostly lower at the disturbed plots than at undisturbed ones, with some exceptions. The most distinct differences on the microbiology of the humus layer between the plot types were lower abundance of tree-symbiotic ectomycorrhizal fungi, and consequently slightly lower microbial and fungal biomasses on both of the disturbed plot types. Those changes were likely related to an assumedly decreased belowground allocation of photosynthates after the mortality of most mature trees on the disturbed plots. However, the living trees remaining on or in close proximity to the disturbed sites probably mitigated the belowground response to disturbance to some extent. Although storms often have a more rapid and intense impact on a forest than more gradually developing *I. typographus* outbreaks, the similarity in soil C and microbiological characteristics between the sites that had been affected by the two disturbance types may be partly related to the different periods of time since the disturbances occurred in the area.

More research on the patterns of disturbances, especially by insects, across wide ranges of explaining environmental characteristics would be important, as their occurrence is often a result of multiple interrelated factors, of which only little is known. Field research on the impacts of natural disturbance on forest C are often limited to the short-term effects of the events. However, longer-term monitoring and combining field studies with ecosystem modeling elucidate the response and recovery of forest C sink after such events further. As soils are the basis of forest functioning and account for most of boreal forest C stocks, research emphasis should be given to the reflection of disturbances on soil C dynamics and microbial communities. Furthermore, examining predisposition to storm and insect disturbance and their impacts on ecosystem C across forests with varying tree species composition and age structures might provide important and practical information. All such studies would help to develop forest management strategies that result in a better balance between forest ecological functions, economical aims as well as optimization of C sequestration in a changing climate and with intensified disturbances.

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