Impacts of bark beetle infestation on soil fungal community composition in Swedish boreal forests

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Degree project/Independent project • 60 credits
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Department of Soil and Environment
Soil, Water, and Environment
Examensarbeten / Institutionen för mark och miljö, SLU
Partnumber 2025:09
Uppsala 2025

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Credits:	60 credits
Level:	Advanced (A2E)
Course title:	Master Thesis in Environmental Science
Course code:	EX0899
Programme/education:	Soil, Water, and Environment- Master's program
Course coordinating dept:	Soil and Environment
Place of publication:	Uppsala
Year of publication:	2025
Partnumber:	2025:09
Series title:	Examensarbeten / Institutionen för mark och miljö, SLU

Keywords:	boreal forest, bark beetles, forest disturbance, ECM fungi, saprotrophic fungi, fungal community

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Abstract

Ongoing global change and forestry practices are increasing stress on boreal forest ecosystems, making them more susceptible to insect infestations. In Sweden, outbreaks of the spruce bark beetle (*Ips typographus*) have become more frequent, leading to increased infestation levels in spruce (*Picea abies)* stands. These disturbances in aboveground vegetation may profoundly affect soil fungi, particularly the symbiotic relationship between trees and ectomycorrhizal fungi, which play key roles in boreal soil nutrient and carbon cycles, potentially affecting ecosystem processes.

Soil samples of organic horizons were collected from twelve spruce stands in the region surrounding Uppsala, Sweden, in a paired setup, where infested sites showed different infestation vulnerabilities, measured on the ratio of infested to total spruces. In contrast, nearby paired control sites showed no sign of infestation. I introduced the term “infestation vulnerability” to compare the infestation intensity of infested sites to the paired un-infested control sites. The impact of infestation on fungal community composition was assessed using DNA sequencing of the ITS2 and LSU regions, focusing on shifts in the relative abundance of fungal guilds between infested and control sites and along infestation vulnerability.

Ectomycorrhizal fungi were significantly less in relative abundance at bark beetle-infested sites compared to un-infested control sites, while saprotrophic fungi showed the opposite pattern. Along with increasing infestation vulnerability, ECM fungi declined in relative abundance, whereas saprotrophs increased. Interestingly, the abundance of ECM fungi in non-infested control sites increased with the level of infestation observed in their paired infested sites. Soil properties at both site types correlated with the infestation vulnerability, suggesting decreased soil fertility, possibly making trees susceptible to bark beetle infestation and their outbreaks more pronounced. At the same time, ECM fungi increase due to a higher need of trees for symbiotic support.

Keywords: boreal forest, bark beetles, forest disturbance, ECM fungi, saprotrophic fungi, fungal community

Acknowledgements:

First, I would like to give special thanks to my supervisor, Tamlyn Gangiah, for supporting me throughout this year in the field, the lab, and all aspects of bioinformatics. Thanks for always being available and making time for me, even on holidays. Special thanks to Björn Lindahl for making this thesis possible, giving me the freedom to design my own project. Thanks to both of you for showing interest in my work and guiding me with knowledge and experience to stay on the right track, especially in the end. I thank Tamnlyn Gangiah, Andrea Törnqvist, Anna Knaapi, Cora Blasinski, Clara Kieschnick-Llamas, Erica Packard, and Péter Garamszegi for company and help during my field work, as well as Leo Zdansky Cottle for providing his car for spontaneous field trips. I thank Katharina Ihrmark and the Forest Mycology and Plant Pathology lab for providing an excellent lab space and for their help with practical questions. Thanks to the whole Soil Biology group for including me, helping me with various questions, inspiring me to get deeper into fungal taxonomy this coming fall, and motivating me to stay in academia. I thank NEFOM for giving me the unforgettable experience of presenting my ideas at the start of my thesis and getting valuable feedback during the annual conference. I thank Sara Overud Wissman from Länsstyrelsen for recommending several areas with previously recorded bark beetle infestations, making the sampling location assessment much easier. I thank my examiner, Thomas Ranius, and opponent, Johanna Ringstam, for constructive feedback. Last but not least, I am very thankful for all the support I got from my family, friends, colleagues and fellow master students throughout all the stages of my thesis. Without all the help and support, this thesis would not have been possible.

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Abbreviations

Abbreviation	Description
Al	Aluminium
AM	Arbuscular mycorrhizal
C	Carbon
CCS	Circular consensus sequencing
DNA	Deoxyribonucleic acid
ECM	Ectomycorrhizal
Fe	Iron
HTS	High Throughput Sequencing
ITS	Internal transcribed spacer
LSU	Large subunit
N	Nitrogen
OM	Organic matter
OTU	Operational taxonomic unit
PacBio	Pacific Biosciences
PCR	Polymerase chain reaction
SH	Species hypothesis
SOM	Soil organic matter

1. Introduction

1.1 The Boreal Forest Ecosystem

The boreal forest ecosystem represents the second largest forest biome (Astrup et al. 2018), covering approximately 11 % of the Earth's landmass (Bonan & Shugart 1989). It represents one-third of the global forest (Hansen et al. 2010; FAO 2020), forming a circumpolar belt extending across Fennoscandia, Russia and North America, lying between the Arctic and temperate zones (Brandt 2009). This ecosystem is characterised by a cold continental climate with short, mild summers and long, harsh winters (Saucier et al. 2015).

The vegetation in this region has evolved to these extreme climatic and environmental conditions, resulting in a rather homogenous structure with a low diversity in tree species (Esseen et al. 1997; Gauthier et al. 2015). This is also true for Sweden, where roughly 70 % of the land is covered with an even-aged, low-diversity forest shaped by forestry (Nilsson et al. 2021). The dominant trees are conifers of the genera *Picea* (spruce), *Pinus* (pine), *Larix* (larch) and *Abies* (fir). Deciduous trees are mainly represented by the genera *Betula* (birch), *Populus* (poplar), *Alnus* (alder), *Sorbus* and *Salix* (willow). Globally, coniferous trees dominate this ecosystem, especially the Norway spruce *Picea abies* and the Scots pine *Pinus sylvestris* (Esseen et al. 1997; Saucier et al. 2015; SLU 2024). Pines thrive rather on dry, nutrient-poor sandy soils, with a more continental climate and a higher fire frequency, whereas spruce prefer a more oceanic climate and moist soils that are more fertile (Esseen et al. 1997; Saucier et al. 2015), being more dominant in the south of Sweden (Nilsson et al. 2021). In Sweden, boreal understory vegetation consists of three main components: ericaceous dwarf shrubs, reindeer lichens and mosses (Nilsson & Wardle 2005). *Vaccinum myrtillus* (bilberry), *Vaccinum vitis-idaea* (lingonberry) and *Empetrum hermaphroditum* (crowberry) are the dominant shrub species in Swedish boreal forests (Nilsson & Wardle 2005).

Plant communities in boreal forests are shaped by soil conditions, such as nutrient availability, hydrology, and soil acidity (Lahti & Väisänen 1987), which are further addressed as “soil fertility”. At the same time, vegetation influences soil properties through root exudates, plant litter input and mycorrhizal symbioses (Lundström et al. 2000; Smith & Read 2008; Taylor & Bhatnagar 2024). Soils with low fertility, like Podzols, are the most dominant soils in the boreal forest and in Sweden (Thiffault 2019; Frelich 2020). They are characterised by a specific Iron/Aluminium (Fe/Al) chemistry, nutrient scarcity, low pH and are defined by a thick organic horizon of recalcitrant plant biomass, with a clearly separated mineral horizon that can be further divided into two distinct layers. The upper layer is called the eluvial horizon and has a distinct grey colour and low pH, where organic matter

(OM), Al, and Fe are leached out. Below is the illuviated horizon where the leached OM and metals are re-depositioned (Frelich 2020). Histosols are also very common in the boreal forest and are created through waterlogging and slow organic matter decomposition (Thiffault 2019; Frelich 2020). This leads to an accumulation of OM, forming peatlands that store substantial amounts of carbon (C) (Thiffault 2019). With increasing soil fertility, the abundance of deciduous trees, the pH, and the abundance of soil fauna increase, leading to a more mixed soil profile (Haimi & Einbork 1992).

Boreal forest soils are characterised by reduced rates of decomposition and evapotranspiration, which contribute to the accumulation of organic matter in the topsoil and overall slow nutrient cycling during forest succession (Read et al. 2004; Kielland et al. 2007). These slow nutrient and C cycling processes are largely driven by environmental constraints such as low temperatures, acidic soil pH, and recalcitrant plant tissues (McLaren & Turkington 2013; Frelich 2020), and poor drainage conditions (van Cleve & Alexander 1981; Nilsson & Wardle 2005). This makes these ecosystems a significant C storage (Bradshaw et al. 2009), containing approximately one third of terrestrial C (Pan et al. 2011; Astrup et al. 2018; *IPCC 2007* n.d.). However, this C pool of purely organic topsoil is relatively unprotected (Deluca & Boisvenue 2012), making boreal forest soils particularly sensitive to environmental changes. C enters the ecosystem by long-term sequestration in plant or microbial biomass (Nilsson & Wardle 2005). Most of this C is stored belowground (Bradshaw & Warkentin 2015), originating from fine roots and root-associated microorganisms, and not primarily from plant litter as previously thought (Clemmensen et al. 2013). This belowground C allocation promotes microbial growth, representing half of the soil respiration in these forests (Högberg et al. 2001). Therefore, plant-soil interactions and belowground processes are crucial in global C cycling.

In boreal forest ecosystems, nitrogen (N) has been identified as the primary limiting factor for plant growth (Vitousek et al. 1997; Högberg et al. 2001; Hyvönen et al. 2008). Despite the abundance of N in the soil, it is predominantly bound in complex organic compounds resistant to decomposition and too large for direct plant uptake (Vitousek et al. 2002). The microbial depolymerisation of these macromolecules is therefore a critical and rate-limiting step in N mineralisation and availability (Schimel & Bennett 2004). Boreal vegetation has been observed to conserve N within biomass, producing litter with low carbon-to-nitrogen (C/N) ratios (Persson 1980; van Cleve & Alexander 1981). This process leads to the accumulation of recalcitrant organic matter, which in turn restricts the availability of N within the ecosystem. Consequently, intense competition for N between soil microorganisms and plants affects nutrient cycling and ecosystem processes (Jäderlund et al. 1998).

1.1.1 Impacts of Disturbances on the Forest Ecosystem

Over the last two centuries, the boreal forest ecosystem has been increasingly affected by forestry and intensive management, leading to significant changes in its structure and biodiversity (Östlund 1993; Östlund & Zackrisson 1997). Sweden's boreal forests have undergone major structural changes over the past century, contributing to a decline in plant and animal species diversity (Östlund & Zackrisson 1997). The predominant forestry practice - clear-cutting of even-aged forest stands - has transformed forests with diverse tree communities into more uniform, monospecific landscapes, reducing their natural complexity (Siitonen 2001).

In addition to forest management practices, environmental changes of anthropogenic origin are altering ecosystems worldwide (Hansen et al. 2006; *IPCC 2013* n.d.). These effects are particularly pronounced in the high latitudes of the Northern Hemisphere (Hansen et al. 2006), with the boreal forest experiencing more rapid warming than other forest biomes (Gauthier et al. 2015; Seidl et al. 2017). The potential effects of climate change on the ecosystem are very diverse. They can be either direct, as changes in temperature or precipitation, or indirect in the form of changes in vegetation and natural disturbance regimes, significantly increasing tree mortality (Astrup et al. 2018). Temperature, for example, is correlated with tree growth (Anthony et al. 2022) and decomposition rates (van Cleve & Alexander 1981), where changes make forests more susceptible to secondary effects such as fires, windthrow, and insect outbreaks, ultimately increasing tree mortality (Anderson-Teixeira et al. 2013; Astrup et al. 2018; Jönsson & Lagergren 2018). The combination of both pressures, multiple climate change risks and intensive management (Moen et al. 2014; Gauthier et al. 2015), increases vulnerability and hampers resilience to disturbance and insect attack in the future (Singh et al. 2024). Norway spruce (*Picea abies*) is particularly sensitive to rising temperatures (Singh et al. 2024), where increased tree mortality has been documented following more frequent droughts and heat waves (Gazol & Camarero 2022). In southern Sweden, spruces are more vulnerable to windthrow, spring frost, summer drought, and bark beetle infestations (Bolte et al. 2010; Grundmann et al. 2011), which have been shown to increase in number and intensity (Kjellström 2014). This is due to milder and wetter winters (Felton et al. 2016) which are also more frequently expected in the future (Seidl et al. 2014).

Studies have suggested that these changes affect the ecosystem's C cycle (Bonan 2008; Hayes et al. 2011), weakening the C sink capacity of boreal forests and possibly even turning some areas into C sources (Bonan 2008; Kurz et al. 2008). Given the current trajectory of climate change and increasing atmospheric CO_2 concentrations, this general trend poses a significant environmental risk.

1.2 The Spruce Bark Beetle *Ips typographus*

Next to fires, storms and droughts, bark beetle outbreaks, particularly those of the Eurasian spruce bark beetle *Ips typographus*, represent a major threat to the boreal forest (Seidl et al. 2017; Hlásny et al. 2021; Senf & Seidl 2021).

Bark beetles (Coleoptera: Curculionidae: Scolytinae) are distributed globally, and they play a crucial role in nutrient cycling, biodiversity, and plant succession. Most bark beetles breed exclusively in dead trees, playing an important role in deadwood decomposition and are therefore vital for forest succession (Hofstetter et al. 2015; Raffa et al. 2015). Some species can colonise stressed or dying trees (Hlásny et al. 2021), where they feed on the phloem tissue between wood and bark, disrupting nutrient and water transport in the tree, leading to tree mortality (Raffa et al. 2015). With an increasing number of infested trees, bark beetle populations can proliferate and reach an epidemic threshold. Due to their high number, they can then overcome the defences of even healthy trees, increasing forest mortality (Hlásny et al. 2021).

Bark beetle infestations alter forest structure above ground by damaging trees and drive significant changes in soil properties below ground. The reduction in trees and shallow fine root biomass (Cigan et al. 2015) has interconnected impacts on biotic processes as well as abiotic variables such as soil pH, soil moisture, microbial activity, root exudates, litter inputs, and soil nutrient dynamics (Cigan et al. 2015; Custer et al. 2020; Hlásny et al. 2021). However, in unmanaged forests, all vegetational biomass remains in the system, providing an input of C and nutrients (Morehouse et al. 2008). Reduced canopy cover leads to increased soil moisture (Mikkelson et al. 2013) but also exposes the forest floor to greater temperature fluctuations (Hais & Kučera 2008; Park Williams et al. 2013). These changes can enhance decomposition rates and nutrient leaching (Tong et al. 2024), which in turn can lead to higher C losses, further diminishing the C storage below ground (Mayer et al. 2020). Additionally, C input into the soil is disrupted after tree mortality, due to the cessation of fine root biomass production as well as mycelial growth (Baldrian et al. 2013; Clemmensen et al. 2013; Kyaschenko et al. 2019). With decreased root deposits and the cessation of base cation uptake, the pH of the soil can increase, elevating the buffer capacity of the soil (Custer et al. 2020). Tree mortality affects soil nutrient cycling, particularly N dynamics, by halting N uptake and increasing N and phosphorus (P) availability through biomass input and reduced plant demand (Morehouse et al. 2008; Mikkelson et al. 2013; Cigan et al. 2015). This effect might increase along a gradient of increasing infestation (Griffin et al. 2011; Keville et al. 2013; Štursová et al. 2014). Premature litterfall after bark beetle infestation has been shown to have higher N concentrations in the needles (Morehouse et al. 2008). The pulse of increased input of high-N litter could alter soil N cycling by increased inputs through leaching, reduced plant uptake, increased mineralisation or decreased immobilisation (Mooshammer et al. 2014).

In Sweden, the combination of climate change, altered hydrology, soil acidification, and widespread clear-cutting followed by planting of monospecific spruce stands has reduced forest resilience, increasing susceptibility to bark beetle outbreaks (Schelhaas et al. 2003; Breshears et al. 2009; Seidl et al. 2011; Strengbom et al. 2011). At the same time, warming temperatures are enhancing the survival, reproduction, and spread of bark beetles by accelerating and extending their brood development (Hinze & John 2020; Hlásny et al. 2021), further stressing forest ecosystems (Seidl et al. 2017; Venäläinen et al. 2020). In the future, forests in Sweden are expected to have increased levels and frequencies of infestations (Seidl et al. 2014), since outbreaks are predicted to shift towards higher latitudes and elevations (Dale et al. 2001; Jönsson et al. 2011). This alteration of aboveground vegetation in turn shapes soil communities, especially those of soil fungi (Veselá et al. 2019a; Custer et al. 2020; Otsing et al. 2021).

1.3 Soil Fungi

Fungi play a crucial role in key ecosystem processes (Averill et al. 2019), such as C and N cycling through the decomposition of soil organic matter (SOM) and influence tree nutrition and productivity via mutualistic root associations (Treseder & Lennon 2015; van der Heijden et al. 2015; Baldrian 2017; Averill et al. 2019). They account for a major portion of microbial biomass and activity in forest soils (Högberg et al. 2001; Joergensen & Wichern 2008; Kohout et al. 2018) and their diversity makes them essential for forest ecosystem functioning and dynamics (Clemmensen et al. 2013; Bahram et al. 2018).

1.3.1 Trophic Guilds

Fungal communities can be categorised into four distinct trophic guilds: endophytic, pathogenic, saprotrophic, and mycorrhizal fungi (Pérez-Izquierdo et al. 2021). Endophytic fungi can live within the tissues of plants without causing harm, while the opposite is true of pathogenic fungi, which typically cause death of host tissues (Zanne et al. 2020).

Saprotrophs

Saprotrophic fungi are free-living primary decomposers that facilitate the breakdown of plant litter, wood, and soil organic matter (SOM), obtaining energy and nutrients from these organic substrates (Leake et al. 2004; Lindahl et al. 2007). In forest soils, these organisms are typically dominant in upper soil layers with labile C complexes, where they are efficient in colonising new plant-derived litter (Lindahl et al. 2007; Clemmensen et al. 2013; Kyaschenko et al. 2017a). Their decomposition processes are key in regulating soil C cycling (Kyaschenko et al. 2017a; Fukasawa 2021; Manici et al. 2024) and soil formation (Boddy et al. 2008),

thereby significantly contributing to soil respiration and CO_2 release (Cairney & Meharg 2002; Floudas et al. 2012). However, the growth of saprotrophic decomposer fungi is limited by the competition of other fungi for nutrients and space (Bödeker et al. 2016).

Mycorrhiza

Mycorrhizal fungi establish symbiotic relationships with plant roots, therefore dominating deeper soil layers, enhancing nutrient and water uptake of their host in exchange for photosynthetic C (Lindahl et al. 2007; Smith & Read 2008; van der Heijden et al. 2015; Pérez-Izquierdo et al. 2021). This mutualistic symbiosis gives mycorrhizal fungi a competitive advantage over other fungi (Lindahl et al. 2010). During this process, plants channel a significant amount of photosynthetic C into the soil and fungal biomass (Clemmensen et al. 2013; Johnson & Jansa 2017; Jansa & Kohout 2019), where their necromass represents a considerable C pool (Wang et al. 2021; Hawkins et al. 2023). Mycorrhizal fungi have been observed to be associated with approximately 90 % of plant families, supplying up to 80 % of their N and 90 % of their P requirements (van der Heijden et al. 2015). This is achieved by scavenging and mining recalcitrant structures that are otherwise unavailable for root uptake. This symbiotic relationship has been demonstrated to enhance overall plant growth and fitness (Smith & Read 2008; Anthony et al. 2022) and to increase tolerance to biotic and abiotic stresses (Bahadur et al. 2019; Branco et al. 2022) increasing plant species success and shaping ecosystem dynamics (Read 1991). Furthermore, the expansion of their mycelial networks contributes to soil stability and the formation of soil organic matter (van der Heijden et al. 2015).

The diversity of mycorrhizal associations reflects the varied environmental conditions, with each type adapted to specific ecological niches. For instance, ericoid mycorrhiza, primarily from the fungal phylum Ascomycota, form symbiosis with plants in the Ericaceae family. These symbioses are observed to thrive in acidic, nutrient-poor soils such as heathlands, peatlands, and boreal forests (Pérez-Izquierdo et al. 2021).

Arbuscular mycorrhiza, formed by fungi in the Glomeromycota phylum, represent the most widespread type, forming tree-like hyphal structures inside plant root cells to facilitate nutrient exchange (Pérez-Izquierdo et al. 2021) and associate with roughly 80 % of all plants. These fungi are more abundant in P-limited ecosystems characterised by high N mineralisation rates (Bunn et al. 2024), playing a crucial role in facilitating P uptake for their host plants (Smith et al. 2011).

In contrast, ectomycorrhizal (ECM) fungi, which belong to the Basidiomycota and Ascomycota phyla, form a mantle around roots and a Hartig net around epidermal root cells (Tedersoo et al. 2010; Pérez-Izquierdo et al. 2021) with almost all boreal forest plants (Dahlberg 2002a; Brundrett 2009). ECM communities seem

to control the degradation of recalcitrant organic N sources in the soil (Talbot et al. 2013), decomposing soil organic matter (SOM) while mining for nutrients (Talbot et al. 2008; Lindahl & Tunlid 2015; Shah et al. 2016). In comparison to their saprotrophic ancestors, ECM, like some *Laccaria* (Martin et al. 2008) and *Amanita* (Wolfe et al. 2012) species, have lost their capacity to decompose cell wall material (Kohler et al. 2015). Therefore, the high presence of ECM fungi was thought to slow down decomposition rates by competing with saprotrophs. This leads to an accumulation of OM and lower rates of N and C mineralisation, which is known as the 'Gadgil effect' (Gadgil & Gadgil 1971; Averill et al. 2014; Kyaschenko et al. 2017b). This effect is particularly present in nutrient-limited coniferous forests. However, ECM may both promote and hamper the accumulation of OM belowground (Frey 2019), since members of the genus *Cortinarius* have been found to have retained the capacity to decompose complex phenolic molecules, such as lignin or humic substances, from their white rot litter saprotrophic ancestors (Bödeker et al. 2014; Clemmensen et al. 2015; Kyaschenko et al. 2017a). Along with a decline in ECM fungi after tree mortality (Pérez-Izquierdo et al. 2021), the presence of *Cortinarius* species has been linked to lower levels of below-ground C storage due to higher decomposition activity (Clemmensen et al. 2021; Lindahl et al. 2021). Thanks to their ability to mobilise nitrogen (N) from organic matter (OM) and provide it to their hosts, these trees thrive in ecosystems with slow nitrogen cycling and low mineralisation rates (Read 1991; Shah et al. 2016). Furthermore, several ECM fungi can utilise peptides and proteins as nitrogen sources (Abuzinadah & Read 1986).

Fungi are N-rich organisms, representing a substantial N store in the soil. Therefore, the N limitation of plants can lead to increased C allocation in the soil, stimulating fungal growth and, by that, their need for N, further depleting N from the soil (Näsholm et al. 2013; Franklin et al. 2014). Still, plants in the boreal forest largely depend on the mycorrhizal symbiosis (Read 1991; Lindahl et al. 2002).

C accumulation in boreal forests is largely influenced by the interaction of symbiotic mycorrhizal fungi and free-living saprotrophs (Talbot et al. 2013; Averill et al. 2014; Kyaschenko et al. 2017a). Differences in fungal biomass production and necromass decomposition might determine long-term accumulation of C, and these traits vary considerably between fungal species (Fernandez & Koide 2012; Wallander et al. 2013). ECM fungal forests, or even individual trees, can host a great diversity of ECM fungal species (Read 1991; Tedersoo et al. 2010), creating a community in just a small space. Species´ richness and composition are primarily shaped by environmental factors, with forest type and climatic region playing the most dominant roles (Tedersoo et al. 2014; Bahram et al. 2018). Additional factors influencing soil fungal communities include soil chemistry and local climate (Castaño et al. 2018; Tedersoo et al. 2021), as well as tree species, which determine root exudates and leaf litter composition (Kennedy et al. 2009; Pérez-Izquierdo et

al. 2017). Over time, forests have developed their specific fungal community structure, where, especially in old-growth forests with diverse fungal communities, rare and specialised fungi dominate (Dvořák et al. 2017; Majdanová et al. 2023). Given these dependencies of fungi and their host plants, forest fungal communities are highly sensitive to changes in vegetation structure and dynamics.

1.3.2 Impacts of Disturbances on the Soil Fungal Community

The impacts of forest ecosystem disturbances, like vegetation loss, on the soil fungal communities depend on their ecological guilds. The effects of large-scale forest disturbances on the soil microbiome have been well studied (Stendell et al. 1999; Dahlberg 2002b; Cairney & Bastias 2007), and there seems to be a greater impact of abiotic factors, such as fire or harvest, compared to biotic factors, such as insect attacks or pathogens (Holden & Treseder 2013).

Fires have been shown to have the most drastic impact on soil fungal biomass, followed by clear-cutting and insect outbreaks (Holden & Treseder 2013). Forest management, clear cutting, and the resulting cessation of photosynthetic C from the trees to the soil have negative impacts on soil fungi (Bonet et al. 2012; Tomao et al. 2020), such as decreasing fungal biomass by 20-40 % (Kohout et al. 2018).

However, these disturbances affect soil fungal trophic guilds in different ways. ECM fungi are particularly sensitive to vegetation disturbances in contrast to saprotrophic fungi, given their symbiotic lifestyle (Lindahl et al. 2007; Smith & Read 2008; van der Heijden et al. 2015; Pérez-Izquierdo et al. 2021). Disturbances can reduce ECM fungal biomass and diversity, alter species composition, and shift abundance ratios (Jones et al. 2003; Twieg et al. 2007; Grebenc et al. 2009; Lindahl et al. 2010; Hartmann et al. 2012; Kyaschenko et al. 2017a). Declines in ECM fungi have been widely documented after forest disturbances due to loss of host trees (Štursová et al. 2014; Kyaschenko et al. 2017a; Pec et al. 2017; Hopkins et al. 2018; Kohout et al. 2018; Veselá et al. 2019a; Tomao et al. 2020). At the same time, saprotrophic fungi seem to proliferate, possibly due to the sudden availability of deadwood and leaf litter as well as the decreasing competition from ECM fungi (Lindahl et al. 2010; Treu et al. 2014; Štursová et al. 2014; Bödeker et al. 2016). The increase in saprotrophic fungi may accelerate organic matter decomposition (Gadgil & Gadgil 1971), potentially leading to increased CO_2 emissions and N availability (Pérez-Izquierdo et al. 2021). This could explain higher C losses from soil after tree removal through clear cuts or storms (Kyaschenko et al. 2017a). The specialised species that dominated the forest before are now replaced with more generalist species that thrive in disturbed environments. Depending on the type of disturbance, fungal groups react in different ways (Kouki & Salo 2020). Different studies showed that it can take several years for the ECM fungal communities to

recover to the same diversity and species composition as in older stands (Wallander et al. 2010; Kyaschenko et al. 2017a).

Bark beetle infestations, like other disturbances, significantly impact soil fungal communities and their functioning (Šťursová et al. 2014; Pec et al. 2017), such as fungal biomass and diversity of litter fungi (Przybył et al. 2008; Kohout et al. 2018) and fungal enzyme activity in the rhizosphere (Šťursová et al. 2014). Following a bark beetle attack, root-associated symbiotic fungi are largely replaced by saprotrophic fungi, as shown by Stursova et al. (2014). Furthermore, another study has demonstrated that following a bark beetle attack, ECM fungal communities on seedlings are altered, with more stress-resistant and low-demanding species becoming dominant following disturbance (Veselá et al. 2019b).

These shifts in fungal communities and nutrient dynamics suggest that bark beetle outbreaks disrupt belowground microbial networks and drive cascading effects on ecosystem function and forest regeneration (Mikkelson et al. 2013; Cigan et al. 2015; Treseder & Lennon 2015; Baldrian 2017). Given the fundamental role of fungi in nutrient cycling and C storage, understanding how bark beetle infestations influence fungal communities is essential for predicting the long-term consequences of these disturbances on boreal forest ecosystems (Tomao et al. 2020).

1.4 Research Importance

Boreal forests in Sweden play a vital role in the global C cycle, especially storage, and it is therefore essential to understand the ecological impacts of disturbances such as bark beetle infestations (Bradshaw & Warkentin 2015; Islam et al. 2024; Singh et al. 2024). These outbreaks have been shown to impact biodiversity, C dynamics, and fungal communities significantly (Gauthier et al. 2015; Baldrian 2017; Hawkins et al. 2023). These communities are crucial for nutrient cycling and forest regeneration. However, even though potentially approximately 40 % of Sweden's managed forests are at risk (SLU 2024), and outbreaks are increasing in frequency (Kärvemo et al. 2023), the long-term consequences for ecosystems, climate, and the economy remain uncertain (Singh et al. 2024).

While other disturbances, such as clear-cutting, storms, and wildfires, have been widely studied in relation to soil fungal communities (Jones et al. 2003; Twieg et al. 2007; Kyaschenko et al. 2017a; Kärvemo et al. 2023), the gradual and prolonged effects of bark beetle outbreaks remain rather unexplored. In contrast to abrupt disturbances, which directly terminate input of C to the soil from trees, bark beetle infestations gradually weaken and kill trees over time, subsequently reducing the input of C. This prolonged process may enable fungal communities to adapt to these changing conditions in distinct ways. This could result in shifts in fungal composition that differ from those observed in association with more immediate

disturbances (Holden & Treseder 2013). However, this aspect of forest ecosystem dynamics has received little attention.

1.5 Thesis Aim

To my knowledge, this study is the first to assess how bark beetle infestations influence soil fungal communities in Swedish boreal forests. The aim is to explore how trophic fungal groups, especially ECM- and saprotrophic fungi, are affected by bark beetle infestation. The study will include the collection of soil samples from spruce-dominated nature reserves in the vicinity of Uppsala, Sweden, with the objective of conducting a comparative analysis of fungal communities between bark beetle-infested and healthy stands. Using paired samples ensures that soil conditions are comparable, thereby allowing the primary variable to be the aboveground vegetation and its influence on fungal composition. This study will further examine a gradient of infestation levels, defined as the ratio of infested to total spruces, ranging from 20–90% infestation, to provide insights into how fungal communities change at different stages of tree decline. A low level of infestation may represent an early phase where C exudates into the soil are only slightly reduced. In contrast, a high level of infestation could indicate later stages of tree mortality and therefore strongly reduced C exudates, offering a potential time-scale perspective on community shifts. To compare the results of the un-infested control sites along the gradient of their paired infested sites, I introduced the term "infestation vulnerability". This term serves two distinct purposes. For infested sites, it represents the measured level of bark beetle infestation. For un-infested control sites, it indicates the pairing relationship and represents the expected susceptibility to infestation based on similarity to an infested site.

I used high-throughput sequencing (HTS) of DNA markers (Nilsson et al. 2019) to analyse fungal communities in organic topsoil of boreal forest spruce stands. In recent years, HTS has provided new possibilities to study the enormous, largely uncharted fungal kingdom with its functional diversity and enabled community composition characterisation (Nilsson et al. 2019; Tedersoo et al. 2021), greatly benefiting the understanding of potential functions of so-far uncultivable species (Hug et al. 2016). Especially because species even within fungal families might have different ecologies (Matheny et al. 2006) it is of greatest importance to determine communities confidently to species level to determine their functional groups. In this study, third-generation PacBio sequencing was utilized, which offers increased read lengths and enhanced taxonomic resolution compared to previous generations. This kind of sequencing is more suitable for community analyses than previous ones (Nilsson 2019), because it helps investigate correlations between environmental drivers and soil properties (Sterkenburg et al. 2015). Custom-designed primers, gITS7 (to ensure fungal specificity) and TW13 (to generate an

extensive PCR product), were utilized. This approach enabled us to achieve a high level of taxonomic resolution, facilitating more precise comparison of community compositions.

A deeper understanding of how fungal communities respond to bark beetle outbreaks can contribute to advancing ecological theory and offering valuable insights regarding forest management and climate change mitigation. The findings of this study will facilitate predictions regarding the long-term resilience of boreal forests and inform strategies for maintaining their ecological and climatic functions in a changing world.

1.6 Hypotheses

H1) I hypothesise that bark beetle infestation significantly negatively impacts the symbiotic relationship between ECM and their plant hosts. I predict that ECM fungal abundances will be lower in areas affected by bark beetles compared to areas without infestation.

H2) Furthermore, I predict a shift in fungal community composition along the gradient of increasing infestation vulnerability. I expect the abundance of ECM fungi at un-infested control sites to linearly decrease, while saprotrophic fungi increase with increasing bark beetle infestation vulnerability.

2. Material and Methods

2.1 Field Work

Bark beetle outbreaks in Sweden were intensively investigated and documented by Länsstyrelsen after a heavy drought in 2018 (Bakke et al. 2020) and the storm "Alfrida" in 2019 (SMHI 2019). Fifteen nature reserves with bark beetle-infested spruce stands in a 70 km radius around Uppsala were recommended by Länsstyrelsen. All sites were visited during September 2024, and suitable sampling spots were scouted. During the scouting process, sites were judged based on suitability for the sampling. The criterion for suitable sites were: 1) sites needed to be spruce dominated forest patches; 2) the spruce dominated patch needed to be at least 20x20 m big; 3) infested sites needed to have a similar patch in proximity without any infestation; 4) infested sites needed to differ in the ratio of dead to total spruces to determine a infestation gradient; and 5) sites needed to be safe to work at (no risk of falling trees) and physically accessible. Eight of these locations proved suitable, having both infested and healthy spruce-dominated forest patches of sufficient size and accessibility. At these eight locations, 12 paired sites were sampled in September and October.

The selected sampling locations are in a 50 km radius around the city of Uppsala (59.858561, 17.638924) in the Upplands region of Sweden (Figure 1). The mean annual temperature is 7.1 °C, and the mean annual rainfall is 638 mm in the region measured from 1991 to 2020 (SMHI 2025b). In 2024, the average annual temperature in Uppsala was 8.1 °C, and average precipitation was 606 mm (SMHI 2025a). The average elevation of the sampling site area is 48 ± 8 m. The region belongs to the boreal forest zone, and soil types in this area are

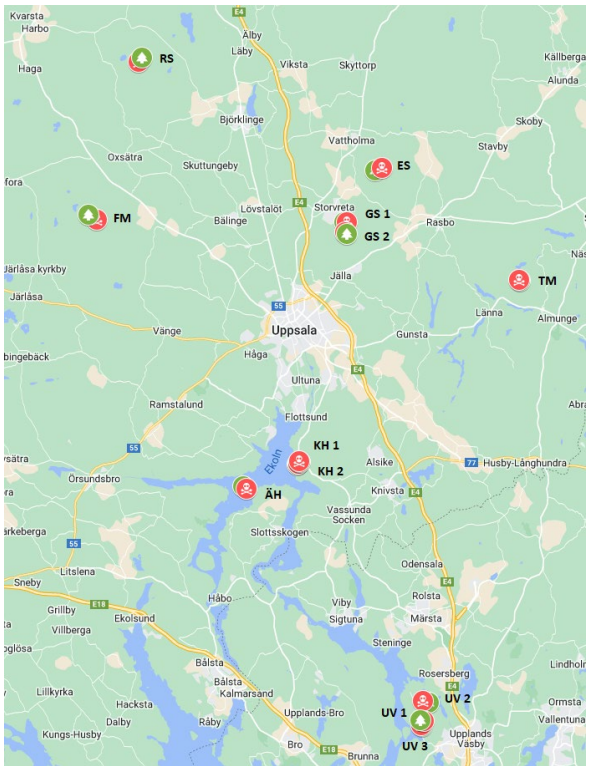

Figure 1: Map of the sampling sites around Uppsala. A red scull represents the infested site, whereas the green tree stands for the paired control site with a healthy spruce stand. Sites are named in abbreviations after the nature reserves or the area (KH = Kungshamm-Morga, TM = Tjäderleksmossen, GS = Gammelskogen, AH =Arnöhuvud, EH = Edhammarskog, UV = Upplands-Väsby, FM = Fäbodmossen, RS = Risboskogen)

Cambisols, Arenosols and Podsols (Swedish Soil Inventory 2024). At three locations (KH, GS, and UV), several sites were sampled, with respective infestation and control site pairs being near each other. A distance of at least 500 m was kept between the sites to ensure that these pairs could be considered as independent samples.

The forests were spruce-dominated, with pine and birch as the following major tree species. At some sites, the soil consisted mainly of large rocks covered with moss, with barely any soil. Others had mostly organic soil, and some only a thin organic layer with mostly mineral soil. Mosses dominated sites, covering an average of 70 % of the total surface area on all sites. The most prevalent moss genera identified were *Ptilium*, *Hylocomium*, and *Sphagnum*. Additional dominant understory vegetation included blueberries (*Vaccinium myrtillus),* grasses, lingonberries (*Vaccinium vitis-idaea*), and ferns, covering on average 20, 17, 12, and 9 % of the area, respectively. Ground vegetation slightly differed between infested and control sites, where mosses and infested sites dominated; control sites showed more ericaceous shrubs, grasses and herbs.

For sampling at each location, two spruce-dominated forest patches, one with and one without bark beetle infestation, were selected. To create a gradient of infestation vulnerability, the ratio of dead to total spruce was first estimated by sight, and then the sampling grid was placed to gain a desired infestation level.

$$Infestation\ vulnerability = \frac{infested\ spruce}{total\ spruce} \quad \{1\}$$

On each site, 25 soil core samples were taken roughly every 5 meters, following a S-pattern direction in a 20x20 m grid (Figure 2). The exact sampling spot was selected randomly to avoid sampling bias. Soil cores of a maximal 15 cm depth were taken with a soil corer of 3 cm diameter. If rocks or big roots hindered a soil core of 15 cm depth, a second sample right next to the original sampling spot was taken, discarding the first one. If the same problem occurred, the soil core was taken as it is. Green living plant parts, such as moss, grass and wood debris, were removed from the soil. Mineral and organic soil horizons were separated and pooled, respectively. The pooled soil samples were frozen the same day and stored at -20 °C until further analyses. The sampling grid was extended by 5 m in all directions, creating a buffer zone for additional tree and vegetation analysis (Figure 3). Trees were counted in the whole 30x30 m grid. Only living spruce and pine trees with a height of 2 m and a trunk of at least 7 cm in diameter at breast height (DBH) were measured. Otherwise, they were classified as saplings or seedlings if the tree height did not exceed 30 cm. Alive and dead trees of other species inside the grid were counted under the same conditions. Ground vegetation was determined, and its surface area cover was estimated.

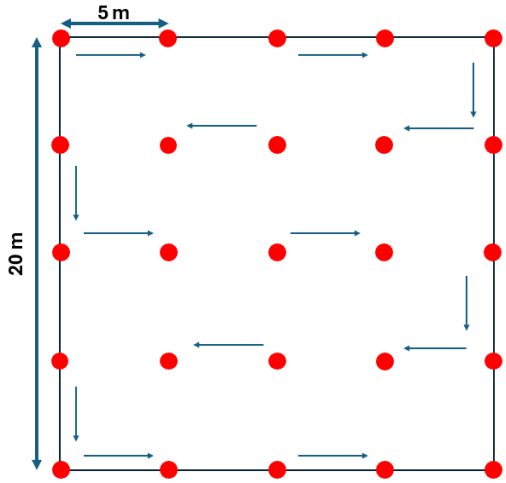

Figure 3: Graphic visualization of the sampling grid and the sampling procedure. Red dots represent soil core sampling plots whereas blue arrows indicate sampling pattern.

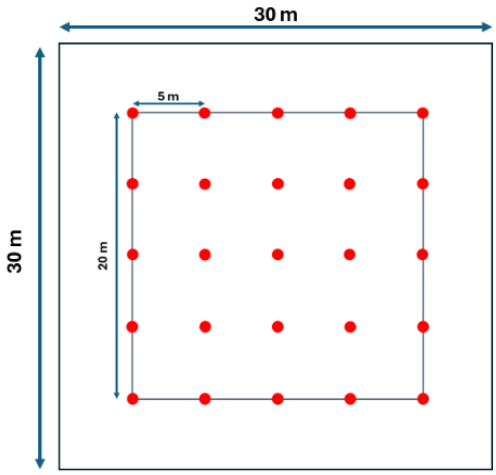

Figure 2: Graphic visualization of the vegetation analysis area, including the soil sampling grid in the centre.

2.2 Laboratory Work

2.2.1 Soil Preparation

Frozen soil samples were milled in a custom-built freeze mill. Random representative subsamples were taken for further analysis. Bigger particles like needles, leaves, roots, or pinecones remaining in the samples were taken apart manually. Subsamples were freeze-dried (4K Modulyo EF4 freeze dryer, Edwards Ltd, UK).

2.2.2 DNA Extraction and Preparation

Freeze-dried soils were ball milled (Mixer Mill MM 400, Retsch GmbH, Germany) at 25 Hz for 45 seconds. Of that milled soil, 1.505 (± 0.005) g was weighed (PG503 DeltaRange, Mettler-Toledo, Switzerland) into a 50 mL centrifugation tube for DNA extraction following the protocol of Clemmensen et al. (2016) with some modifications. DNA was extracted from 1.5 g of milled organic soils using 3 % Cetyltrimethyl ammonium bromide (CTAB) buffer. Forty glass beads (5 mm diameter) were added to milled organic soils. Approximately 25 mL of 3 % CTAB buffer was added and immediately shaken to homogenise the soil with the CTAB buffer. All tubes were shaken in the ball mill at 20 Hz for 30 seconds before incubation and every 15 minutes during the incubation time of 60 minutes at 65°C. After incubation and centrifugation (9600 x g for 5 min), DNA was extracted two times in an 1:1 ratio with chloroform and then precipitated with 1.5 volumes of 2-

propanol over night at -20 °C overnight (Kyaschenko et al. 2017a) and centrifuged the next day (16.500 x g for 10 min.) before discarding the supernatant from the pellet. After washing the pellet in 70 % ethanol and centrifuging at 4100 x g for 5 min., DNA pellets were dissolved in SL2 buffer (NucleoSpin Soil Kit, Macherey-Nagel, GmbH & Co. KG, Germany) and stored at -20°C. 300 µL of each sample was run through the Macherey-Nagel NucleoSpin Soil kit (Düren, Germany) for DNA purification following the instructions, but with volume adjustments for SL3 and SB buffer using 65 and 110 µL respectively. Purified and washed DNA was eluted in 50 µL Elution Buffer and then stored at -20 °C. DNA concentrations were measured with NanoDrop (Thermo Scientific NanoDrop ND-1000 UV/Vis Spectrophotometer, Thermo Fischer Scientific Inc., Waltham, MA, USA) and diluted with mqH_2O to DNA concentrations of 1, 0.5 and 0.1 ng/µL. To find optimal PCR cycles a test PCR was run with three samples – UV2, FM, GS2 (low, medium and high bark beetle infestation). The concentrations 1 ng/µL and 0.5 ng/µL for each sample were used.

For the PCR reaction, 20 µL of MasterMix, 5 µL of a tagged primer mix and 25 µL of DNA were added. The PCR was run under following conditions: 1) Denaturation of the dsDNA for 5 min at 94 °C; 2) 31 cycles of 30 s denaturation at 94 °C, 30 s primer annealing at 56 °C and 60 s DNA replication at 72 °C; 3) Final extension for 7 min at 72 °C. The PCR was stopped after 23, 25 and 28 cycles. To compare the products of the different concentrations and determine the most suitable combination (Castaño et al. 2020) and cycle numbers all products were run through a 1 % agarose gel (300 V, 180 mA, 20 min). The PCR was run again in triplicates for all the samples, this time with optimised PCR conditions using the 1 ng/µL dilution and 26 PCR cycles. Therefore, 25 µL of DNA was mixed with 5 µL of tagged primer mix and 20 µL of MasterMix. For this PCR, the uniquely tagged forward and reverse primers gITS7 (CXXXXXXXXT – GTGARTCATCGAATCTTTG) (Ihrmark et al. 2012) and TW13 (CAxxxxxxxx – GGTCCGTGTTTCAAGACG) (Tedersoo et al. 2017) were used. The reverse primers TW13, located in LSU, have strong affinities for all eukaryotes (Tedersoo et al. 2015) making them highly universal. Each sample became an individual tagged primer for possible separation of the DNA products later. However, the same tagged primer was used for the respective triplicates of a sample.

The AMPure XP Bead-Based Reagent Kit (Beckman Coulter Life Sciences Inc., Indianapolis, IN, USA) was used to clean the PCR products. Triplicates of each sample were pooled, diluted 1:1 with AMPure magnetic bead solution and transferred to a PCR plate. The cleaned PCR product concentrations were measured with the QuBit dsDNA Quantification High Sensitivity Assay Kit (Thermo Fischer Scientific Inc., Waltham, MA, USA).

44.7 ng of DNA for each sample respectively was pooled. The total volume of that sample was measured and further washed following the E.Z.N.A Cycle Pure

Kit for Centrifugation (Omega Bio-tek Inc., Norcross, GA, USA). Sample concentration and pureness was measured with NanoDrop (xxx - Thermo Fischer Scientific Inc., Waltham, MA, USA) and the DNA 7500 Kit for 2100 Bioanalyzer Systems (Agilent, Santa Clara, CA, USA). Fungal amplicons were sequenced using the Pacific Biosciences (PacBio) PSII SMRT method at SciLifeLab Uppsala, Sweden. PacBio was chosen to minimise size variation bias (Castaño et al. 2020).

2.2.3 DNA Processing and Bioinformatics

Fungal DNA sequences were quality filtered and clustered using the bioinformatics pipeline SCATA (https://scata.mykopat.slu.se) (Ihrmark et al. 2012). All DNA sequences were screened for gITS7 and TW13 primers and identification tags, requiring a minimum alignment length of 90 % and reverse complemented if necessary. Sequences with incomplete products, missing tags and reads with a mean quality score < 20 were removed. Penalties for mismatch, gap opening and extension were set equally to 1. All sequences only occurring once in the entire dataset (global singletons) were removed, and homopolymers were collapsed to 3 bp before clustering (Ihrmark et al. 2012). Sequences were clustered into species hypotheses (SH) using single-linkage clustering with a minimum similarity of 99 % threshold distance to the closest neighbour.

For each SH, I extracted the large subunit (LSU) and the ITS2 region using ITSx extractor (Bengtsson-Palme et al. 2013). The ITS2 region was used for taxonomic annotation, since its high variability reveals slight genetic differences, improving the differentiation between closely related species (Schoch et al. 2012). The highly conserved LSU, which shows small changes over evolutionary time, helped to estimate phylogenetic distances and relationships at higher taxonomic levels (James et al. 2006). Chimaeras were filtered out of all ITS2 sequence clusters. Only the species contributing to the top 80 % of total reads per site were kept for all further analyses, since species with low read counts would not contribute to the relative abundance while potentially reducing the statistical power. Further, I refer to them as “working species”.

Selected clusters were blasted against the reference database UNITE (https://unite.ut.ee/) (Kõljalg et al. 2013) to obtain identification of species hypothesis (hereafter, species) (Kõljalg et al. 2013). Unidentified clusters were manually identified with the help of the UNITE database and NCBI's BLASTn database (https://blast.ncbi.nlm.nih.gov) if they showed at least 98 % similarity. Species were then manually sorted into functional groups using SLUs Artdatabanken Artfakta (https://artfakta.se/). The following functional groups were included: 1) ectomycorrhizal fungi (“ECM”), 2) saprotrophic fungi (“sap”), 3) other agaricomycetes that could not be assigned to either (“unknown”), and 4) all other fungi that were not agaricomnycetes (“others”).

MUMU (https://github.com/frederic-mahe/mumu), an updated version of LULU, was used to remove remaining erroneous SHs by identifying and merging rare `daughter' SHs and combining them with similar and more abundant 'parent' SHs (Frøslev et al. 2017). MAFFT (http://mafft.cbrc.jp/alignment/server/large.html) was applied to improve cluster alignment using the LSU region. Maximum likelihood trees were created with RAxML (Kozlov et al. 2019) and visualised as a phylogenetic tree on iTOL (https://itol.embl.de/itol.cgi). SHs that were still not identified were assigned based on their neighbour joining species in the phylogenetic tree.

2.3 Soil Property Analysis

Soil moisture was determined by measuring the weight loss during freeze drying:

$$Moisture\ (\%\ of\ FW) = \frac{(FW-DW)*100}{FW} \quad \{2\}$$

FW is fresh soil weight before, and DW is dry weight after freeze drying.

One milled soil sample remained at -20 °C for later enzyme activity assays and pH measurement. The organic matter content of both organic and mineral soil was determined by the loss of ignition method using approximately 3 g of freeze-dried organic soil. Since the mineral soil samples were not freeze-dried, crucibles with soil were first dried at 60 °C. All crucibles were muffled for 6 h at 550 °C.

$$OM\ content\ (\%) = \frac{WS-WA}{WS} * 100 \quad \{3\}$$

WS is the weight of the soil pre-ignition, and WA is the weight of the remaining ash after ignition.

For pH measurements, a soil slurry with a 1:5 soil/water ratio was created using fresh organic soil and deionised water (Radiometer PHM 93 pH Meter, Radiometer Medical ApS, Denmark).

2.4 Statistical Analysis

All statistical analyses were executed in RStudio (v.4.3.3). Two-sided two-tailed t-tests were performed to test significant differences in soil properties such as pH, organic matter content, and soil moisture, as well as DBH of spruce and pine between the control and infestation sites. Linear mixed models (LMM) were used to assess the effect of infestation vulnerability on soil properties and fungal community parameters, while keeping the sites as a random factor. PERMANOVA (pairwiseAdonis) was used to test the effect of infestation vulnerability on fungal

community composition, comparing both site types. Results were visualised in a non-metric multidimensional scaling (NMDS) plot. A principal component analysis (PCA) was used to create a soil fertility index using OM content and soil moisture of both the mineral and organic soil layers, as well as pH.

For the analysis, all measured soil and vegetation properties and fungal abundances of both site types are plotted against infestation vulnerability. This was done to examine the effect of site properties on the data, comparing both sites. Since I assumed that soil properties between un-infested control and infested sites are similar due to spatial proximity, I disregarded the site factor between paired samples as a driver of fungal community composition.

3. Results

3.1 Vegetation

Table 1: Averages and standard error of vegetation parameters of control and infested sites, including the p-value of a pairwise t-test between control and infested values.

	type	Control	Infested	p value
Spruce	Circumference (cm)	54.5 ± 7.1	59.3 ± 3.9	0.57
	alive trees	80.7 ± 9.7	25.8 ± 3.7	< 0.001
	basal area (cm^2)	4412.1 ± 571.2	1523.6 ± 260.4	< 0.001
Pine	Circumference (cm)	94.6 ± 12.0	72.1 ± 12.9	0.20
	alive trees	8.5 ± 2.0	8.3 ± 3.5	0.96
	basal area (cm^2)	778.1 ± 229.2	621.9 ± 293.7	0.64

The number of spruces was significantly lower on infested sites than control sites ($p < 0.001$). Pines were significantly less abundant than spruces ($p < 0.001$). DBH of living spruces did not differ significantly between control and infested sites, but differed between the tree species, where pines on average had a higher DBH ($p < 0.01$) (Table 1).

On the infested sites, the infestation vulnerability ranged from 21 % at UV2 (Appendix 1, 2) to 88 % at GS2 (Appendix 3, 4). The total number of living spruces on control sites increased along the infestation vulnerability, while the number decreased at infested sites. Pine abundance exhibited a slight decline in both site types along the infestation gradient (Figure 4). However, none of these trends could be significantly supported, as neither infestation vulnerability nor site type seemed to affect the number of abundant trees.

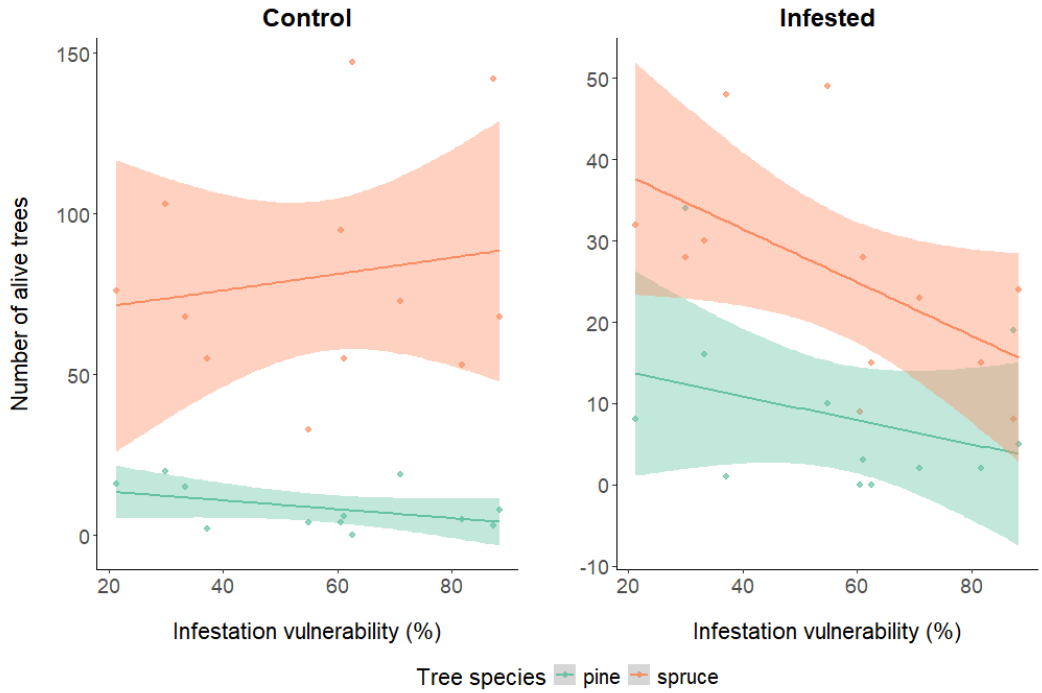

Figure 4: Total number of alive pine (green) and spruce (red) against the infestation vulnerability at control and infested sites.

3.2 Fungal Communities

Hypothesis 1

Of all 14,040,953 PacBio reads, 2,136,399 sequences passed quality control with a mean read length of 908. The average species richness per site was 102, ranging from 41 (ES.C) to 142 (KH1.C). No significant effect of site type (control versus infested) on species richness was detected ($p = 0.15$). Total read counts ranged from 5,748 (KH1) to 33,153 (TM.C), averaging 20,024 reads per site.

Duplicates, chimeras and plant species were removed, and the remaining sequences clustered in 617 Species Hypotheses (SHs). Of these, 164 were ECM fungi, 128 were saprotrophic fungi, and 20 had an unknown trophic status. The remaining 305 species, mainly Ascomycetes, were categorised as 'others'. Relative abundances of assigned fungal guilds varied between sites and site types. The following analyses are executed with the working species, representing species contributing to the top 80 % of all reads.

The relative abundance of ECM fungi was significantly lower at infested sites than at control sites ($p = 0.013$). Saprotrophic fungi showed a higher relative abundance at infested sites, though this difference was not statistically significant ($p = 0.29$). There is no significant difference between the relative abundance of

ECM and saprotrophic fungi at control sites, but on infested sites (Figure 5). The model showed a significant negative main effect of infestation on the relative ECM fungal abundance ($p = 0.03$). An additional, even stronger effect was observed in the interaction between site type and fungal guild ($p = 0.018$).

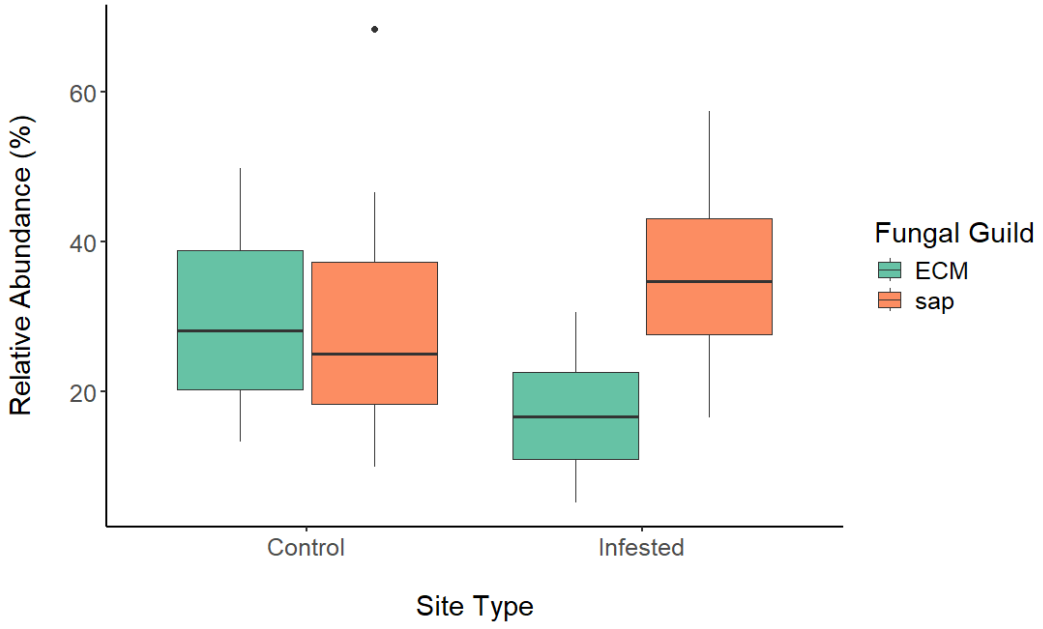

Figure 5: Relative abundance of ECM and saprotrophic fungi, comparing control and infested sites.

The 15 most abundant species comprised 32 % of the total reads, consisting of three ECM and nine saprotrophic fungal species and three species that were not Agaricomycetes. The most abundant species in the whole dataset are *Mycena* sp., *Luellia recondita, Piloderma byssinum, Piloderma bicolor,* and *Mycena galopus*. The abundances of species varied between the control and infested sites, whereas un-infested control sites had two ECM fungal species (*P. byssinum, P. bicolor*) in their top five most abundant species. In contrast, only *Mycena* spp. and *Luellia recondita* are present on the infested sites. On the infested sites, saprotrophic fungi dominate, while on control sites, ECM fungi also have high abundances. Comparing the most abundant ECM fungal species between sites, I could not see a difference in species but in the order of these species. Next to several *Piloderma* spp. and *Cenococcum geophilum* (coll.), I found *Cortinarius stilatitius, Tylosppora fibrilosa* and *Lactarius tabidus* at control sites *and Russula velenovsky, Lactarius camphoratus* and *Cortinarius evernius* at infested sites. Comparing saprotrophic species between sites, *Mycena* species (*M. galopus, M. rosella, M. sanguinolenta, M. vulgaris, M. metata*) and *L. recondita* dominated just in different orders.

Hypothesis 2

ECM fungi showed a clear decline in relative abundance as infestation vulnerability increased, while saprotrophic fungi exhibited the opposite pattern, increasing with greater vulnerability (Figure 6). Infestation had a significant negative main effect on ECM fungal abundance ($p = 0.014$), and an additional effect was observed in the interaction between site type and infestation vulnerability ($p = 0.019$). Infestation vulnerability alone did not significantly affect ECM abundance ($p = 0.36$). The observed increase in saprotrophic fungi relative abundance, while visually apparent, was not statistically significant.

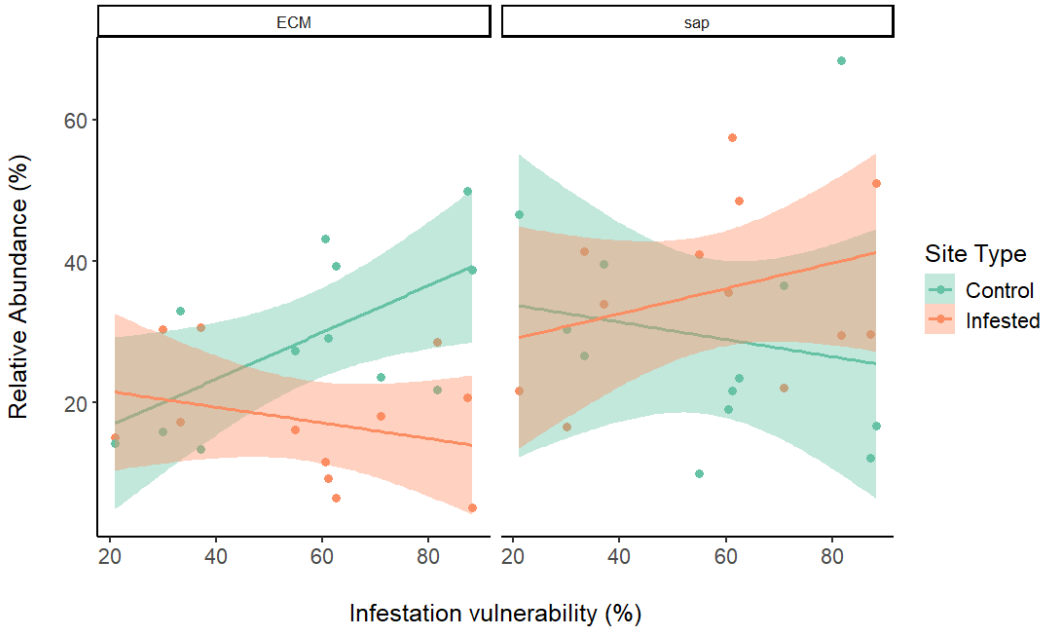

Figure 6: Relative abundance of fungal reads for ECM fungi and saprotrophic fungi along the infestation vulnerability, comparing control (green) and infested (red) sites.

Linear mixed-effects models indicated a positive relationship between ECM fungal abundance and infestation vulnerability at un-infested control sites ($p = 0.098$). The interaction between site type and infestation vulnerability was almost significant for the abundance of ECM fungi ($p = 0.055$). For saprotrophic fungi, the model showed a significant positive relationship between infestation vulnerability and site type ($p = 0.047$).

The community structure of fungi did not seem to change between the sites significantly (Figure 7, Appendix 5). While fungal communities at control sites appeared slightly more homogeneous than those at infested sites, site type did not significantly affect community composition ($R^2 = 0.05$, $p = 0.26$). In comparison, bark beetle infestation itself seemed to influence fungal communities ($R^2 = 0.068$, $Pr(>F) = 0.041$).

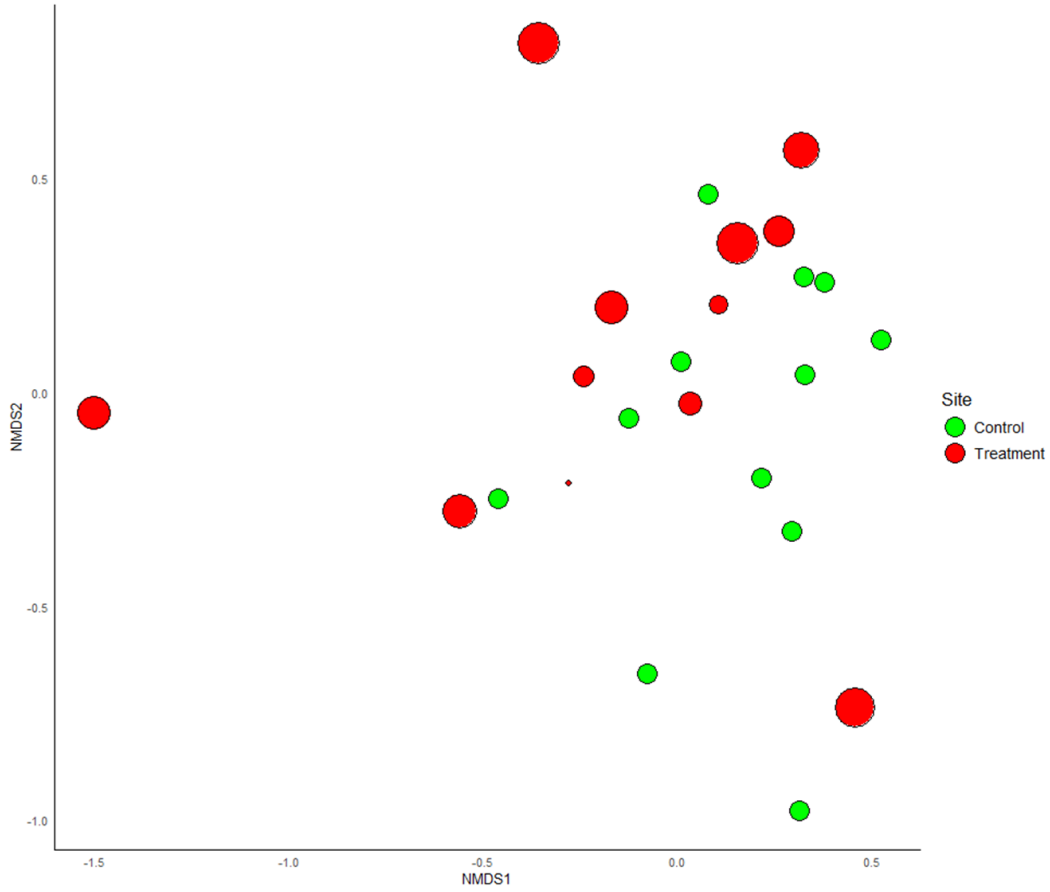

Figure 7: Nonmetric multidimensional scaling (NMDS) ordination plot based on the Bray-Curtis distance of samples for each sampling site. Comparison between control (green) and infested (red) sites, where increasing circle size represents the increasing level of infestation vulnerability.

3.3 Soil Properties

Given the changes in fungal communities at un-infested control sites in the opposite direction of the infested sites, I looked deeper into the relationship between soil properties and the infestation vulnerability.

Table 2: Averages and standard error of soil properties for all control and infested sites, including the p-value of a pairwise t-test between control and infested values.

	type	Control	Infested	p value
Soil moisture (%)	organic soil	56.2 ± 2.1	60.2 ± 2.7	0.28
	mineral soil	24.3 ± 3.8	31.1 ± 2.3	0.15
pH	organic soil	4.5 ± 0.1	4.8 ± 0.2	0.25
OM content (%)	organic soil	72.1 ± 4.6	69.5 ± 4.9	0.72
	mineral soil	14.0 ± 5.4	10.5 ± 1.5	0.55

Soil properties did not significantly differ between infested and control sites, but did between organic and mineral soil samples. Soil moisture and pH were slightly higher at infested sites, whereas the OM content was slightly higher at un-infested control sites (Table 1).

Both soil moisture and OM content exhibited similar trends across the infestation vulnerability, with an increase in organic soils and a decrease in mineral soils (Figure 8). However, I only present the trend of the OM content since it shows a significant trend in comparison to soil moisture ($p = 0.05$).

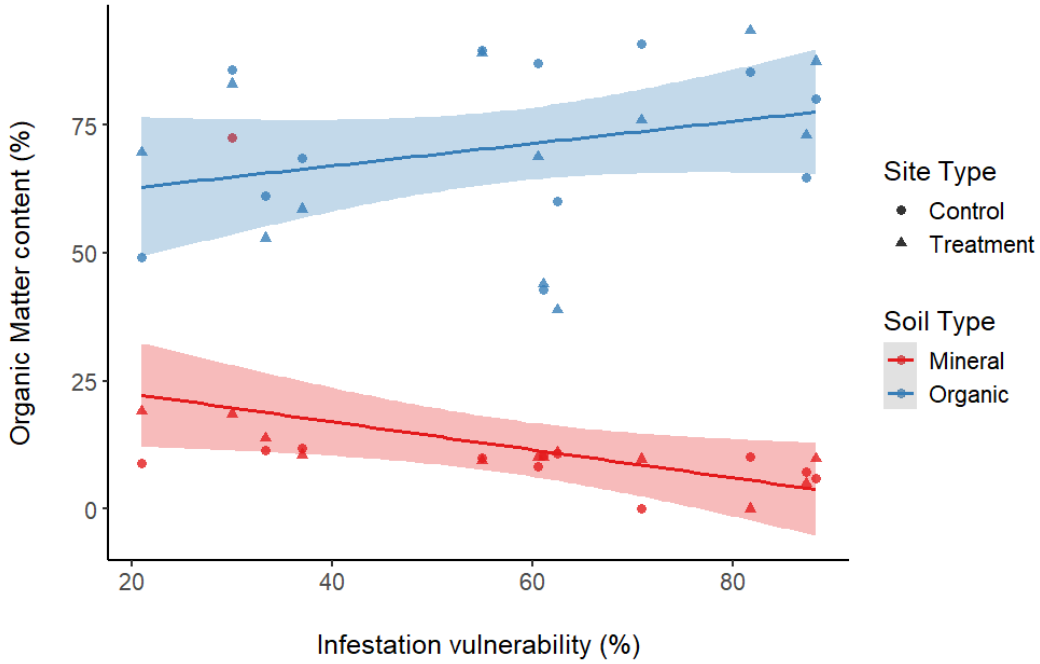

Figure 8: Organic matter contents of mineral (green) and organic (red) sites in % along the gradient of infestation level (%).

Soil pH showed a non-significant negative correlation to the infestation vulnerability at both sites (Figure 9).

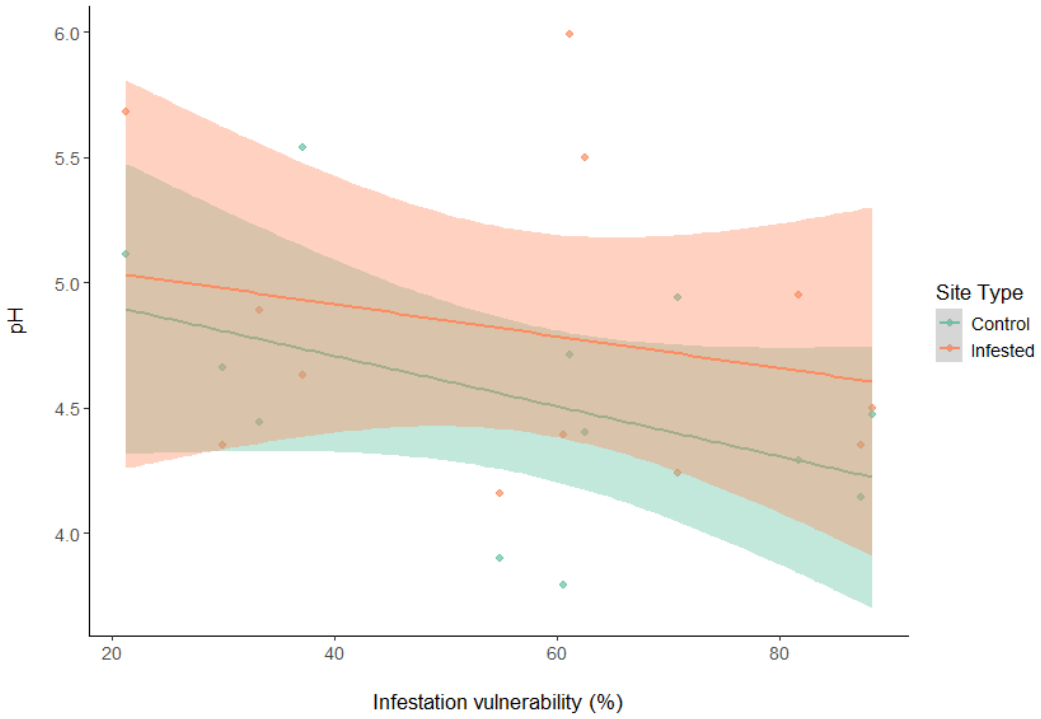

Figure 9: Soil pH values of control (green) and infested (red) sites along the gradient of infestation level (%).

ECM fungal relative abundance showed a negative correlation to increasing pH (Figure 10), significant at un-infested control sites ($p = 0.0047$). However, ECM abundance remained relatively stable at infested sites across the pH gradient, showing no clear response to pH changes. (Figure 10).

The created soil fertility index showed no difference between infested and control sites and the infestation vulnerability. There was no statistically significant effect of infestation vulnerability on site type detectable. Along with the infestation vulnerability, the soil fertility index increases slightly (Figure 11).

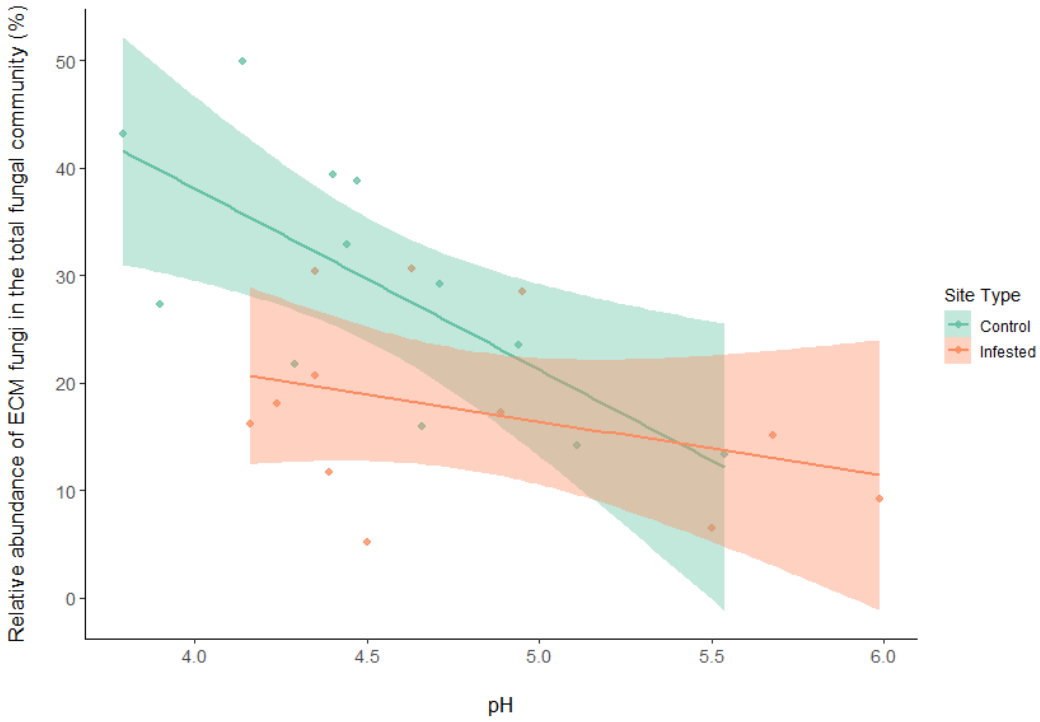

Figure 11: Relative abundance of ECM fungi of control (green) and infested (red) sites against soil pH.

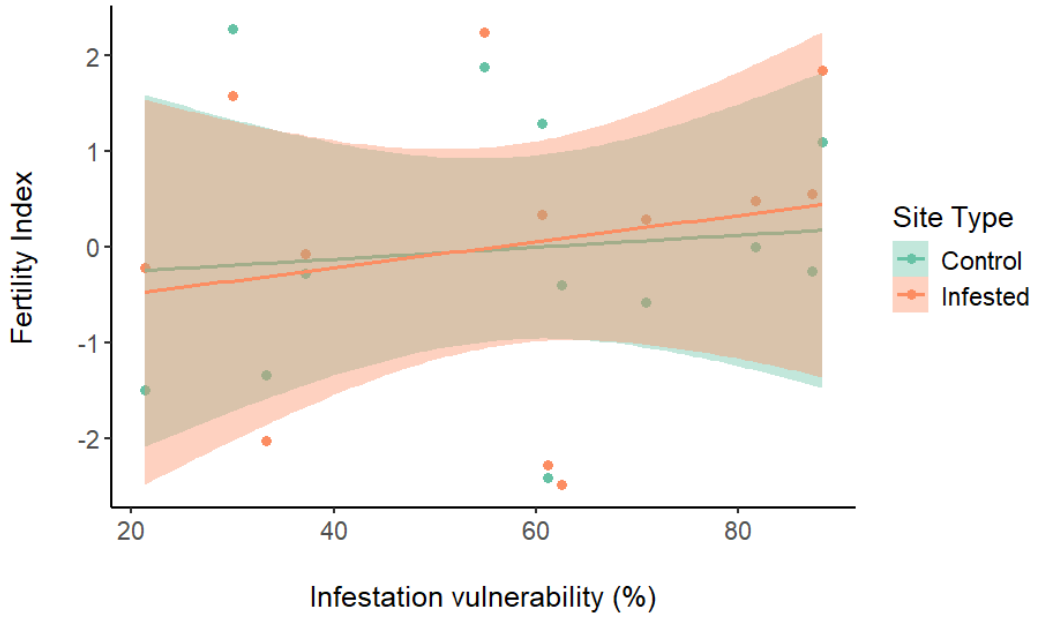

Figure 10: Soil fertility gradient created with PCA containing organic matter content, soil moisture and pH against the infestation vulnerability gradient comparing un-infested control sites (green) with infested sites (red).

4. Discussion

H1 – Infestation vs. no-infestation

The study revealed that the relative abundance of ECM fungi was significantly lower at infested sites compared to non-infested control sites, while saprotrophic fungi were more abundant, although not significantly so (Figure 5). These findings support the first hypothesis that bark beetle infestation leads to lower relative abundance of ECM fungal species, thereby facilitating the proliferation of saprotrophic fungi. This shift can be attributed to the reduced allocation of photosynthetic carbon to ECM fungi following beetle-induced tree mortality (Table 1), which diminishes the competitive advantage over saprotrophic fungi (Kohout et al. 2018; Choma et al. 2023).

In accordance with the 'Gadgil-effect', the proliferation of saprotrophic species is anticipated to result in enhanced decomposition rates (Gadgil & Gadgil 1971), potentially emitting significant amounts of CO_2 (Custer et al. 2020; Taylor & Bhatnagar 2024). This effect is evident in my data, where the OM content at infested sites is slightly lower compared to un-infested control sites (Table 2). Concurrently, bark beetle-induced tree mortality leads to premature litterfall and tree death, increasing the input of OM into the system, creating favourable conditions for saprotrophs, enhancing their diversity and activity (Lindahl et al. 2010; Cigan et al. 2015; Pérez-Izquierdo et al. 2021).

Soil moisture and pH levels were slightly elevated at infested sites (Table 2), likely due to diminished water uptake and reduced evapotranspiration, which is a result of tree loss. Previous studies have shown similar results, where infestation and tree removal positively impact these properties (Wardle et al. 2004; Uroz et al. 2016; Custer et al. 2020; Šamonil et al. 2020). Soil pH usually increases when trees are removed due to the cessation of organic acid exudates from tree roots, while their uptake of base cations stops, increasing the buffer capacity of the soil (Brand et al. 1986).

Given their close relationship to soil properties and soil fertility, fungal communities showed differences in relative abundance between control and infested sites (Guo et al. 2020). The most abundant ECM fungal species (*P. byssinum* and *P. bicolor)* were reduced by half in their relative abundance at infested sites compared to un-infested control sites. These two species are found in cold, N-poor, undisturbed forests (Larsen et al. 1997; Toljander et al. 2006; Larsson et al. 2024), explaining their decline in disturbed forests. They specialised in mining for recalcitrant organic N sources, with their abundance negatively correlated with N deposition (Lilleskov et al. 2024). Therefore considered nitrophobic (van der Linde et al. 2018), their decline in relative abundance at infested sites indicates an increase in mineralised N, contradicting the assumption of increased soil fertility.

However, these results are based on the relative abundance of sequencing reads. Future studies should integrate complementary methods alongside DNA-based analyses to achieve a more precise understanding of fungal community function and abundance. Although sequencing provides valuable taxonomic insights, incorporating a phospholipid fatty acid (PLFA) analysis can offer a more accurate estimation of fungal biomass than sequence reads alone, providing a quantitative perspective (Joergensen & Wichern 2008; Wallander et al. 2013). Enzyme assays could reveal actual fungal activity by measuring extracellular enzyme production, detecting shifts towards saprotrophic fungi at the metabolic level, and providing a functional perspective (Sinsabaugh et al. 1991; Burke et al. 2011; German et al. 2011; Kyaschenko et al. 2017a).

In summary, I can say that my first hypothesis is supported, and that the data is in alignment with previous studies, showing lower ECM fungal abundance and higher abundance of saprotrophic fungi after bark beetle infestation (Štursová et al. 2014; Veselá et al. 2019a).

H2 – Effect of infestation gradient

The intensity of the bark beetle infestation significantly affected soil fungal communities. The abundance of ECM was negatively correlated with infestation vulnerability at infested sites. At the lowest infestation vulnerability, ECM relative abundance was highest, decreasing along the gradient. Conversely, saprotrophic fungi exhibited a contrary trend along the infestation vulnerability (Figure 6). This finding supports the second hypothesis, stating that the effect of infestation intensifies with increasing infestation vulnerability, thereby reflecting the mutualistic relationship between mycorrhizal fungi and their plant hosts.

Similar trends could be seen at the species level. Heavily infested sites were dominated by saprotrophic species (*Mycena* spp.), while sites with low infestation vulnerability had ECM fungi (*P. bicolor, P. byssinum*) as the most abundant species. At sites with low infestation vulnerability, the species composition of infested and paired control sites was more similar than on sites with high infestation vulnerability. This change is possibly due to the same effect of tree removal like mentioned above, just along a gradient, but in alignment with previous studies (e.g. Toljander et al. 2006; Pec et al. 2017; Jörgensen et al. 2022).

ECM fungal taxa were still detected even at high infestation levels, where almost no spruces survived (Figure 6), possibly due to the presence of some trees or their roots acting as refugia (Modlinger et al. 2025). This distinguishes bark beetle disturbances from other disturbances, such as clear-cuts or fires, where all trees are rapidly removed, leading to more drastic reductions in ECM communities (Rodriguez-Ramos et al. 2021; Bell-Doyon et al. 2022). Unlike these disturbances, bark beetle infestations leave the aboveground forest structure, vegetation, and

organic layer mostly unaffected. This distinction could explain the relatively low significance of the decrease in ECM fungal abundance along the infestation vulnerability gradient, given the lower intensity of the disturbance (Rodriguez-Ramos et al. 2021). Additionally, the presence of surviving trees in the ecosystem after bark beetle attacks has positively affected ECM fungal abundance (Sterkenburg et al. 2019). Therefore, tree retention in managed forests is crucial for the fungal community and forest succession (Hopkins et al. 2018). Consequently, disturbances such as clear-cuts and fires potentially have longer-lasting negative effects on fungal communities than beetle infestations, having a more prolonged effect closer to natural forest succession (Tomao et al. 2020; Bell-Doyon et al. 2022). In these more severe disturbances, communities may require a longer time to re-establish due to the lack of remaining ECM fungi (Hartmann et al. 2012).

It is also important to consider that the sampled sites are located in nature reserves, which may significantly impact the results and their interpretation. Spruce monoculture production forests, in comparison, are more susceptible to bark beetle infestations given their low biodiversity (López-Andújar Fustel et al. 2024). Additionally, the fungal community in spruce production forests may be less diverse and, therefore, less prone to disturbances (Smith & Read 2008; Tomao et al. 2020; Anthony et al. 2022). The infested areas at the investigated sites were seldom bigger than the vegetation analysis grid of 30x30 m. This is in alignment with previous studies, which showed that production forests are more likely to be affected by infestations (Hlásny et al. 2021), while nature reserves buffer the intensity of outbreaks (Seidl et al. 2017). This underscores the importance of maintaining diverse forest stands to enhance the resilience of fungal and tree communities to various disturbances. To further support these results, future studies should consider how long a forest has been designated as a nature reserve, given that fungal diversity has been shown to increase with the age of the forest stand (Kyaschenko et al. 2017a). It should be noted that sites potentially differ in their soil properties and therefore fungal communities, which makes comparing communities challenging. These differences might be the result of previous land use (Uroz et al. 2016; Malik et al. 2018; Carneiro de Melo Moura et al. 2025). For instance, sites near disturbed areas may harbour early successional fungi, whereas more remote locations within protected forests will likely maintain stable, old-growth fungal communities (Sterkenburg et al. 2019).

Moreover, future studies could improve the parameter of infestation vulnerability by including the number of dead trees and whether they are still standing or have already fallen. This approach could provide insights into the duration of the infestation process, potentially leading to a stronger understanding of changes in the fungal community.

Notably, substantial alterations in fungal communities were also detected at un-infested control sites, indicating the presence of an underlying factor independent of infestation (Figure 6). This is opposite to the trend at infested sites and suggests an underlying driver shaping fungal communities, which is unrelated to the infestation. Although there were no differences in soil properties between infested and control sites, further investigation revealed correlations between vegetation composition and soil characteristics along the infestation vulnerability. This suggests that site conditions such as soil fertility, rather than infestation itself, are the primary drivers of these trends. This means that soil fertility is not low on sites with high infestation vulnerability; instead, trees are more susceptible to infestation at sites with low fertility, which decreases their resistance to bark beetles and results in higher infestation vulnerability.

High levels of infestation and tree loss were particularly associated with reduced tree density and basal area, as well as shifts in soil structure and chemistry. This aligns with studies that link bark beetle outbreaks to altered belowground ecological processes (Twieg et al. 2007; Sterkenburg et al. 2015; Choma et al. 2023).

Soil OM content and moisture exhibited stratification patterns (Figure 8) while pH decreased (Figure 9) consistent across both infested and un-infested control sites along the infestation vulnerability. This further supports the assumption that vegetation and soil type have a greater influence than infestation.

Soil pH, a key factor in determining fertility (Mitsuta et al. 2025), exhibited a non-significant negative trend with increasing infestation vulnerability, suggesting the possibility of ongoing podzolisation (Lundström et al. 2000). Previous studies report an increase in soil pH following tree mortality and cessation of root exudates (Custer et al. 2020). My data reflects this effect to some extent, documenting slightly higher pH values at infested sites than un-infested controls (Figure 9). However, the negative trend at both site types suggests other factors have a stronger effect on pH than infestation and tree removal. The relative abundance of ECM fungi at control sites was found to be highest at low pH (< 4) and to decline with increasing pH, thus suggesting a pH optimum for ECM dominance (Figure 10)(Sterkenburg et al. 2015). However, the optimum for fungi in general has been suggested to be at a pH of 5 (Sterkenburg et al. 2015), standing in contrast with my data. This optimum is meant for fungi in general, where in this case I focus on ECM fungi, which might have a different pH optimum, given their adaptation to the harsh conditions of boreal forest soils with their lower pH and nutrient scarcity (Tedersoo et al. 2014). The increasing differentiation and stratification of OM contents between the mineral and organic soil layer along the infestation vulnerability further indicate a trend towards podzolisation (Lundström et al. 2000). One possible reason for this could be the absence of bioturbation caused by soil fauna. This finding is consistent with those reported in environments with low pH and low nutrients (Haimi & Einbork 1992). Bioturbation may be more prevalent in areas with low vulnerability to infestation, where acidification is less advanced

(Gustafsson et al. 2001). This leads to the mixing of organic and mineral soil in these areas, which is evident in the lower level of stratification in OM content. Decreasing soil moisture in the mineral soil layer along the infestation vulnerability gradient could further indicate podzolisation, which has the potential to lead to drought stress for trees and to increase their susceptibility to bark beetle infestations (Marini et al. 2017; Singh et al. 2024).

Combining these results, sites with low infestation vulnerability seem to have higher soil fertility than those with high infestation vulnerability. As this trend is evident in both control and infested sites, these results imply that soil fertility is the primary factor influencing tree susceptibility to bark beetle infestation. If bark beetle infestation shapes the soil properties, this trend would only be seen at infested sites. Trees are weakened by factors such as water deficiency in areas with low fertility, increasing the risk of infestations (Seidl et al. 2017; Singh et al. 2024). Additionally, increasing pH seems to decrease the abundance of ECM fungi, further weakening the trees through the lack of nutrient supply (Smith & Read 2008; Anthony et al. 2022). With decreasing soil fertility, trees exhibit increased reliance on symbiotic mycorrhizal partners for nutrient acquisition under reduced soil fertility conditions (Abuzinadah & Read 1986; Averill et al. 2019). This heightened dependence is reflected in the data, picturing an increase in the relative abundance of ECM fungi along with the infestation vulnerability.

However, the soil fertility parameter showed no difference between site types and seemed to slightly increase with infestation vulnerability (Figure 11, Appendix 6). There was no significant correlation between site type, infestation vulnerability, and the soil fertility index. This highlights the importance of future studies to include more soil parameters in the soil fertility index to improve the understanding of the complex interactions between soil properties, fungal communities, and vegetation. Documenting soil horizons and measuring the thickness of organic and mineral layers could improve soil characterisation. This would aid in verifying observed stratification patterns and the proposed podzolisation process, particularly at sites with high vulnerability to infestation. As fungal communities are vertically structured (Lindahl et al. 2007; Clemmensen et al. 2013), variations in soil layer thickness could significantly impact both abundance and diversity.

This study highlights the significant impact of bark beetle infestation on soil fungal community composition, primarily through the decline of ECM fungi and the corresponding increase in saprotrophic species. Although infestation plays a significant role, the infestation vulnerability reveals that soil fertility parameters exert an even stronger influence on fungal dynamics; however, not combined in an index. All soil properties correlated with infestation vulnerability across both infested and un-infested control sites, while the relative abundance of ECM fungi positively correlated with gradients in pH. This correlation suggests a podzolisation

of the soil, which is linked to long-term ecological processes rather than short-term disturbances. These findings indicate that soil fertility influences not only fungal community composition but also mediates tree susceptibility to bark beetle attack. Understanding this interplay is crucial for predicting forest vulnerability and informing management practices that aim to maintain forest health and biodiversity.

5. Conclusion

This study is the first to examine the impact of spruce bark beetle (*Ips typographus)* infestations on soil fungal communities in Swedish boreal forests, with a particular focus on ECM and saprotrophic fungi. This study reveals that infestations significantly reduce the amount of ECM fungi in Swedish spruce forests, where the vulnerability to infestation increases this effect. Concurrently, saprotrophic fungi dominate, accelerating decomposition and CO_2 emissions and potentially converting forests into carbon sources. These shifts in the fungal community may have long-term negative impacts on forest health and succession.

However, it is important to note that bark beetle outbreaks are not the sole cause of these changes. Pre-existing site conditions, particularly the low fertility of podzolic soils, seemed to shape fungal communities and spruce vulnerability. Spruces in low-fertility soils experience greater physiological stress, making them more susceptible to beetle attacks. This highlights the fundamental role of soil fertility in ecosystem stability, with un-infested control sites emphasising the importance of soil properties in determining vulnerability to infestation.

The study, however, has limitations, including the lack of an in-depth analysis of soil fertility parameters and other fungal community properties, such as fungal biomass and enzymes. Further site parameters, such as land use history or the duration of infestation, could provide a more comprehensive interpretation of the results. Future research could incorporate these analyses to potentially strengthen the findings.

In conclusion, this study has provided valuable insights that contribute to advancing ecological theory and offer valuable information for forest management and climate change mitigation. Understanding how fungal communities respond to outbreaks of bark beetles is crucial for predicting the long-term resilience of boreal forests and for developing strategies to preserve their ecological and climatic functions in the face of changing environmental conditions.

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Popular science summary

As global climate change progresses and forest management intensifies, boreal forests are increasingly stressed, making them more susceptible to bark beetle infestations. In Sweden, outbreaks have become more frequent and severe, threatening forest ecosystems. These disturbances impact not only the trees but also the world beneath them, particularly the fungi living in the soil. While fungi are often recognised for their aboveground fruiting bodies, which many of us enjoy picking and eating, their crucial role in forest ecosystems is often overlooked. This study focuses on two key groups of soil fungi: ectomycorrhizal (ECM) fungi and saprotrophic fungi. ECM fungi form a mutually dependent symbiotic partnership with trees, providing essential nutrients that enable trees to grow in the nutrient-poor boreal forests. In return, these fungi receive sugars produced by the trees during photosynthesis. This partnership gives ECM fungi a competitive advantage over saprotrophic fungi, which decompose dead plant material for energy, allowing ECM fungi to dominate boreal forest soils.

In this study, I investigated how bark beetle outbreaks affect these soil fungi. By using DNA sequencing, I compared the relative abundance of ECM and saprotrophic fungi between infested and non-infested sites. Soil samples were collected from twelve spruce-dominated forests around Uppsala, Sweden. At each forest, samples were taken from sites with varying intensities of bark beetle infestations, measured as the ratio of infested to total spruces, and from nearby control sites showing no signs of infestation.

The results revealed a lower abundance of ECM fungi in areas infested by bark beetle infestations compared to un-infested areas, whereas saprotrophic fungi were more abundant. This shift became more pronounced with higher levels of tree infestation, likely because the beetles killed trees, disrupting the symbiotic relationship between trees and ECM fungi, making space for saprotrophs. Interestingly, the soil fungal communities in the un-infested control sites also changed along with the infestation levels of their paired forest sites, but in the opposite direction, suggesting that factors other than bark beetles influence soil fungi. To explore this further, I examined soil properties and found they were correlated with infestation levels, indicating lower soil fertility at sites with high bark beetle infestation. Assuming similar soil properties at paired sites, trees at sites with low soil fertility appear more stressed and thus more susceptible to bark beetle infestations. Additionally, ECM fungi were most abundant at these low-fertility sites without infestation, as trees rely more on their symbiotic partners when nutrients are scarce. This study highlights the complex interplay between aboveground disturbances and belowground ecosystems and the importance of soil fertility, stressing the importance of understanding these dynamics to better manage and protect our forests.

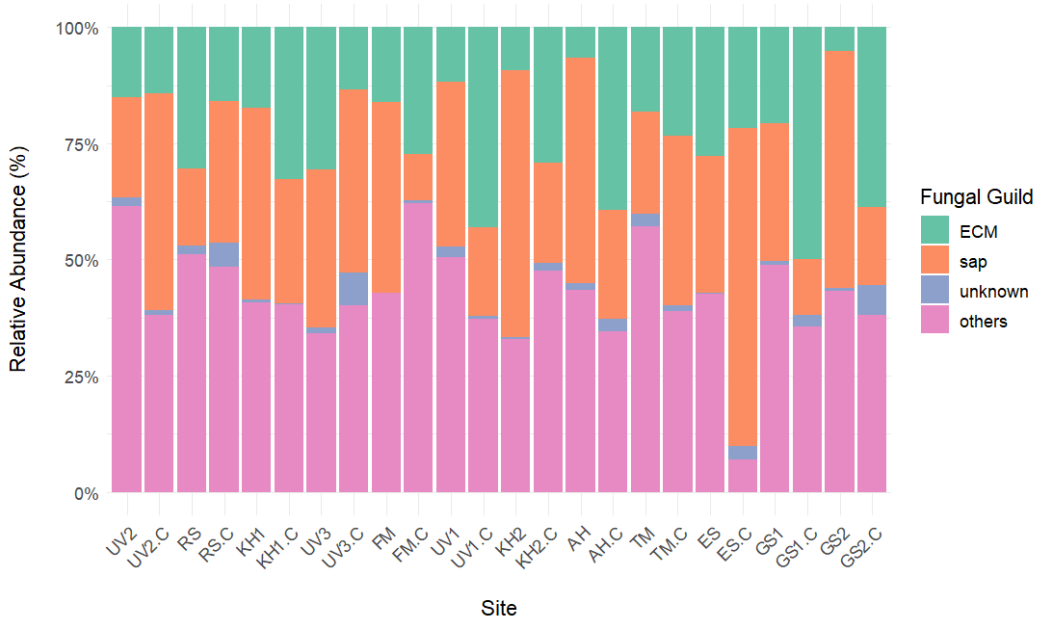
Appendix

Appendix 1: Picture of the site UV2, which showed the lowest level of infestation vulnerability.

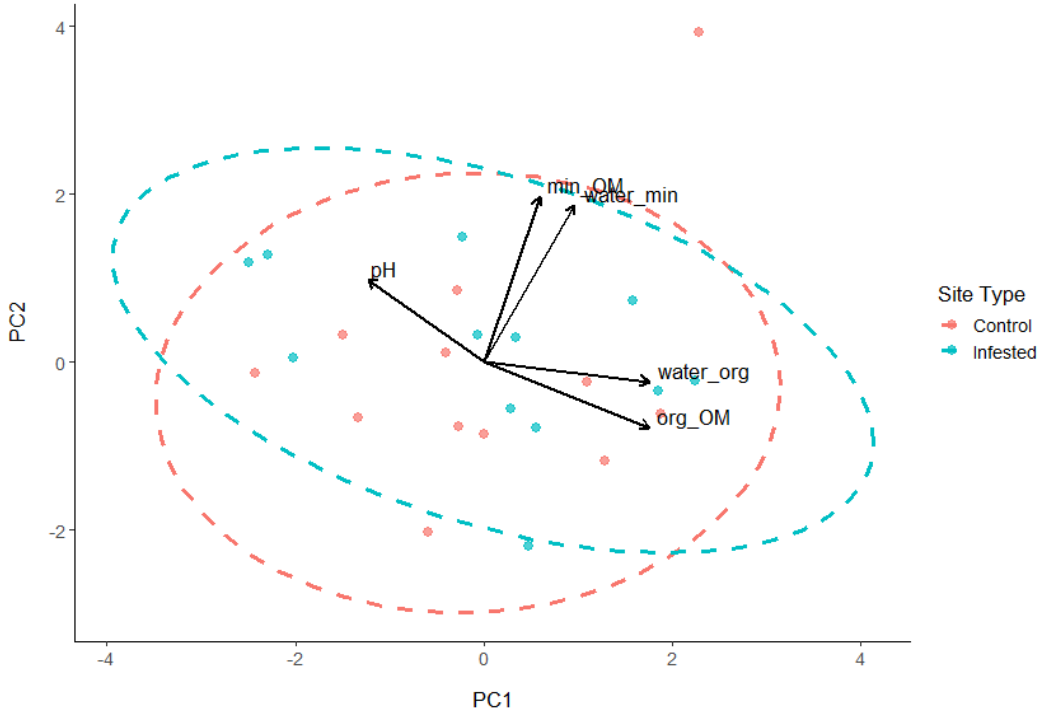
Appendix 2: Picture of the site UV2 C, which is the non- infested, paired control site to UV2.

Appendix 3: Picture of the site GS2, which showed the highest level of infestation vulnerability.

Appendix 4: Picture of the site GS2 C, which is the non- infested, paired control site to GS2.



Appendix 5: Relative abundance of the determined functional guilds - ECM (green), saprotrophs (orange), unknown Agaricomycetes (blue), and other fungi (pink) - for each sampled site.



Appendix 6: PCA of soil fertility properties, including soil moisture, organic matter content and pH comparing both site types. The first dimension explains 43 % and the second dimension explains 31.1 % of the variation in the data.

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