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Integrating mechanistic disturbance models and stand dynamics of Norway spruce

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Academic dissertation

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ABSTRACT

Disturbances, caused by abiotic and biotic agents, are discrete events in time disrupting the ecosystem and resulting in the reduction of plant biomass. They play a key role in forest ecosystems, but in the managed forests pose a risk to forest productivity. The projected climate change is expected to increase the risk of various disturbances in the boreal forests. In Europe, the major risks threatening the Norway spruce (*Picea abies*) dominated stands are caused by *Heterobasidion* root rot, wind storms, and European spruce bark beetle (*Ips typographus*). *Heterobasidion* root rot causes growth losses, mortality and decreases the timber quality. It also decreases the mechanical stability of the tree against wind load and increases the stand vulnerability for wind damages. Bark beetles benefit from the low resistance breeding material, i.e., wind damaged trees, when the population is low and can emerge as outbreaks in the right conditions. This thesis presents a simulation framework WINDROT to simulate the interactive dynamics of these disturbance agents. WINDROT consists of four simulation models, each responsible for either the dynamics of the host or one of the disturbance agents. A stand level decision support system, MOTTI, simulates the growth and dynamics of tree stands as affected by forest management, and provides inputs for mechanistic models Hmodel, HWIND and BBDYN simulating the dynamics and effects of disturbance agents. The model performance analyses in tree and stand scale showed that; i) the *Heterobasidion* dynamics are driven by primary and secondary infections on large stumps; ii) increasing intensity of *Heterobasidion* root rot damages increases the risk for wind damages; and iii) the increasing wind damages increased the subsequent bark beetle damages. The simulation framework can be used to analyze the sensitivity of different forest management regimes to the risks posed by these damages alone and in various combinations.

Keywords: disturbance, root rot, bark beetle, wind, mechanistic modelling, *Picea abies*

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“Ja tosta se alkaa!” – Jussi Koskela

With these words in mind, I started my journey in the world of science several years ago. Little did I know what it had in store for me. During these years I have come to realize the true meaning of collaboration in science. It is not a journey to walk alone.

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I am more than grateful to all of my co-authors in the substudies of this thesis. I’ve enjoyed long talks on *Heterobasidion* life with Tuula Piri, sharing ideas on root systems and their physiology with Tuomo Kalliokoski, discussions on the development of young stands with Jouni Siipilehto as well as reasoning the disturbance interactions with Heli Peltola. Juha Heikkinen provided me essential insights to statistical aspects of this work, while Mika Lehtonen, Hannu Salminen, and Hannu Väisänen, all helped me with programming of the models.

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Urjala, May 2017

Juha Honkaniemi

LIST OF ORIGINAL ARTICLES

This thesis includes the introductory review and the following four research articles. These articles are referred throughout the text with Roman numerals **I-V**. Articles **I**, **II** and **III** are reprinted with the kind permission of the publishers, while article **IV** is a manuscript.

I **Honkaniemi**, J., Ojansuu, R., Piri, T., Kasanen, R., Lehtonen, M., Salminen, H., Kalliokoski, T. and Mäkinen, H. (2014). Hmodel, a Heterobasidion annosum model for even-aged Norway spruce stands. Canadian Journal of Forest Research 44(7): 796–809. https://doi.org/10.1139/cjfr-2014-0011

II **Honkaniemi**, J., Piri, T., Lehtonen, M., Siipilehto, J., Heikkinen, J. and Ojansuu, R. (2017a). Modelling the mechanisms behind the key epidemiological processes of the conifer pathogen *Heterobasidion annosum*. Fungal Ecology 25: 29–40. https://doi.org/10.1016/j.funeco.2016.10.007

III **Honkaniemi**, J., Lehtonen, M., Väisänen, H., and Peltola, H. (2017b). Effects of wood decay by *Heterobasidion annosum* on vulnerability of Norway spruce stands to wind damage: a mechanistic modelling approach. Canadian Journal of Forest Research 47(6): 77-87. https://doi.org/10.1139/cjfr-2016-0505

IV **Honkaniemi**, J., Ojansuu, R., Kasanen, R., and Heliövaara, K. (2017c). Integrating mechanistic model for bark beetle dynamics to simulation framework WINDROT to simulate the interactions between root rot, wind damages and bark beetles. Manuscript.

Author’s contribution

The author is solely responsible for the compilation of this thesis. In all of the articles the author was responsible for drafting the article as well as designing the model structures jointly with the co-authors. Programming of Hmodel, WINDROT and BBDYN was mainly carried out by the author.

The connection between MOTTI and other models in articles **I**, **II**, **III** and **IV** was designed and carried out jointly by the author, Mika Lehtonen, Hannu Salminen and Risto Ojansuu. HWIND used in articles **III** and **IV** was tailored for the use here by Hannu Väisänen.

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ABBREVIATIONS AND DEFINITIONS

Abbreviations:

t_W	User specified time for the stand to be exposed to wind effects

Definitions:

model	Mathematical description of an entity described with the hypothesized relationship between variables
simulation	The process of running a model.
simulation model	Computer program including the model algorithms and equations.
simulation framework	Framework including various simulation models.
mechanistic model	Model consisting of the hypothetical relationships between the variables describing the relationship mechanistically with underlying biological processes in different scales.
submodel	Part of a larger mechanistic model (i.e. algorithm or equation) describing an underlying biological process or processes.
statistical model	Model consisting of the hypothetical relationships between variables aiming to describe the data in the best possible way.

INTRODUCTION

Natural disturbances and forest management

Natural disturbances are a key part of forest ecosystems and driving force of regeneration in natural forests (Pickett and White, 1985; Kuuluvainen and Aakala, 2011). Disturbances are discrete events in time disrupting the ecosystem structure, community or processes and thus leading to destruction plant biomass (Pickett and White, 1985; Grime, 2001; White and Jentsch, 2001). The disturbances are caused by abiotic and biotic agents, such as windstorms, pathogens and insects, and the sum of all the different disturbances affecting an ecosystem are its disturbance regime (White and Jentsch, 2001). The disturbance events occur in the ecosystem at certain probabilities posing risks (Kaplan and Garrick, 1981). In managed forests, the different abiotic and biotic disturbance agents cause significant damage and economic losses posing risks to forest management (Woodward et al., 1998; Schelhaas et al., 2003; Grégoire et al., 2015). In Finland, according to the latest 11th National Forest Inventory (2009-2013) (Nevalainen et al., 2015), disturbances were estimated to occur in 51% of the area available for forest management (94 000 km^2), but disturbances decreasing the quality of the stand only in 24.5% (45 000 km^2) of the area. A total of 33% of the disturbances were abiotic and 30% biotic, but up to 30% of the causes of the disturbances are recorded as unknown and thus there is a rather large degree of uncertainty in the observations.

In many regions climate change is altering the disturbance regimes and the risk of disturbances for forest management is increasing in many regions under the projected climate (Dale et al., 2001; Thom and Seidl, 2016). The increasing damages may have a large effect on the management strategies (Seidl et al., 2014b). In addition, the damages caused by various disturbance agents affect the carbon storage of the forests (Seidl et al., 2014b; Healey et al., 2016). A good example of this are the recent large-scale disturbances by bark beetles in the western coast of North America (Safranyik and Wilson, 2006), where the forests have turned from carbon sinks taking in carbon as they grow to carbon sources due to large scale mortality (Kurz et al., 2008; Dymond et al., 2010). Recent study also suggests possible underestimation of the effects of root diseases on the forest carbon balance, which may be greater than insect damages and equal to the effect of wildfires on carbon balance in North America (Healey et al., 2016). Therefore, it is crucial to consider the integration of comprehensive risk management plans to forest management in the future to decrease the negative effects of climate change on forests (Lindner et al., 2010, 2014; Hanewinkel et al., 2011; Kolström et al., 2011; Seidl et al., 2011b; Subramanian et al., 2015; Thom and Seidl, 2016).

Disturbance dynamics in managed even-aged Norway spruce stands

Norway spruce and the key disturbances

Norway spruce (*Picea abies* L. (Karst.)) is one of the most important coniferous tree species in Eurasia, it is an important species in the boreal and subalpine conifer forests and it is also widely planted beyond its natural range (Caudullo et al., 2016). In Finland, Norway spruce covers approximately 30% of the growing stock volume of forest land and is the second-most common tree species after Scots pine (*Pinus sylvestris* L.) (Kaila and

Ihalainen, 2014). Norway spruce is an adaptable tree species often growing best on moist and fertile sites as it prefers humus-rich soil to support its shallow root system (Puhe, 2003). However, the shallow root system also makes it vulnerable to various abiotic and biotic disturbances.

Wind and snow are the most important abiotic disturbance agents of Norway spruce in Finland causing uprooting and breakage of the trees, such damage are found in approximately 8% of the Norway spruce dominated forest management stands (Nevalainen et al., 2015). Since 2000, strong winds in different storm events have caused losses of over 24 million m^3 of timber in total (Gregow, 2013; Zubizarreta-Gerendiain et al., 2016). Root and stem rot causing pathogens (e.g. *Heterobasidion* sp, *Armillaria* sp.) and bark beetles (e.g. *Ips typographus* L, *Pityogenes chalcographus* L.) are the most important biotic disturbance agents of Norway spruce in Finland (Nevalainen et al., 2015). The Norway spruce dominated stands in southern Finland are especially high-risk areas for root and stem rot damage (Mattila and Nuutinen, 2007). Herbivory and browsing by voles may cause significant local damages in young stands from time to time (Huitu et al., 2009). The seed production of Norway spruce is weather dependent (Sarvas, 1962; Zamorano et al., 2016) and often affected by pests and pathogens (Tillman-Sutela et al., 2004).

The damage risks due to root rot, wind and bark beetles are all expected to increase with the predicted changing climate in the northern Europe. The vulnerability of the forests to root rot is increasing in warmer climate due to longer growing season and increasing metabolic rate of the fungi leading to increased sporulation and mycelial growth (e.g. Gonthier et al., 2005; La Porta et al., 2008; Müller et al., 2014). The effect of strong winds on forests is expected to increase due to the shorter frozen soil period that currently improve tree anchorage during the winter months (Blennow et al., 2010; Kellomäki et al., 2010; Gregow et al., 2011). Bark beetles are expected to benefit from the warmer temperatures by increased reproduction and having more generations with full life cycles (Bale et al., 2002). In addition, Norway spruce is expected to suffer under the projected climate in southern Finland and may be able to survive only on the most fertile sites due to the increasing occurrence of drought events (Kellomäki et al., 2008). This may increase the vulnerability of Norway spruce to other disturbances. However, forest management regimes and especially the selection of tree species during regeneration and the tending of the young stand can offer tools to adapt to the changing climate and therefore it is of great importance to be able to react to future risks early (Kolström et al., 2011).

Heterobasidion root rot

The *Heterobasidion annosum* species complex (= *Heterobasidion annosum* s.l., from here on *Heterobasidion*) is one of the most destructive groups of fungal conifer pathogens causing great economic losses throughout the Northern Hemisphere (Woodward et al., 1998). The species complex consists of five necrotrophic pathogens considered to cause some of the most destructive diseases of conifers: three native species in Eurasia and two in North America (Korhonen et al., 1998; Otrosina and Garbelotto, 2010). In addition, *Heterobasidion irregulare*, another North American species, is an invasive alien species in Europe posing a serious threat to forestry (Gonthier et al., 2007, 2014).

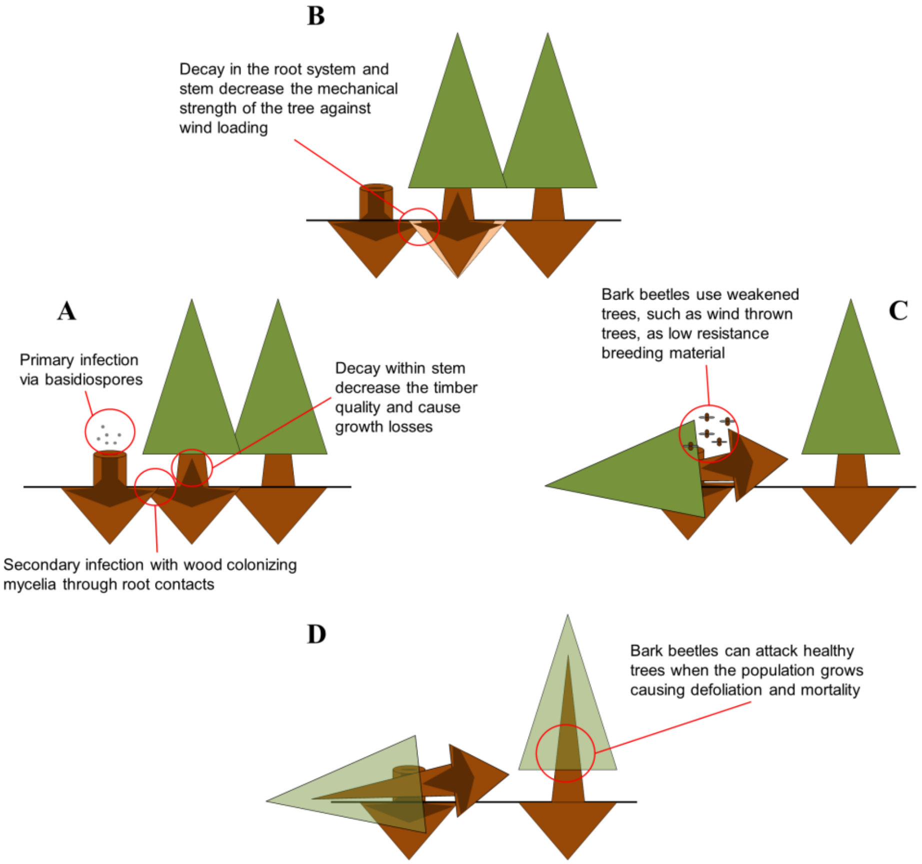

Figure 1. Interactive disturbance dynamics on Norway spruce including; (A) the primary and secondary spread of *Heterobasidion* root rot, (B) the decreasing effect of wood decay on tree mechanical strength, (C) wind disturbance and the low resistance breeding material for bark beetles, and (D) defoliation and mortality due to bark beetles.

Two species of the *Heterobasidion* complex currently exist in Finland (Korhonen, 1978; Korhonen et al., 1998). *Heterobasidion annosum* (Fr.) Bref. s.s. is able to infect a wide range of tree species including Norway spruce, Scots pine and several deciduous species, while *Heterobasidion parviporum* Niemelä & Korhonen is specialised for Norway spruce. In Southern Finland, approximately 90% of the *Heterobasidion* infections in Norway spruce are caused by *H. parviporum* (Korhonen and Piri, 1994).

Heterobasidion has two primary mechanisms of spreading; primary, long-distance dispersal via basidiospores on fresh wood tissue (Rishbeth, 1951) and secondary, short-distance dispersal via mycelia through root contacts and root connections (Garbelotto and Gonthier, 2013). Basidiospores are produced in basidiocarps, usually found in the roots of wind thrown trees or in decayed stumps. In natural conditions, fresh wood tissue is rarely available and therefore *Heterobasidion* is quite uncommon in natural forests. However, intensive forest management has created an optimal niche for *Heterobasidion* primary spread via fresh stump surfaces during loggings. In addition, logging wounds enhance the spreading possibilities although their significance is smaller (Isomäki and Kallio, 1974).

The spore deposition has high spatio-temporal variation (Möykkynen and Kontiokari, 2001; Gonthier et al., 2005). Summertime loggings in Fennoscandia create fresh stumps susceptible to spore infection as the basidiospores are produced mainly during the summer months (Kallio, 1970; Brandtberg et al., 1996). Recent studies have shown that annual temperature sum cannot explain the spatial variation in the spore deposition (Kasanen et al., 2011; Witzell et al., 2011). The spatial variation most likely derives from the amount of basidiocarps in the vicinity of stands (Garbelotto and Gonthier, 2013) as the majority of the basidiospores are distributed only within a few hundred metres from the basidiocarp (Kallio, 1970; Möykkynen et al., 1997).

Once the fungus has infected the stumps, it will start to spread towards the root system as wood-colonising mycelia. The fungus can spread from the infected stumps to adjacent stumps and living trees through root contact or root grafts (Garbelotto et al., 1997; Garbelotto and Gonthier, 2013). Once established in a stand, the fungus is capable of surviving for several tree generations as it is able to spread to the subsequent tree generation; young Norway spruce understorey and planted seedlings (Piri, 2003a; Piri and Korhonen, 2007; Piri and Valkonen, 2013).

After the fungus has infected a living tree it spreads from roots to stem bases entering the stems at the border of heartwood and sapwood. In Scots pine the heartwood is rather decay resistant limiting the fungus to the sapwood leading to growth losses and eventually tree death as the water transportation of the tree decreases (Stenlid and Redfern, 1998). However, in Norway spruce *Heterobasidion* mainly decays the dead heartwood continuously challenging the nutritious sapwood (Stenlid and Redfern, 1998). Trees need to allocate resources to resist these pathogen attacks by forming a reaction zone (Shain, 1971, 1979), which decreases the sapwood area and leads to growth losses (Bendz-Hellgren and Stenlid, 1995, 1997; Oliva et al., 2010, 2012) and in some cases to mortality (Swedjemark and Stenlid, 1993). *Heterobasidion* is a rather slow decomposer and may decay the heartwood of Norway spruce for years without any symptoms of decay. The economic losses on Norway spruce take place when the tree is cut down and the valuable timber is lost to low quality pulpwood or bioenergy (Mäkelä et al., 1998).

Heterobasidion infections can be controlled in various ways. The main control methods are: change of tree species, chemical or biological stump treatment to prevent new spore infections and the timing of forest management operations (Piri, 2003b). In addition, mixed species stands have been reported to have less decay than pure stands of Norway spruce (Piri et al., 1990; Lindén and Vollbrecht, 2002). Delayed thinnings and reducing the number of thinnings have also been suggested to improve the economic outcome of forest management in infected stands (Möykkynen and Pukkala, 2010) as the intensity of the damages increases even after winter time thinnings without new spore infections (Piri and Korhonen, 2008). The growth rate of the fungus in stump roots is 3 times the growth rate in the roots of a living tree (Bendz-Hellgren et al., 1999) and therefore each stump and dead tree supports the spread of *Heterobasidion*.

Wind storms

Wind is the most significant disturbance in Europe (Schelhaas et al., 2003) causing mechanical loading on the canopy and stem leading to tree failure if the mechanical resistive strength of the tree is overcome. In the managed forests wind storms cause severe losses as wind damage events may reschedule logging operations and thus cause great economic losses. Wind damaged trees may also cause subsequent damages as bark beetles and other insects use them as breeding material (e.g. Komonen et al., 2011). Trees recently exposed to wind (in thinned stands or stands adjacent to clear-cut stands) which are not yet adapted to the new wind conditions are especially susceptible to wind damages (Laiho, 1987; Zubizarreta-Gerendiain et al., 2012; Suvanto et al., 2016) as well as are stands infected with root diseases, such as *Heterobasidion* root rot (Whitney et al., 2002; Oliva et al., 2008).

Trees bend under the wind load due to the horizontal forces created by the wind and the vertical forces created by gravity, their sum being the overall bending moment of the tree (Peltola, 2006). Tree resists uprooting against the bending moment with the supportive moment from the anchoring root system, which is most often described as a function of the root–soil plate dimensions (i.e., root radius, mass, rooting depth) (Peltola, 2006). Similarly, tree resists stem breakage with the stem resistance moment, which is a function of the modulus of rupture (Jones, 1983; Morgan and Cannell, 1994) and tree diameter at breast height. Further, tree fails under static wind load if the maximum resistive moment of the tree is overcome by the bending moment of the tree (Peltola, 2006). These forces and eventually the wind disturbance dynamics are affected by local wind climate (wind speed, occurrence etc.) and by tree and stand characteristics, such as tree species, height and diameter, canopy length and area, biomass, rooting depth, root radius, soil type or stand density (Peltola et al., 1999; Ancelin et al., 2004; Suvanto et al., 2016).

Wind disturbances are a major part of the disturbance dynamics interacting with several other disturbance agents such as snow, pathogens and insects (Peltola et al., 1999; Bouget and Duelli, 2004; Giordano et al., 2012). Root rot, caused by fungal pathogens such as *Heterobasidion* sp. and *Armillaria* sp., decreases the mechanical strength of wood in the roots and stem and hence affects the resistive moments of the root soil plate and stem making the trees more vulnerable to uprooting and stem breakage (Bazzigher and Schmid, 1969; Gordon, 1973; Whitney et al., 2002; Oliva et al., 2008). Decay in the root system and especially in the large, anchoring roots decreases the mechanical strength of the root system decreasing the effective size of the root-soil plate (Fraser, 1962; Bergeron et al., 2009; Giordano et al., 2012). In the stem, the decay creates a hollow structure that affects the resistive moment of the stem (Ossenbruggen et al., 1986; Smiley and Fraedrich, 1992).

Wind damages can be controlled by forest management (e.g. timing and intensity of thinnings) as the tree resistive moments and the overall stand vulnerability are determined by many factors affected by forest management. Integration of wind disturbance models in forest planning could significantly reduce the risk of wind damages at the landscape level (Heinonen et al., 2009, 2011).

Bark beetles

The European spruce bark beetle (*Ips typographus*) is one of the most destructive pests of Norway spruce and it has caused severe and extensive economic and ecological losses especially in Central Europe after the 1990s (Nageleisen, 2001; Schelhaas et al., 2003;

Gilbert et al., 2005). It belongs to the family of Coleoptera:Curculionidae as the subfamily Scolytinae with several other bark beetle species of which *Ips typographus* is the most destructive in Europe. The distribution currently covers almost the entire boreal and temperate regions of Eurasia, where spruce are grown.

Bark beetles bore under the Norway spruce bark to reproduce and prefer living trees as a food source for the larvae, although e.g. wind damaged trees are attacked over a year after the storm event (e.g. Eriksson et al., 2005; Louis et al., 2016a, 2014). The flight activity and development of the overwintered beetles starts in the spring as the air temperature rises above 20 °C (Annila, 1969). After the beetles have developed to adults, they fly and attack trees in order to reproduce. Bark beetles can travel long distances and in pheromone-free environments only 1% remains within one hectare from the mother tree (Franklin and Grégoire, 1999).

Bark beetle males pioneer the attacks on the trees and the very first beetles start to produce aggregating pheromones to attract other beetles to attack the same tree and to overcome the tree’s resistance (Bakke et al., 1977; Wood, 1982). Trees fight against the attacking bark beetles with resin production (Paine et al., 1997) and changing the quality of the food for bark beetles around the entrance holes (Rohde et al., 1996). However, the trees can allocate resources only to some extent. This limit of tolerance for bark beetles is considered as the resistance threshold, which is linked to the annual growth and the sapwood area (Raffa and Berryman, 1983; Mulock and Christiansen, 1986). Bark beetles start the production of anti-aggregation pheromones after the resistance is overcome to avoid overpopulation in one tree (Bakke et al., 1977).

Successfully attacked trees are used for reproduction. On average each attacked male breeds with two females laying 60–80 eggs along the maternal gallery (Annila, 1971). The reproduction rate is related to the female density in a tree and the overall number of offspring to the optimal bark area for reproduction in each tree (Anderbrant et al., 1985; Anderbrandt, 1990; Weslien and Regnander, 1990). *Ips typographus* can reproduce under bark with a minimum thickness of 2.5 mm, whereas there seems not to be any maximum bark thickness (Grünwald, 1986). Intraspecific competition of the bark area leads to decreased reproduction rate (Anderbrant et al., 1985). Interspecific competition between different bark beetle species is segregated by different preferences for bark thickness for reproduction (Grünwald, 1986). In Fennoscandia, *Ips typographus* usually only produces one generation although there have been observations of two generations (Annila, 1969; Pouttu and Annila, 2010). Some beetles may re-emerge after attack to reproduce a sister brood (Anderbrant, 1986). After the reproduction, infested trees die due to a blue-stain fungi infection carried by the bark beetles (Horntvedt et al., 1983).

The bark beetles benefit from weakened trees and especially from storm events creating suitable forest edge habitat (Peltonen, 1999; Hedgren et al., 2003; Kautz et al., 2013) as well as low resistant breeding material (Louis et al., 2014, 2016a). Wind damaged trees may help the bark beetle population grow to level where healthy trees are colonized (e.g. Bouget and Duelli, 2004; Komonen et al., 2011).

The bark beetle damages are controlled to minimize the attacks on living trees. The most used control methods are the removal of wind damaged trees, sanitation fellings of infested stands, mass trappings and the debarking of timber (Wermelinger, 2004). Small amounts of wind damaged trees (< 5–20 trees ha^{-1}) can be left in the forest for biodiversity, but larger amounts need to be removed to reduce the subsequent bark beetle risk (Hedgren et al., 2003; Eriksson et al., 2007). The timing of salvage loggings and sanitation fellings is very crucial as trees which are used for reproduction during the logging are the only ones affecting the bark beetle population levels (Stadelmann et al., 2013).

Modelling the disturbance dynamics

Models are simplifications of the real world and can help us to understand the underlying mechanisms of different processes. Disturbances are modelled to analyze their effect on the ecosystem and to understand the processes affecting them. Mathematical models describing disturbances can be roughly divided into two categories; statistical and mechanistic models. Statistical models rely on data and the variables have a hypothesized relationship to best describe the data (i.e. correlation between the model explanatory variables and the dependent variable). In contrast, mechanistic models describe the hypothesized relationship between the variables by describing the underlying biological processes in different scales. Mechanistic models may include statistical models as submodels describing the correlation between input and output variables indirectly.

After the seminal work on disturbance modelling by Pickett and White (1985), the interest in disturbance modelling and research providing data for modelling approaches has accumulated significantly (Seidl et al., 2011a). Statistical models are the most frequently developed models in disturbance modelling, but the development of mechanistic models describing the underlying mechanisms are needed to simulate the complex interactions of disturbance regimes and the effects of changing climate on them (Seidl et al., 2011a; Dietze and Matthes, 2014). The challenges of disturbance modelling include i.a., complex interaction between different agents, a lack of data to describe the key processes and the scalability of disturbances (Seidl et al., 2011a).

Several statistical models to predict the spread and distribution of *Heterobasidion* root rot as well as the incidence and economic losses due to decay have been developed over the years since the 1950s (e.g. Arvidson, 1954; Greig and Low, 1975; Stenlid, 1987; Tamminen, 1985; Vollbrecht and Agestam, 1995; Vollbrecht and Jørgensen, 1995; Woodward et al., 2002). The most advanced mechanistic models include Western Root Disease model (WRDM) (Frankel, 1998) incorporated into the Forest Vegetation Simulator (FVS) (Teck et al., 1996) and Rotstand consisting of three different modules: stand dynamics, fungal dynamics and their interactions (Möykkynen et al., 1998; Pukkala et al., 2005). WRDM is the only root rot model including other disturbance agents, but it does not either describe the interactive dynamics.

The threshold of wind speeds required for tree failure, either uprooting or breakage, have been mechanistically modelled in several simulation models to be able to analyse the amount and probability of wind damages in alternative management regimes based on local wind data (Peltola et al., 1999, 2010; Gardiner et al., 2000, 2008; Ancelin et al., 2004; Byrne and Mitchell, 2013; Seidl et al., 2014a; Dupont et al., 2015). Some of the models include interaction with e.g. snow damages (Peltola et al., 1999), but none of the modelling approaches are widely linked with the interactive effects between winds and wood decay decreasing tree anchorage and stem strength. A few models however take into account the decay cavities for stem breakage (Ossenbruggen et al., 1986; Smiley and Fraedrich, 1992). Tree pulling experiments have been the basis of modelling static wind loading and not many experiments have focussed on comparing healthy and decayed trees although some experiments have included decayed trees as well (Nicoll et al., 2006; Lundström et al., 2007; Bergeron et al., 2009; Giordano et al., 2012).

The broad knowledge on the bark beetle ecology and the driving factors of beetle outbreaks (e.g. Seidl et al., 2016; Wermelinger, 2004) have enabled the development of mechanistic models describing the bark beetle dynamics (Seidl et al., 2007, 2009; Fahse and Heurich, 2011; Kautz et al., 2014; Louis et al., 2016b). In addition, numerous statistical models predicting parts of the *Ips typographus* dynamics have shed light on the processes affecting the bark beetle dynamics (e.g., Anderbrant et al., 1985; Eriksson et al., 2005; Mulock and Christiansen, 1986). A few models consider the interaction between weakened trees (namely wind damaged trees) as a low resistance breeding material for bark beetle reproduction (e.g., Eriksson et al., 2007, 2005; Louis et al., 2016b).

Aims and goals of the thesis

The aim of this thesis was to simulate the interactive dynamics of root rot, wind disturbance and bark beetles as affected by forest management. To achieve this aim, a simulation framework consisting of different simulation models was developed to provide a tool for future research to estimate the economic and ecological losses caused by these disturbance agents on a larger scale.

The goals during the framework development were to:

1. Develop a simulation model for *Heterobasidion* dynamics with a biological basis (**I**) to analyse the processes of *Heterobasidion* epidemiology and to improve the model if needed (**II**).
2. Develop submodels to simulate the effects of wood decay caused by *Heterobasidion* on stand vulnerability against wind (**III**)
3. Develop a simulation model for *Ips typographus* dynamics with a biological basis (**IV**)
4. Carry out model performance analysis for the simulation models of the framework together and separately in tree and stand scale to study the dynamics of each agent separately as well as together (**I**, **II**, **III**, **IV**)

The hypotheses for the stand scale simulations were:

1. The intensity of the damages caused by *Heterobasidion* species is driven by primary and secondary infections on large stumps. (**II**)
2. Wood decay caused by *Heterobasidion* species affects the vulnerability of a tree to wind damages. (**III**)
3. The intensity of damages caused by *Heterobasidion* species affects the intensity of damages caused by other disturbance agents, namely wind and bark beetles in even-aged Norway spruce forests. (**III**, **IV**)

MATERIALS AND METHODS

WINDROT simulation framework

General description of the simulation framework

The WINDROT simulation framework was developed to simulate the dynamics of Norway spruce dominated stands and the three major disturbance agents posing a risk to the forest management of those stands. WINDROT consists of four simulation models; MOTTI, Hmodel, HWIND and BBDYN, each responsible for one part of the interactive dynamics of either the host or one of the disturbance agents (Fig. 2). The use of each model in the substudies is described in Table 1. The MOTTI stand-level decision support system (Salminen et al., 2005; Hynynen et al., 2014, 2015) simulates the stand growth and dynamics as affected by forest management and the environment. The Hmodel (**I**, **II**) is the basis for disturbance agent dynamics as the *Heterobasidion* dynamics are simulated over the whole rotation and the simulation of the spatial layout is included in the Hmodel. HWIND (Peltola et al., 1999) is a mechanistic model to simulate the wind dynamics for each tree of the stand. BBDYN (**IV**) simulates the bark beetle dynamics.

The dynamics of the disturbance agents, especially *Heterobasidion*, depend highly on the stand spatial structure. However, MOTTI is not a spatially explicit model, and is instead based on sample trees representing the trees within the stand. Therefore, Hmodel was designed to include simulating the spatial layout with random coordinates for each tree (Fig. 3). Trees have a minimum distance between each other, which can be specified by the user prior to simulations. The simulation area was by default a rectangular area of 1 ha (100 x 100 m) with a buffer zone of 8 m on each side (Fig. 3.). The buffer zone was assumed to appear as the simulation area including the same forest management.

The WINDROT simulation framework includes stochastic features in the spatiality of the stand concerning the location of trees and stumps. Randomisation was also included in the initial stump diameters as well as with all probabilistic parameters (e.g. initial *Heterobasidion* genet distribution, colonization of the stump by *Heterobasidion*, annual wind speed, dispersal of bark beetles). This means that simulations with the same initial situation and input values, but a different seed number for the random number generator gives different outputs.

Table 1. Use of different models in the articles included in this thesis.

Article Model	I	II	III	IV
MOTTI	x	x	x	x
Hmodel	x	x	x	x
HWIND			x	x
BBDYN				x

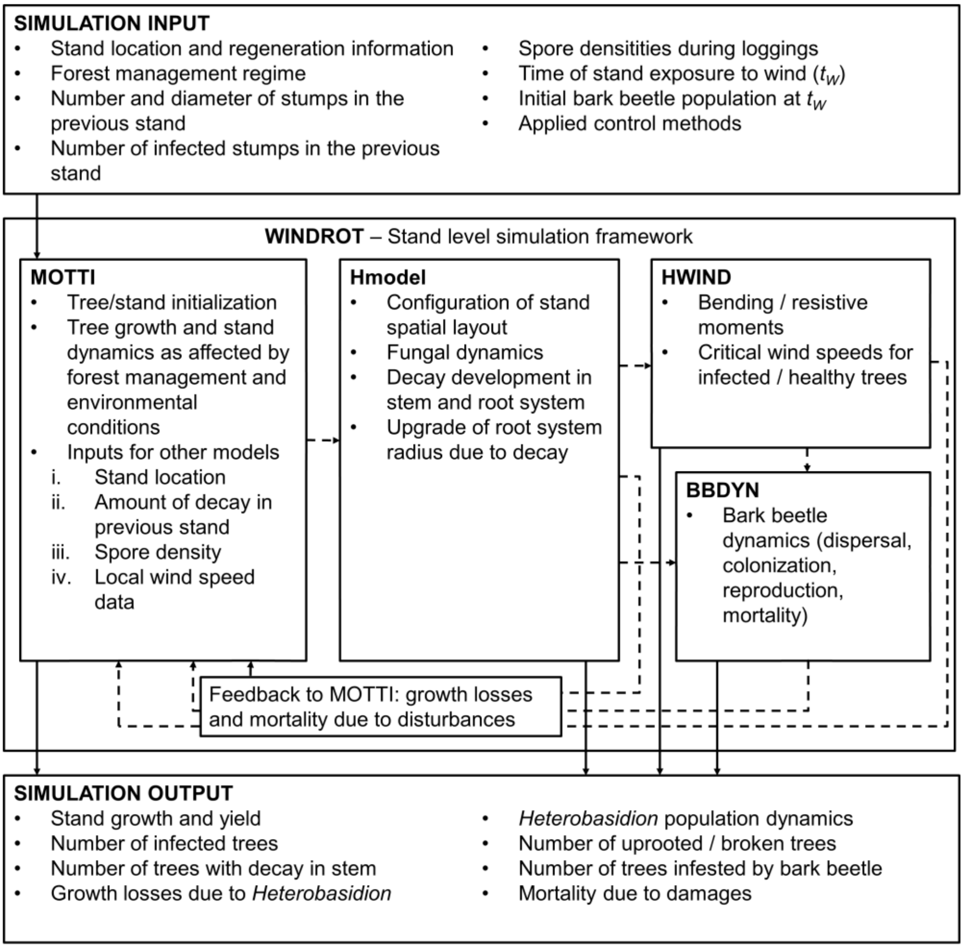

Figure 2. Conceptual diagram for WINDROT simulation framework including four simulation models (MOTTI, Hmodel, HWIND and BBDYN), their major contribution as well as the input and output variables of the framework.

MOTTI

The stand-level decision support system MOTTI (Salminen et al., 2005; Hynynen et al., 2014, 2015) simulates tree growth and stand dynamics in even-aged stands as affected by forest management and environmental conditions (e.g. temperature sum, elevation). The stand dynamics in MOTTI are simulated in two stages. First, the dynamics of a young stand from regeneration to the dominant height of the stand of less than 8 m are simulated with stand-level models with distribution models providing the link to the second stage. The second stage is the dynamics for an old stand (dominant height > 8 m) with spatially implicit individual-tree-level models simulating the stand dynamics based on sample trees representing the trees within one hectare (Hynynen et al., 2014; Siipilehto et al., 2014).

The basic assumption for stand dynamics for MOTTI in the WINDROT framework is that the simulations always start from stand regeneration and are run for one rotation length. Input for MOTTI includes the stand location, soil and site type, soil preparation prior to regeneration, regeneration process (i.e. planting, sowing or natural regeneration) and further also the number of seedlings/seeds and seedling survival rate. Forest management can be by either the forest management recommendations for Finnish forestry practice (Äijälä et al., 2014) or modified to user preferences. Forest management regime options include the timing for the tending of the young stand, timing and intensity of thinnings and the rotation length.

During each simulation step (by default 5 years with interpolation if needed), MOTTI first simulates the tree growth and stand dynamics providing input for the disturbance models. Hmodel simulates the trees in the spatial layout deriving the tree information from the MOTTI sample trees. At the time of the user-specified time for wind exposure (t_W), HWIND simulates the wind damages and BBDYN the subsequent bark beetle dynamics. During the simulation period for wind and bark beetle dynamics the simulation step is by default one year. After each simulation step, MOTTI receives feedback from the disturbance models and adjusts the growth and mortality of the trees within the stand (Fig. 2).

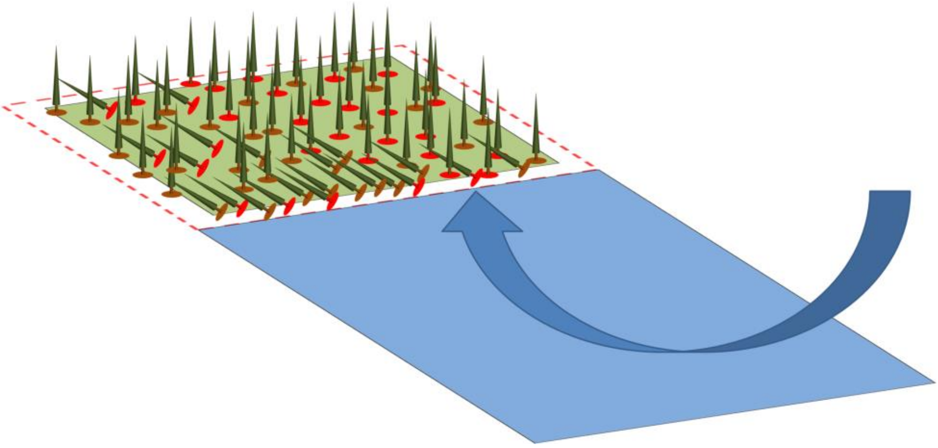

Figure 3. Spatial layout of the simulation area in the WINDROT framework. The green rectangular area represents the one hectare area, the white area delimited with the red dashed line represents the 8 m buffer zone and the blue area represents the upwind gap area as the stand is exposed to wind effects at time t_W. Trees in the stand are either healthy (brown) or infected by *Heterobasidion* (red root system). Trees failure under static wind load and subsequent bark beetle dynamics benefit from the stand edge and wind damaged trees.

Hmodel

Hmodel (**I**, **II**) is a mechanistic model to simulate the *Heterobasidion* dynamics at stand scale. Hmodel (**I**) was developed to study the effects of *Heterobasidion* root rot on the stand dynamics and to assess the effect of forest management on disease development. The overall structure followed the one applied in Rotstand (Pukkala et al., 2005) with modified submodels. The spatial layout described above is included in Hmodel and therefore it was used in all the articles. Hmodel is initialised as MOTTI starts its simulation of stand dynamics of reproduction.

Hmodel consists of several submodels describing different processes of the *Heterobasidion* dynamics. The primary infection process is a function of stump surface area (heartwood and sapwood areas separately) and the spore density and survival probabilities of heterokaryotic mycelia in stumps. Secondary dispersal via wood colonizing mycelia from stumps to living trees and from living trees to each other occur when two root systems overlap each other. Then the probability for infection depends on the area of overlap and the probabilities for transfer in the root system.

From the point of infection, the fungus is assumed to spread at a given growth rate towards the stem base entering it at the border of the heartwood and sapwood. The decay development at the stem base is then modelled as a function of tracheid dimensions and the growth rate of the fungus as it is assumed that the growth in the stem is mediated by the number of cell walls that will be degraded. The fungus was assumed to decay heartwood and sapwood at different rates due to the tree resistance (i.e., the reaction zone). Further spread to the whole root system was assumed to occur when 50% of the heartwood area at the stem base was decayed.

Growth losses due to *Heterobasidion* were modelled as a function of the decayed sapwood area. Mortality due to *Heterobasidion* occurred if the decay area covered the whole tree area at stem base or if the cross-sectional area of decay covered the cross-sectional area in 85% of the main roots at the root collar. *Heterobasidion* survival in the degrading root system of stumps and dead trees was modelled as a function of the diminishing amount of acid hydrolysable components (e.g. cellulose, hemicellulose and lignin).

HWIND

HWIND (Peltola et al., 1999) is a mechanistic model to simulate the effect of static wind load on trees and stands. Submodels to link the *Heterobasidion* root rot and wind disturbance dynamics were developed to simulate the interactive dynamics between wood decay caused by *Heterobasidion* root rot and wind (**III**).

In the WINDROT simulation framework the stand is assumed to be exposed to wind disturbance at a given time t_W specified by the user. It is assumed that at this time a neighbouring stand next to one of the sides of the simulation area is clear-cut, thus exposing the stand (Fig. 3). After the exposure of the stand, the wind disturbance dynamics are simulated in one year simulation steps for a given number of years specified by the user. Annual maximum wind speeds are given to be compared with the critical wind speeds predicted by HWIND. Stand edge dynamics (i.e., change of the stand edge due to wind damages) are calculated after each simulation step.

HWIND predicts wind speeds (given at a height of 10 m at the edge of the upwind gap) needed for uprooting and stem breakage of trees for different stand configurations (Peltola et al., 1999), using tree and stand characteristics and in this work as input also root decay and stem decay information provided by Hmodel. In HWIND, the predicted wind speeds required for uprooting and stem breakage of trees are affected by the bending and resistive moments, which are derived from root-soil plate weight (uprooting) and the modulus of rupture (stem breakage). Wind damage is predicted to occur if the predicted wind speeds for uprooting or stem breakage (i.e., critical wind speeds) are lower than simulated annual maximum wind speeds for the stand based on local wind climate data.

BBDYN

BBDYN (**IV**) is a mechanistic individual agent based model to simulate the dynamics of bark beetles on a stand scale. It is based with several modifications on the SAMBIA model by Fahse & Heurich (2011). The most significant modification was to make most of the bark beetle dynamics (e.g. resistance threshold, reproduction rate) tree dependent instead of constant values. BBDYN is initialized after the wind exposure at t_W as optimal stand edge habitat for bark beetle reproduction (Peltonen, 1999) is created as the neighbouring stand is clear-cut (Fig. 3).

BBDYN consists of four submodels; i) dispersal, ii) colonization, iii) reproduction, and iv) mortality of bark beetles. Dispersal of bark beetles is simulated in two phases. First, the bark beetles are dispersed randomly according to their flight abilities. After that, the bark beetles are re-organized in trees according to the possible influence of aggregation or anti-aggregation pheromones or when they are absent, in the nearest tree. There is no preference between weakened and healthy trees in the dispersal stage.

Colonization of a tree is determined by a tree specific resistance threshold (Mulock and Christiansen, 1986). If the number of attacking bark beetle males is greater than the resistance threshold, the tree is colonized and further used for reproduction. If the number of bark beetles is less, the tree resistance kills the attacking bark beetles. The tree resistance is a function of tree vigour index and therefore the resistance for weakened trees is lower than for healthy trees.

Reproduction rate in successfully colonized trees was calculated as a function of female density per bark area (Anderbrant et al., 1985). It was assumed that every male reproduced with two females and the sex-ratio in the offspring was 1:1. The optimal bark area for bark beetle reproduction in one tree was predicted with a new bark area model as a function of minimum and maximum optimal bark thickness.

Bark beetle mortality takes place in three parts of the model. First, intraspecific competition is taken into account in the reproduction submodel. Second, antagonists predating the larvae are modelled as a function of the probability for the antagonists to find a colonized tree and as the survival probability of the larvae if the antagonists find the colonized tree. Third, winter mortality reduces the overall population by 40% (Poolak, 1975; Austarå and Midtgaard, 1986).

Model performance simulation outlines

The simulations to analyse the performance of each model were run at the tree and stand levels. Trees for the tree level simulations varied between studies (see substudies for tree dimensions in each study). Stand level simulations were run in a similar stand mimicking a typical Norway spruce in southern Finland (**I-IV**). The stand was the Myrtillus site type (Cajander 1949) on mineral soil with a temperature sum of 1300 d.d. The forest management was based on the current forest management recommendations for Finnish forestry practice (Äijälä et al. 2014) including mounding as soil preparation before the planting of seedlings (1800 Norway spruce seedlings per hectare), and the timing of the tending of young stands, where naturally regenerated trees were removed and planted spruces along with the 5% mix of Silver birch (*Betula pendula*) left after tending. The timing of the first commercial thinning (from below) depended on the stand basal area and therefore varied between iterations and scenarios in all simulations. In articles **I** and **II**, the timing of the second thinning was also dependent on the stand basal area. In papers **III** and **IV**, the timing of the second thinning was fixed at age 44 and 43 years, respectively. In article **I** the rotation length was 59 years and in articles **II**-**IV** it was 61 years in all scenarios.

Three different scenarios posing a different risk of *Heterobasidion* infection on the stand scale were simulated in each study as the basis scenarios (Table 2). These scenarios (low, medium and high risk) were defined with an increasing inoculum pressure (spore load during the loggings and the number of infected stumps in the previous stand) with slight variation between the substudies. There were no control measures against *Heterobasidion* applied in these simulations and thinnings were assumed to be carried out during winter months with lower spore loads.

Wind disturbances (**III, IV**) were simulated over a 10-year period. The stand was assumed to be exposed for wind effects from one side after the clear-cut of the neighbouring stand, which was set to occur at the same time as the second thinning of the simulation area. The maximum wind speed for each year over the simulation period was randomly predicted based on long-term statistics for the annual mean probability of the maximum 10-min average wind speed at 10 metres high above ground for Helsinki-Vantaa Airport (Peltola et al., 2010). Wind disturbances were assumed to occur during unfrozen soil conditions.

Three different bark beetle scenarios (**IV**) were simulated after the clear-cut of the neighbouring stand as a stand edge favouring bark beetle reproduction was formed along with wind disturbance. The scenarios differed with the initial bark beetle population. The initial population in the low bark beetle risk scenario was 10000 beetles ha^{-1}, in the medium scenario 25000 and in the high bark beetle risk scenario 40000 beetles ha^{-1}.

All the disturbance agent models include stochastic features and therefore the number of simulated replications needed to reduce the simulation error for the model outputs was studied by running 2-400 replications. Hmodel alone was run with 10 simulated replications (**I**, **II**), but the addition of HWIND and BBDYN to the WINDROT framework increased the number of replications needed to 200 simulations (**III**, **IV**).

Table 2. Hmodel inoculum pressure with different *Heterobasidion* risk scenarios

Variable	Value		
	Low	*Medium*	*High*
Share of infected stumps in the previous stand (%)	0	10	30
Probability of spore infection (P_{spore}) (I,II) / Spore density (D_{spore}, m^{-2} hr^{-1}) (II–IV)	0.2 / 200	0.5 / 400	0.9 / 750

RESULTS AND DISCUSSION

Major advancements of the developed models

Hmodel advanced disease modelling by placing the main emphasis on developing a mechanistic model with logical submodels based on the biological processes and concentrating on the underlying mechanisms of *Heterobasidion* dynamics. A similar mechanistic approach has not been widely applied in modelling forest diseases before (e.g. Frankel, 1998; Marçais et al., 1996; Pukkala et al., 2005) as many disease models have been based on descriptive statistical concepts. However, such mechanistic models with strong biological support will be needed in future to predict disease dynamics in various scenarios and under the predicted changing climate (Seidl et al., 2011a). The most significant concepts in the submodels of Hmodel were; the primary infection process as a whole (**II**), using tracheid dimensions to determine fungal growth rates (**I**) and linking them with the annual mean temperature (**II**) as well as modelling the growth losses as a function of reduced sapwood area and therefore linking it to the formation of reaction zone and carbon allocation (**I**).

The primary infection process was based on the assumption that Norway spruce heartwood is more suitable for spore germination and survival than sapwood (Oliva et al., 2013). It included a novel approach to determine the pairing of two homokaryotic spores as heterokaryotic mycelia assumed to be superior in the competition against homokaryotic mycelia. The concept is suitable for use with other fungi with similar needs for heterokaryosis and could potentially be used in ecological studies to analyse interspecific competition in degrading stumps in the future. The concept of using tracheid dimensions to determine the fungal growth rates in different parts of the tree was based on the assumption that the limitation for decay spread is the degradation of cell walls (Fuhr et al., 2011). Explaining the growth losses with decreasing sapwood area and the formation of reaction zone was based on studies by Oliva et al. (2012, 2010). Modelling the growth losses also created a link to the tree resistance and thus to the interaction with bark beetle dynamics.

The connecting of Hmodel and HWIND was the first attempt to mechanistically model the effect of wood decay on the mechanical strength of trees against wind load considering both resistive moments by the root systems and stems. Although several tree-pulling experiments and stand level inventories have shown that root rot plays a major role in increasing tree and stand vulnerability to wind (Fraser, 1962; Whitney et al., 2002; Oliva et al., 2008; Giordano et al., 2012), there are still several gaps in the what is known about the mechanisms especially considering the effect of wood decay on root system strength.

The BBDYN mechanistic model is based on the structure of the individual agent based model SAMBIA (Fahse and Heurich, 2011). The major advancement was the inclusion of the colonisable bark area submodel and further linking the colonisation and reproduction processes to be tree-size dependent. The concept of a colonisable bark area has not been used in simulation models for bark beetle dynamics before and it enables the simulation of interspecific competition in the future as many bark beetles are segregated in the stem for reproduction by the colonisable bark thicknesses (Grünwald, 1986). In addition, we included stand growth dynamics and the random location of trees within the stand.

Model validation

Validation of the WINDROT simulation framework output against field data over the whole rotation length is not possible because obtaining a good dataset for evaluation in the case of all three disturbance agents is nearly impossible considering how much variation and stochasticity is involved in such disturbance event data. Therefore, we have applied partial evaluation of some of the submodels or parts of the model against results from field studies (Table 3). Further validation of the submodels should be done in the future when suitable field data is available.

Sensitivity analyses are another way to study the model performance. Complex mechanistic models, such as the ones described in the substudies of this thesis, consist of several submodels and include several parameters. This can lead to over-parameterization, where two or more of the model parameters correlate with each other. In addition, causality structures may exist among the parameters. The influence of parameters and their combinations to the simulation results either on the submodel or whole model level can be studied by carrying out sensitivity analyses with fixed parameter combinations. Such sensitivity analyses of model parameters were done in the substudies on the tree and stand levels.

Table 3. Comparison and evaluation of different parts of the WINDROT framework against results from field studies.

Part of the model:	Compared against results from:	Article
Hmodel		
Decay growth within the stem. The height to width ratios of the decay.	Tamminen (1985)	**I**
Secondary spread via root-to-root contacts. The diameters of roots where the infection could have occurred.	Piri et al. (1990)	**I**
Genet distributions.	Piri et al. (1990)	**I**
Degradation of stumps and survival time of *Heterobasidion* in them.	Piri (unpublished data)	**I**
Primary infection process. The maximum pairing distance.	Möykkynen and Kontiokari (2001)	**II**
Annual mortality due to *Heterobasidion*.	Swedjemark and Stenlid (1993)	**II**
Hmodel+HWIND		
Decay in stem affecting the stem breakage at the tree level	Gordon (1973)	**III**
Tree anchorage and decrease in the resistive moment due to decay	Lundström et al. (2007), Giordano et al. (2012)	**III**
Location of uprooted healthy and infected trees	Whitney et al. (2002), Oliva et al. (2008)	**III**
BBDYN		
Colonisable bark area used for reproduction	Weslien and Regnander (1990)	**IV**

Key mechanisms of *Heterobasidion* epidemiology

Sensitivity analysis for Hmodel showed that the three most sensitive parameters in Hmodel were: i) the probability of spores colonizing fresh stumps (P_{col}), ii) the growth rate of fungus in the roots of a living tree (rH_{tr}), and iii) the spreading probability of the fungus from stumps to trees ($P_{transferST}$) (**I**). The submodels including these three parameters were considered the key mechanisms of *Heterobasidion* dynamics. These submodels were further analysed and submodels of primary infection process (including P_{col}) and the ones including mycelial growth rate (rH_{tr}) were significantly modified and modelled in more detail to achieve more profound submodels (**II**).

The *Heterobasidion* risk scenarios showed that the increasing amount of infected stumps in the previous tree generation and higher spore densities increased the number of infected trees as well as the number of trees with decay in the stem towards the end of the rotation (**I**, **II**). However, the limited numbers of scenarios in the model performance analyses were not enough to determine the differences between primary and secondary spread processes in the significance for *Heterobasidion* damages. Therefore, large scale simulations are needed to produce more variable *Heterobasidion* risk scenarios with variations in stand options. In addition, simulations should be run over several rotations to take into account the effect of primary infections from thinnings.

The stand level simulations over one rotation showed that several infections on large stumps are more significant than numerous infections in the small stumps created during the early stage of the rotation (i.e., the tending of young stands and the first thinnings). Therefore the number of large stumps can be considered to be the driving factor for *Heterobasidion* epidemiology at the stand scale (**II**) proving the *Hypothesis 1* true. There are two reasons why large stumps are more significant than small stumps. First, they have larger stump surface area for spores to land and thus a higher probability of being colonized. Also, the area of heartwood is a function of diameter and age (Sellin, 1994; Wilhelmsson et al., 2002) and thus the area is larger in large stumps than in small stumps which may still be completely sapwood and thus more resistant to spore infections (Oliva et al., 2013). Second, the large stumps have larger root systems and therefore have higher probabilities of overlapping with other root systems. Large stumps might also have more root contacts and connections compared to small stumps, but this is not taken into account in Hmodel as the transfer probabilities from stump to tree and from tree to tree are not tree-size dependent.

Effects of wood decay on tree vulnerability against wind

The model performance simulations showed that the wood decay caused by *Heterobasidion* root rot affected the critical wind speeds needed for tree failure under wind load (**III**) proving the *Hypothesis 2* true. Both tree and stand level simulations showed that the wood decay affected more the critical wind speeds needed for uprooting than the ones needed for stem breakage (Fig. 4).

Tree pulling experiments have shown that the trees affected by root and stem rot are more prone to failure under mechanical loading (Nicoll et al., 2006; Lundström et al., 2007; Bergeron et al., 2009; Giordano et al., 2012). However, the underlying mechanisms have not been well quantified. In the model, we assumed that the decayed area within the stem and roots would lose all its mechanical strength as HWIND makes its calculation of stem resistive moment using a pipe-like shape (see Jones, 1983). However, on Sitka spruce the effect of decay on the modulus of rupture has been shown to decrease only on average 26% as compared to healthy wood (Pratt, 1979). In addition, the stage of the decay affects the strength as well (Pratt, 1979). Therefore, the WINDROT framework probably overestimates the wind damages. It is crucial in the future to: i) carry out experiments on Norway spruce to estimate the strength losses due to different decay types, and ii) develop more detailed models on the advance of decay within stem and roots.

Seifert (2007) developed a model to estimate the decay advancement within the stem and the inclusion of a similar model should be considered for Hmodel. However, our knowledge of root architecture and structure is still somewhat fragmentary (see Kalliokoski et al., 2010; Lintunen and Kalliokoski, 2010) and the advancement of decay within the root system is not well enough documented to produce a more detailed model. The secondary spread of *Heterobasidion* also weakens the tree first from its root system towards its stem base and after reaching the stem base starts to weaken other roots. Therefore, the mechanical strength of root system in nature is much more heterogeneous than is assumed in the model.

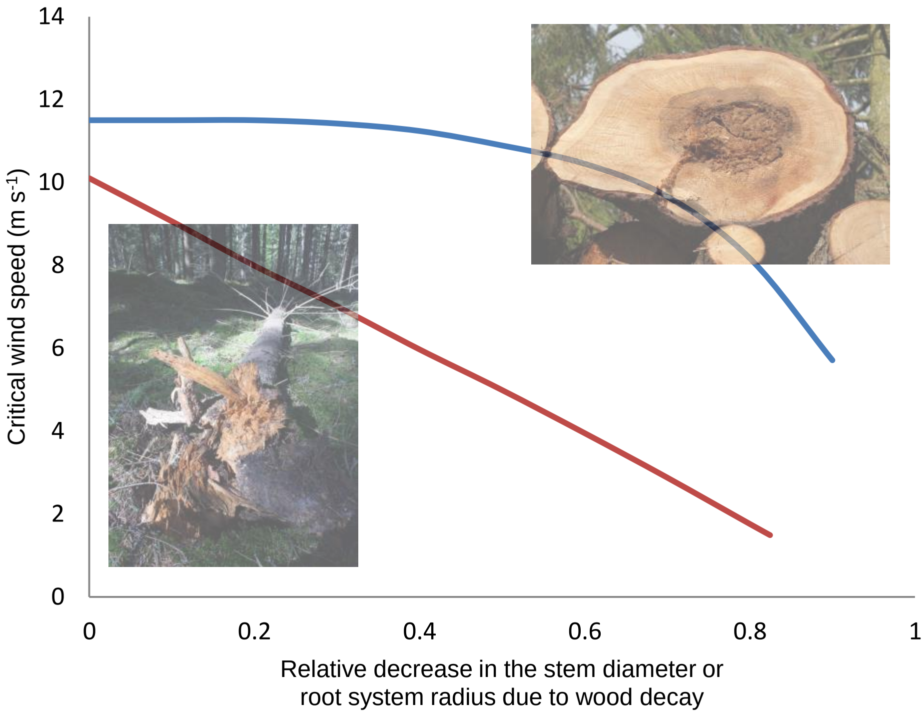

Figure 4. The effect of relative decrease in stem diameter (blue) or root system radius (red) due to wood decay in a tree with diameter of 20 cm and height of 20 m.

Interaction between disturbance agents

The intensity of damages caused by *Heterobasidion* species (i.e., the number of infected trees) affected the intensity of wind damages after the stand was exposed to wind by a clear-cut of a neighbouring stand at t_W (Fig. 5) (**III**, **IV**) proving the *Hypothesis 3* partly true. In all scenarios the majority of the wind damages occurred during the first year after exposure mainly due to the accumulation of highly vulnerable decayed trees over the years before the exposure. On average 6% of all trees in low, 19% in medium and 35% in high risk scenarios were uprooted during the first year. However, a similar effect was not seen for stem breakages as the relative decay diameters of the stem diameters at breast height were below 0.6 in all scenarios and therefore did not significantly affect the stem mechanical strength.

The number of living trees killed by bark beetles (excluding the trees killed by *Heterobasidion* or wind during the same simulation step) slightly decreased with the intensity of wind damages, but increase relative to the number of trees within the stand (**IV**). The number of wind damaged trees attacked by bark beetles increased with the intensity of wind damages. However, stand level simulations did not show any direct interaction between *Heterobasidion* decreasing the tree growth and thus lowering the tree resistance against bark beetle attacks (**IV**) leaving the *Hypothesis 3* partly untrue.

The initial bark beetle population was a significant factor for the mortality of trees due to bark beetles over the simulation period. The population of 10000 beetles ha^{-1} in the low bark beetle risk scenarios was clearly not enough for the population to lead to an outbreak and attack living trees although the population successfully attacked wind damaged trees (**IV**). Mortality due to bark beetles was observed on average for a few years in the medium and for 4-5 years in the high bark beetle risk scenario. Variations in the mortality of trees were high in the medium and high bark beetle risk scenarios.

The simulation results were well in line with several field studies observing the increase of stand vulnerability to wind due to root rot (Whitney et al., 2002; Oliva et al., 2008; Suvanto et al., 2016). However, the significance of wind damaged trees to the potentiality of bark beetle outbreak was not observed as clearly as it is often in many field studies (e.g. Eriksson et al., 2005; Komonen et al., 2011). This may be due to the small size of the simulation area and the effects of landscape level simulations could better show the significance of wind damages on subsequent bark beetle damages. The initial bark beetle population had a much more significant effect on the stand scale and was well in line with field data (Weslien et al., 1989).

The stand level simulations show that many more trees are infected and decayed by *Heterobasidion* than are wind damaged or killed by bark beetles (Fig. 5). However, the nature of these disturbances should be taken into account. *Heterobasidion* slowly affects the trees over the rotation length decreasing the timber quality, causing growth losses and making the trees more vulnerable to wind damages. Wind and bark beetle damages are more discrete events and influence the stand dynamics in a short period of time by killing trees and thus instantly reducing the number of trees in the stand. Economic analysis should be carried out in future to compare the effects of different disturbance agents on forest management.

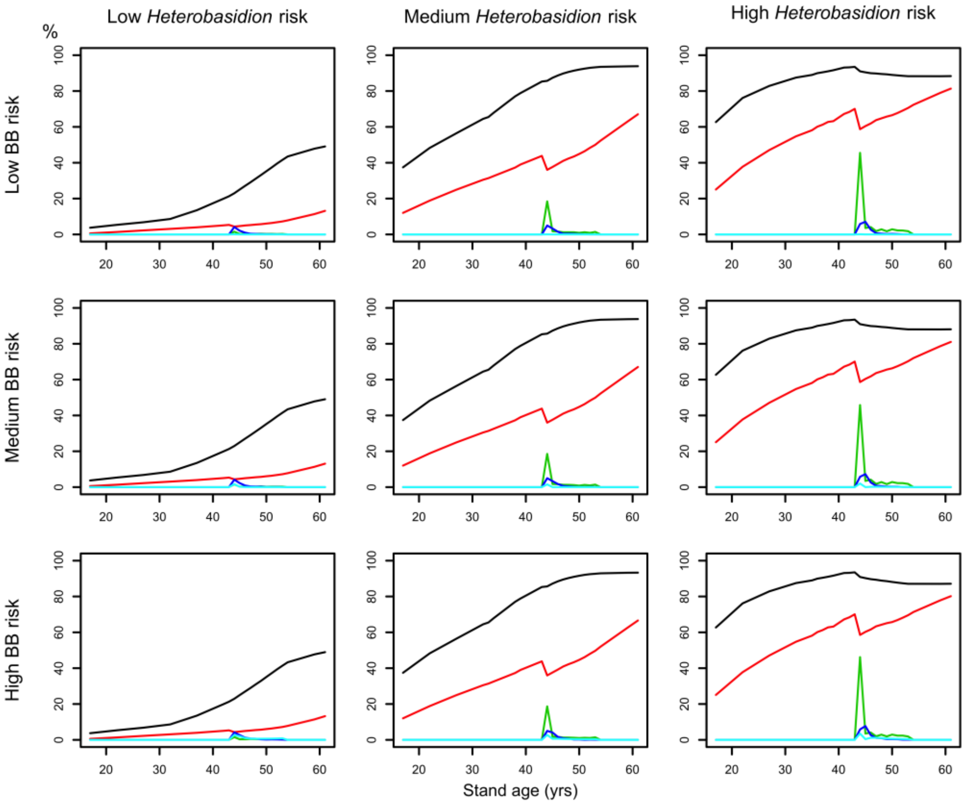

Figure 5. Percentages out of all trees (living + time from death 0 years) for the *Heterobasidion* infected trees (black), trees with decay in their stems (red), uprooted (green) and stem broken trees (dark blue) as well as trees killed by bark beetle attacks (light blue).

CONCLUSIONS AND FUTURE PROSPECTS

The WINDROT simulation framework represents a novel approach in disturbance modelling that takes into detailed consideration interactive stand dynamics and various disturbance agents. The simulation framework aims to integrate abiotic and biotic disturbance dynamics and risk assessments as an active part of future forest management simulation scenarios. It is intended as a tool for researchers to analyse the risk posed by various disturbance agents to forest management under different scenarios and to deliver information for forest policy actors and decision makers at the national and EU-levels.

Seidl et al. (2011a) reviewed the development of disturbance modelling since Pickett and White (1985) and found that the disturbance agent interactions were especially modelled with statistical concepts. However, statistical models have limitations when it comes to disturbances, which are in most cases highly stochastic events. In addition, the complex interactions between disturbance agents, forming disturbance regimes, modelled with statistical methods limit the understanding of the underlying mechanisms. Therefore, Seidl et al. (2011a) concluded that there were the following four challenges for disturbance modelling: i) a better understanding of the key mechanisms with novel statistical methods, ii) development of mechanistic models to be applied in the changing world, iii) integration of disturbance models in ecosystem models, and iv) solving scalability issues from even cell-level processes to the landscape level. The development of the WINDROT simulation framework improved mechanistic modelling for *Heterobasidion* and *Ips typoghraphus* dynamics as well as introducing novel ways to incorporate interactive dynamics between different disturbance agents. The inclusion of the disturbance models with the MOTTI decision support system integrated the disturbances into a platform used actively to support decision making. The scalability was developed from the cell (e.g., tracheid dimensions in Hmodel) to the stand levels. However, the future challenge for the development of the WINDROT simulation framework is its scalability from the stand to landscape levels, which will require better models for landscape level dispersal. In addition, the inclusion of climate change effects on the disturbance dynamics is an area for future development. Economic evaluation of the results should also be incorporated in the model in the future to better estimate the economic losses caused by different disturbances as well as to economically justify various control measures.

The main ambition of the model development was to take advantage of the vast amount of existing literature on the disturbance dynamics. The dynamics of each disturbance agent in this study have been extensively studied over the past decades and the biology and epidemiology of *Heterobasidion* species or *Ips typographus* are among the most well-known (e.g., Garbelotto and Gonthier, 2013; Wermelinger, 2004).

Modelling disturbance dynamics is a complex task and the mechanisms and processes affecting the model must be simplified. Therefore, it is crucial to understand that models are simplifications of the real world. However, they can help us to understand the underlying mechanisms of different processes. The limitations of model development and performance analyses raised several issues that will need further research in the future. New quantitative results are needed focusing on the key processes of the dynamics of each disturbance agent as well as their interactions with each other. For example the mechanisms related to the underground secondary spread of *Heterobasidion* and to the root system dynamics should be studied. In addition, the underlying mechanisms regarding the decrease of mechanical strength due to wood decay should be studied in greater detail.

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