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**Interaction of disturbance agents on Norway spruce: a mechanistic model of bark beetle
dynamics integrated in simulation framework WINDROT**

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26 Abstract

27

28 Interaction of disturbance agents may cause cascading effects in forests. The three most
29 important disturbance agents of Norway spruce (*Picea abies*) in northern Europe are
30 *Heterobasidion* root rot, wind and the European spruce bark beetle (*Ips typographus*). In this
31 study, we present a mechanistic individual agent based model to simulate the dynamics of the
32 bark beetle and integrate it in the simulation framework WINDROT to further study the
33 interactive dynamics of root rot, wind and bark beetles. We carried out model performance
34 analysis concluding that the model is sensitive to the parameters of optimal bark thickness for
35 reproduction. Stand level interaction between wind and bark beetle disturbances was also
36 evaluated against field data. The stand level simulations show the interaction between the
37 disturbance agents; the root rot increases wind disturbance and bark beetles benefit from
38 wind fallen trees. No direct interaction was found in the simulation study between the root rot
39 and bark beetles. Further experimental research and large scale simulation studies are needed
40 to better understand the underlying mechanisms in the interaction between the disturbance
41 agents.

42

43 Keywords: bark beetle, *Ips*, disturbance interaction, *Picea abies*, wind disturbance, root rot

44

1 Introduction

46

47 Bark beetles are well-known to cause significant disturbances all over the globe in the
48 coniferous forests (Raffa et al., 2015). Recently, the most serious large-scale outbreaks have
49 occurred in western North America by the mountain pine beetle (*Dendroctonus ponderosae*
50 Hopkins) (Safranyik and Wilson, 2006). In Europe, *Ips typographus* (L.), Coleoptera,
51 Curculionidae, Scolytinae is causing significant damages in Central and northern Europe
52 (Seidl et al., 2011). Many bark beetle species attack trees in high numbers to overcome tree
53 resistance, which is dependent on the tree vigor (Mulock and Christiansen, 1986; Raffa and
54 Berryman, 1983). Hence, when the bark beetle population is low, weakened trees with low
55 resistance are required for breeding and when population increases, the beetles can attack
56 healthy, living trees.

57

58 Norway spruce (*Picea abies* (L.) Karst.) is economically one of the most important tree
59 species in northern Europe. The managed Norway spruce stands currently face three major
60 disturbance agents; root and butt rot caused by *Heterobasidion* species complex, wind storms
61 and European spruce bark beetle (*Ips typographus*). All of these agents cause significant
62 economic losses, and their impact is predicted to increase under the projected climate change
63 (Müller et al., 2014; Peltola et al., 2010; Seidl et al., 2014).

64

65 Interaction in the disturbance dynamics may lead to cascading effects when disturbances
66 increase the subsequent disturbances caused by another agent (Buma, 2015). On Norway
67 spruce dominated forests in northern Europe, the most well-known regime of compounding
68 disturbances is the one including root rot, wind and bark beetles: wood decay decreases the
69 tree stability against wind (Giordano et al., 2012), bark beetles benefit from weakened, wind-

70 fallen trees (Bouget and Duelli, 2004; Komonen et al., 2011) and the root and butt rot is
71 spreading rapidly in dead trees, roots and stumps (Bendz-Hellgren et al., 1999). One of the
72 best examples of the cascading effects is the winter storm Gudrun in 2005 in the Götaland
73 province in Sweden, where approximately 75 Mm³ of trees were fallen (Anonymous, 2006).
74 The stands with root decay were the most vulnerable for wind disturbance (Oliva et al.,
75 2008). The operations to salvage the wind-thrown trees took time, which facilitated bark
76 beetle mass attack in the landscape causing also serious disturbance in the subsequent years
77 (Långström et al., 2009).

78

79 Even though the dynamics of the major disturbance agents affecting Norway spruce have
80 been described with mechanistic models over the years (e.g. Fahse and Heurich, 2011;
81 Gardiner et al., 2000; Honkaniemi et al., 2014; Peltola et al., 1999; Pukkala et al., 2005; Seidl
82 et al., 2007), there are very few models including the interactive dynamics between these
83 disturbance agents. Several bark beetle models include interaction with wind disturbance (e.g.
84 Louis et al., 2016b; Potterf and Bone, 2017) and Western Root Disease Model (WRDM;
85 Frankel, 1998), developed for similar system in North America, incorporates multiple agents
86 in the simulations. However, the WRDM lacks the underlying interactivity between
87 disturbance agents as the interactions are user-specified input values.

88

89 Honkaniemi et al. (2017a) presented a simulation framework WINDROT to simulate the
90 interaction between root and butt rot caused by *Heterobasidion* species complex and wind
91 disturbances. In this study, we present a mechanistic agent based model for *Ips typographus*
92 integrated into the WINDROT framework. The biology of bark beetles and the factors
93 affecting the outbreaks are rather well known (Seidl et al., 2016; Wermelinger, 2004) and
94 there are already several mechanistic models to simulate the bark beetle dynamics (Fahse and

95 Heurich, 2011; Kautz et al., 2014, 2013; Louis et al., 2016b; Potterf and Bone, 2017; Seidl et
96 al., 2007). Even though many of the models include the interaction between wind disturbance
97 and subsequent bark beetle dynamics, they lack other agents or the underlying mechanisms
98 and dynamic interactions. Our aim was to include dynamic interaction in the simulations by
99 combining mechanistic models for three different disturbance agents.

100

101 Root rot on Norway spruce is most often caused by *Heterobasidion* species in the Nordics.
102 They cause great economic losses throughout the Northern Hemisphere (Woodward et al.,
103 1998) by reducing the timber value as well as causing growth losses and mortality. In
104 addition, they decrease the supportive strength of the trees against wind storms (Giordano et
105 al., 2012). *Heterobasidion* species spread by two mechanisms; spores infect fresh wood
106 surfaces and subsequent mycelia grows through root contacts from tree to tree (Garbelotto
107 and Gonthier, 2013; Piri and Valkonen, 2013; Piri, 2003). Forest management and especially
108 fresh stumps have created an optimal spreading route for the disease. The spore deposition
109 has high spatio-temporal variation and in the Nordics the highest infection probabilities occur
110 during the summer months (Brandtberg et al., 1996; Möykkynen and Kontiokari, 2001;
111 Witzell et al., 2011). In case of Norway spruce, root rot advances from root system up into
112 the stem mainly decaying the heartwood (Stenlid and Redfern, 1998). However, it can
113 challenge the tree vigor by entering into functional sapwood and therefore causing growth
114 losses (Bendz-Hellgren and Stenlid, 1997; Oliva et al., 2012, 2010).

115

116 Wind causes mechanical loading on the canopy and stem which lead to tree failure if the tree
117 resistive strength is exceeded. The overall bending moment is a sum of the horizontal forces
118 created by the wind and the vertical forces created by the gravity (Peltola, 2006). The
119 mechanical support of the root system resists these forces against uprooting and stem

resistance moment against stem breakage (Peltola, 2006). The trees break or uproot if the wind load exceeds the tree mechanical strength. Because several variables affecting this strength, such as tree species, height-diameter ratio and rooting depth, are subject to forest management (Ancelin et al., 2004; Peltola et al., 1999), it plays a significant role in the control of wind disturbances.

European spruce bark beetle males pioneer the attacks and produce the aggregation and anti-aggregation pheromones released during the attack on the trees (Bakke et al., 1977) to overcome the tree resistance threshold. Trees suitable for bark beetle attack need to have bark that is thick enough to offer protection and nutrition for the bark beetles during their life stages under the bark. This limits the trees to have at least a 2.5 mm thick bark (Grünwald, 1986). If a suitable tree is found and the tree resistance is overcome, bark beetles can use the tree for reproduction. Due to preference for the weakened trees as reproduction material when the population is low, bark beetle outbreaks are often subsequent to wind disturbances providing massive amounts of timber in the forest (Bouget and Duelli, 2004; Eriksson et al., 2005; Komonen et al., 2011).

The objective of this paper is to describe an individual agent based model for European spruce bark beetle and include that in a simulation framework WINDROT (Honkaniemi et al., 2017a) to study the potential interactions between the three disturbance agents; root rot, wind and bark beetles. We present the model in detail as well as test the submodel sensitivity and evaluate parts of the model against field data following the principles of pattern-oriented modelling (POM) (Grimm and Railsback, 2012). To our knowledge, this study is the first simulation work considering these three disturbance agents and their interactive dynamics. In

addition, we have carried out simulations to analyze the model performance and sensitivity in tree and stand scale.

2 Materials and methods

2.1 Model description

The new mechanistic model BBDYN, described in this article, is developed to simulate the bark beetle dynamics within an existing simulation framework WINDROT (Honkaniemi et al., 2017a). The model is based on the basic structure presented in SAMBIA model (Fahse and Heurich, 2011) with several modifications and parametrizations. The novelty of BBDYN lies in the development of key mechanisms of bark beetle dynamics (reproduction, aggregation and tree colonization) to be tree-size dependent as the underlying interaction mechanisms between different disturbance agents could be only related to tree growth and the disturbance effects on tree growth. We present submodels where the reproduction is related to the colonizable bark area of each tree based on the optimal bark thickness for *Ips typographus*. The aggregation caused by pheromones and the overcome of tree resistance are based on the tree growth.

The basic structure of the BBDYN model was based on the SAMBIA model (Fahse and Heurich, 2011) with several modifications. The key differences between the models are: i) change from grid-based spatial layout (SAMBIA) to random coordinates of trees (BBDYN); ii) addition of absent host dynamics (SAMBIA) to complex stand dynamics affected by forest management simulated with MOTTI stand level decision support system (Hynynen et al., 2014; Salminen et al., 2005) (BBDYN); and iii) replacement of static, non-size-dependent

parameters (SAMBIA) with tree-size-dependent parameters with bark thickness model (BBDYN). The preference of weakened trees for bark beetle reproduction was included in SAMBIA, but the weakened trees were randomly selected from the landscape rather than including the interactive dynamics.

BBDYN model was included in the simulation framework WINDROT (Honkaniemi et al., 2017a) including already three previously published models (i.e. MOTTI, Hmodel and HWIND, see Appendix 1 for more description of these models). In this framework MOTTI stand level decision support system (Hynynen et al., 2014; Salminen et al., 2005) simulates the tree growth and stand dynamics affected by different forest management options. Hmodel (Honkaniemi et al., 2017b, 2014) simulates the *Heterobasidion* species complex dynamics in space and time in stand scale and decreases the tree anchorage as well as causes growth losses and tree mortality. HWIND (Peltola et al., 1999) simulates the wind disturbance by calculating critical wind speeds for each tree of the stand, which are further compared to the annual maximum wind speed on the location of the stand. WINDROT framework simulations are by default run on a rectangular area of 1 ha (100 x 100 m) with a buffer zone of 8 m on each side of the area (see Appendix 1). The stand environment is assumed uniform with similar forest continuing beyond the simulation area borders.

The model description follows the ODD (Overview, Design concepts, Details) protocol for describing individual- and agent-based models (Grimm et al., 2010, 2006). The abbreviations used in this paper are presented in Table 1 with explanations as well as with parameter values if applicable.

2.2 Purpose

194

195 The purpose of the model is to simulate the *Ips typographus* dynamics in Norway spruce
 196 stands. In addition, the model integrates the economically most important disturbance agents
 197 of Norway spruce into the stand dynamics and simulates the potential interactions and
 198 compounding effects between these disturbance agents, in the WINDROT simulation
 199 framework.

200

201 2.3

202

203 BBDYN model includes beetles as entities interacting with three other agents (trees,
 204 *Heterobasidion* and wind) included in the other models of the WINDROT framework. Each
 205 bark beetle individual is described with state variables of flying ability (groups of “strong”,
 206 “average” and “weak” bark beetles) and gender (only flight of males is simulated). Reaction
 207 to aggregation and anti-aggregation is dependent on the individual’s flying ability. Species-
 208 specific optimal bark thickness (minimum and maximum bark thicknesses for reproduction)
 209 defines which trees are suitable for bark beetle colonization and reproduction. The population
 210 is formed of individuals with different flying abilities forming groups of beetles which are
 211 further divided into two flying cohorts each. This way all the beetles do not disperse at the
 212 same time.

213

214 Trees are described with state variables of diameter at 1.3 m height (*dbh*) and height (*h*).
 215 MOTTI describes the stand as a group of sample trees represented by the state variables and
 216 each sample tree representing a certain number of trees. Hmodel then creates a spatial stand
 217 based on these sample trees (see full details in (Honkaniemi et al., 2017b, 2014). Hmodel
 218 adds information on trees whether they are infected or not, the extent of decay in root system

and stem and whether the tree suffers growth losses due to root rot. HWIND predicts critical wind speeds for each tree and comparison of those against local wind data provides information whether trees can tolerate the wind effect or not (uprooted/broken). Bark beetle individuals attack trees and if they exceed the tree's resistance threshold, colonize the tree for further reproduction. Unsuccessful attacks (ie. number of attacking beetles less than tree resistance threshold) result in the death of the beetles and the tree remains uninfested.

2.4 Process overview and scheduling

The default time step of BBDYN model is one year. During this time step, the order of models in WINDROT framework is following; stand dynamics and tree growth in MOTTI, fungal dynamics in Hmodel and wind disturbance dynamics in HWIND. After wind disturbance dynamics, the bark beetle dynamics are simulated through the following processes in the following order; (i) dispersal, (ii) colonization, (iii) reproduction, and (iv) mortality (Fig. 1). Within the dispersal process the individual beetles disperse according to their flying ability ("strong", "average", "weak"). These groups are further divided into flying cohorts flying in consecutive waves, in order to be exposed to pheromones. Calculated values are assigned to beetles after each cohort simulation. Beyond the dispersal, beetles are considered as one population and values are assigned after calculating them for the whole population. This principal of scheduling applies also to other models with trees, fungi and wind.

2.5 Design concepts

2.5.1 Emergence

Interactions between wind and bark beetles or root rot and bark beetles are not fixed in the model and are expected to emerge from simulations. Interactions depend on the growth of the trees. In addition, the number of attacking bark beetles per tree is not fixed to any limit, but is regulated by the reactance of individuals to aggregation and anti-aggregation pheromones. There is one major built-in feature in the model affecting the behavior of individuals. The initial beetle population is assumed to be only on the stand edge, whereas later generations disperse within the stand in more random pattern.

2.5.2 Adaptation

Beetles adapt to the population levels in trees by emitting aggregation and anti-aggregation pheromones during the dispersal and thus trying to avoid overpopulation of trees which affects the reproduction success. Re-emergence of beetles is not included.

2.5.3 Objectives

Each beetle generation is grouped into three groups by their expected flying ability (“strong”, “average” and “weak”). These groups of individuals are formed with an objective to avoid overpopulation in trees by affecting their i) dispersal range and ii) reactance to pheromones.

2.5.4 Sensing

Bark beetles sense during the dispersal stage only the pheromones emitted by other beetles attacking a tree. They do not sense tree state variables such as if a tree is uprooted or otherwise weakened. However, the weakening of a tree (death, growth losses by root rot) reduces the tree resistance against beetles and thus when that limit is met earlier compared to intact trees, the beetles start emitting their anti-aggregation pheromones earlier in weakened trees.

269

270 2.5.5 Interaction

271 The interactions between different disturbance agents and bark beetles are indirect and
272 mediated through the tree growth.

273

274 2.5.6 Stochasticity

275 Stochasticity is included in the WINDROT simulation framework in forming the spatial stand
276 structure (ie. locations of trees and stumps, stump diameters not provided by MOTTI). In
277 addition all probabilistic parameters included stochasticity. In the BBDYN model the
278 dispersal of beetles was random along with probabilistic parameters included in other
279 submodels.

280

281 2.5.7 Collectives

282 Individuals belong to three groups by their expected flying ability (“strong”, “average” and
283 “weak”). These groups are further divided into cohorts whom then fly one after another.

284

285 2.5.8 Observation

286 Tree level output includes information of the number of beetles attacking the tree, success of
287 the attack, the number of beetles reproducing and the number of offspring. Other tree level
288 output includes tree state variables and tree level data regarding other disturbance agents (e.g.
289 decay dimensions within stem, critical wind speeds). In stand level output the number of trees
290 killed by bark beetles is collected along with number of trees affected by other disturbance
291 agents (see Honkaniemi et al., 2017a, 2014).

292

293

2.6 Initialization

The simulation for stand and *Heterobasidion* dynamics start from regeneration after clear-cut of the previous tree generation. In WINDROT framework, Hmodel is responsible for creating the spatial structure of the stand within 100m*100m square with 8m buffer (see Honkaniemi et al., 2017b, 2014). Tree and stump locations are random with minimum between-tree distances determined by the user. This creates stochasticity in the initialization of the WINDROT framework. The BBDYN model described in this paper is initialized after stand exposure for wind disturbance at the time t_w after the clear-cut of a neighboring stand on one side of the simulation area including the buffer zone on that side (Honkaniemi et al., 2017a). An initial bark beetle population (pop_{BB}) for that time is given by the user. The clear-cut creates a stand edge adjacent to the simulated stand, which has a warming effect favoring bark beetle reproduction (Peltonen, 1999). This effect in the model is included however only through the first dispersal of initial bark beetle population (pop_{BB}) at the stand edge. After the initialization of BBDYN the framework proceeds at default on simulation steps of one year for a period of 10 years.

2.7 Input data

The user-defined input variable of the BBDYN model is the initial number of bark beetles in the simulation area at t_w (pop_{BB}). We assume that the initial sex ratio of pop_{BB} is 1:1. In BBDYN, only the movement of males is simulated and only males are considered to contribute to the initial attacks and aggregation to overcome the tree resistance. Hence, the initial pop_{BB} is divided by two. Otherwise, the model does not use any data outside from the data that is within the WINDROT framework.

2.8 Submodels

(i) Dispersal

Bark beetles are distributed in two ways into the trees within the stand depending on the simulation step. At t_W , the first simulation step for bark beetle dynamics, the males of the initial bark beetle population ($0.5*pop_{BB}$) are distributed randomly along the stand edge. In the consecutive simulation steps, dispersal of bark beetles from reproduction trees is simulated as described by Fahse and Heurich (2011) using Gaussian Kernel Random Walk (Eq. 1), where the probability for the bark beetle to fly from its origin (0, 0) to location (x, y) is modeled as a function of landing coordinates (x, y), diffusion coefficient D and time for dispersal t_D . As time step by default is one year, $t_D=1$, each bark beetle is given a single random coordinate to fly to.

$$(1) P(x, y, D, t) \sim \exp\left(-\frac{x^2+y^2}{4Dt_D}\right)$$

We divided the bark beetle generation into three groups by their expected flying ability (“strong”, “average” and “weak”), in a similar way that was done in SAMBIA model (Fahse and Heurich, 2011). Each of these groups are further divided into two flight cohorts forming a total of six flight cohorts, as all the bark beetles do not fly at the same time in the nature. Cohorts were flying in order from strongest to weakest (i.e. strong1, strong2, average1, average2, weak1, weak2). The diffusion coefficient D was transformed to correspond meters used in our simulation framework compared to the grid approach by Fahse and Heurich (2011) (Table 1). The values for each of the groups flight ability were 644, 286 and 72 m^2 season⁻¹ for “strong”, “average” and “weak”, respectively.

344 After the first dispersal, the bark beetles are redistributed to suitable host trees (living or one
 345 year time from death at maximum) (e.g. Eriksson et al., 2005; Louis et al., 2016a, 2014)
 346 based on possible i) aggregation or ii) anti-aggregation pheromones from trees in the vicinity.
 347 If such trees do not exist, the bark beetle is moved to a nearest suitable tree ($A_{bark} > 0$). If trees
 348 are not in the vicinity (< 13.5 m), the bark beetle is considered to die due to loss of energy.
 349 The surroundings of the simulated hectare is assumed to continue similar behind the borders
 350 (except the upwind gap) and thus, if the random coordinates of a bark beetle exceed the
 351 simulation area, another bark beetle from the surroundings would replace it with a random
 352 coordinate within the simulation area.

353

354 The limit values for the production of aggregation and anti-aggregation pheromones were
 355 assumed to be related to a tree-specific threshold of resistance (D_{def} , see section 2.2.2
 356 “Colonization and mortality of trees”). We assumed that aggregation pheromones are
 357 produced by the first bark beetles entering the tree and pheromone production changes from
 358 aggregation to anti-aggregation when the tree resistance threshold is achieved (Birgersson,
 359 1989). The first two cohorts of “strong” bark beetles do not react to pheromones (Nêmec et
 360 al., 1993). However, bark beetles from “average” and “weak” flying cohorts react to the
 361 aggregation as they are assumed to have lower body weight and therefore to react more
 362 strongly to aggregation (Nêmec et al., 1993). In addition, only beetles of the group “strong”
 363 are affected by the anti-aggregation pheromones (Schlyter et al., 1989). Individuals from the
 364 same flight cohort were not affected by pheromones produced by the same flight cohort (i.e.
 365 one flight cohort was assumed to fly at the same time and disperse unrelated to each other).
 366 The effective radii of a catchment area around a tree where pheromones are produced were
 367 13.5 and 4.5 m for aggregation (r_{agg}) and anti-aggregation (r_{antagg}), respectively (Fahse and
 368 Heurich, 2011).

369

370 (ii) Colonization and mortality of trees

371

372 Successful attack of bark beetles occurs when the number of bark beetles attacking the tree
 373 overcomes the threshold of the tree resistance (Mulock and Christiansen, 1986; Raffa and
 374 Berryman, 1983). This threshold is related to the tree vigor index ($tvig$) which is the relative
 375 area of annual growth of sapwood area ($tvig = BAI/SA$). The threshold value for tree defense
 376 (N_{def}) is thus tree-specific variable depending on the tree growth (i_{dbh}) and tree diameter (dbh)
 377 (Eq. 2) based on the study by Mulock and Christiansen (1986). Trees where N_{def} is overcome
 378 by the attacking beetles are categorized first “infested” and after reproduction “dead”.

379

$$380 \quad (2) \quad N_{def} = 90 \cdot \exp(0.24 \cdot tvig)$$

381

382 (iii) Reproduction

383 Reproduction occurs in successfully colonized “infested” trees. Reproduction rate and the
 384 number of offspring (D_{fl} , Eq. 3) are based on the density of female bark beetles (D_{fem}) per
 385 100 cm^2 colonizable bark area obtained from Anderbrant et al. (1985) including the intra-
 386 specific larval mortality. We assumed that on average every male, which has successfully
 387 infested a tree, reproduces with two females (Annala, 1971). To produce the overall number
 388 of offspring from one tree (N_{fl}), the density of offspring produced in 100 cm^2 (D_{fl}) is further
 389 multiplied with the colonizable bark area (A_{bark}) (Eq. 4) and assumed to have sex-ratio of 1:1
 390 for next simulation step population.

391

$$392 \quad (3) \quad D_{f1} = D_{fem} \cdot 38.8 \cdot e^{-0.87 \cdot D_{fem}^{0.45}}$$

393

$$(4) N_{f1} = Df1 \cdot A_{bark}$$

To predict the colonizable bark area for reproduction in each tree of the stand (A_{bark}), the bark thickness in tree j (B_{lj}) at different tree heights (l) was modeled based on the data by Vuokila and Väliaho (1980) including 1024 Norway spruce from 128 sample plots in Finland. Data included bark thicknesses from 9 relative tree height ($x=0.01, 0.02, 0.06, 0.10, 0.20, 0.30, 0.50, 0.70, 0.85$).

A linear mixed model (*nls* from *nlme* package) (R Development Core Team, 2015) was fitted for the bark thickness (B_{lj}) as a function of section height within tree (l). The polynomial formulation was based on the Fibonacci series used for stem curve model by Laasasenaho (1982) (Eq. 5). Model parameters, the standard deviation of the random effect of tree j (u_j), and the standard deviation of the random measurement effect (ε_{lj}) are presented in Table 2.

$$(5) B_{lj} = a_1x_j + a_2(dbh \cdot x)_j + a_3x_j^2 + a_4x_j^3 + a_5x_j^5 + a_6x_j^8 + a_7x_j^{13} + u_j + \varepsilon_{lj}$$

$$(6) x = 1 - \frac{l}{h}$$

The main fixed independent variables were relative point of the height (x , Eq. 6) and diameter at breast height (dbh). The first degree depends on the dbh , where tree was the grouping variable j . Autocorrelation within the data (ϕ , Table 2) (measurements within single tree are not independent) was taken into account by first order continuous autocorrelation function (*corCAR1*).

Further, the height within tree for minimum ($B_{min}=2.5$ mm (Grünwald, 1986)) and maximum bark thickness ($B_{max}=no\ limit$ (Grünwald, 1986)) for bark beetle reproduction, l_{Bmin} and l_{Bmax} , were calculated, respectively. The total colonizable bark area was finally calculated as a sum of 10 equal length trapezoid parts of the colonizable bark area (Eq. 7):

$$(7) A_{bark} = \sum_{i=0}^9 \frac{(p(l_{max}+i \cdot (0.1 \cdot h_{Abark})) + p(l_{max}+(i+1) \cdot (0.1 \cdot h_{Abark})))}{2} (0.1 h_{Abark}) \cdot 100$$

Here p is the perimeter at height l , l_i , and l_{i+1} are the heights of the begin and end of the i :th part and $0.1 \cdot h_{Abark}$ is tenth of the height of the colonizable bark area ($0.1 \cdot h_{Abark} = 0.1 \cdot (l_{min} - l_{max}) \cdot h$). The perimeters at each relative height were predicted according to the stem taper curve by Laasasenaho (1982). Finally, the area was transformed to 100 cm^2 to correspond the reproduction rate equation.

(iv) Mortality of bark beetles

Mortality of bark beetles occurs in BBDYN in three different ways; i) intra-specific competition at the larval phase, ii) predation by antagonists and iii) winter mortality. The intra-specific competition is included in the reproduction rate by Anderbrandt et al (1985) in section “Reproduction”.

For the predation effect of antagonists, we used the full submodel for antagonists from SAMBIA (see Fahse and Heurich 2011, section 2.2.5 part 4d and Appendix A for mathematical description), where the submodel for antagonist effects consists of two parts; i) probability for the antagonists to find a colonized tree used for bark beetle reproduction, and ii) survival probability of the larvae under predation. Fahse and Heurich (2011) studied the submodel in detail and presented sensitivity analysis for the submodel parameters. We chose

to use constant values for the sigmoid curve parameters of the probability for antagonists to find an infested tree. These upper and lower limit parameter values were $p_{find}(1)=0.999$ and $p_{find}(0)=0.03$, respectively. If the antagonists would find the colonized tree, then the constant survival probability for the larvae under predation was 0.05. According to Fahse and Heurich (2011), by using this survival probability the risk for outbreak is medium (~ 0.5).

The winter mortality after each simulation step affected the population at the end of the growth season. Winter mortality was parametrized to be 0.4 for this simulation study (Austarå and Midtgaard, 1986; Faccoli, 2002; Poolak, 1975).

2.5 Outline of simulations

The new submodel of BBDYN, colonizable bark area model within the reproduction process, was evaluated in two parts. First, tree level simulations were carried out to analyze the sensitivity of the reproduction to changes in colonizable bark area (A_{bark}). Colonizable bark area was calculated for three individual trees of different diameters at breast height ($dbh=20$, 30 and 40 cm) and tree height ($h=20$, 25 and 30 m) with combinations of different minimum and maximum bark thicknesses ($b_{min}=[2.0, 2.5, 3.0 \text{ mm}]$ and $b_{max}=[4.0, 5.0, \text{no limit mm}]$). Second, the colonizable bark areas from stand level simulations (see below) were evaluated against field data including measured bark areas in attacked trees of various sizes (Weslien and Regnander, 1990) (Table 3).

The simulated stand was set up to represent a typical Norway spruce stand growing on a *Myrtillus* site type (Cajander, 1949) in southern Finland on mineral soil with temperature sum ($tsum$, sum of degrees by which the daily average temperature exceeds $+5 \text{ }^{\circ}\text{C}$) of 1300 d.d.

The site was prepared before planting trees with density of 1800 ha^{-1} , and seedling survival was 90 %. Forest management followed the current management recommendation for Finnish forestry (Äijälä et al., 2014). The rotation length was fixed to 61 years in all scenarios, and the second thinning was set to take place at the age of 44 years at the same time with the final cut of the neighboring stand. This exposed the stand to wind disturbance. The timing of the first commercial thinning depended on the stand basal area and varied between simulated replications and scenarios. This also created variable stand densities and dimensions prior to the second thinning. The default simulation step in the simulations (beyond the wind/bark beetle period) was 5 years, but it adjusts to the timing of forest management operations. The effect of root rot by *Heterobasidion* was simulated using three different root rot risk scenarios used earlier also by Honkaniemi et al. (2017a); low-, medium- and high-risk scenarios (Table 4). These scenarios address both infections mechanisms of the fungi; primary spread via basidiospores and secondary spread through root contacts. The previous stand was clear-cut in the summer-time during active spore production season and all thinnings were winter-time operations with zero spore loads. No control measures were taken to prevent *Heterobasidion* infections.

The wind disturbances were simulated for a 10-year period in simulation steps of one year after the second thinning as described by Honkaniemi et al. (2016). Long-term statistics for the annual probability of the maximum 10-min average wind speed at 10 meters high above ground for Helsinki-Vantaa Airport (Peltola et al., 2010) were used. Maximum winds were assumed to occur when there was no frost in the ground. Subsequent bark beetle dynamics were then simulated in three scenarios (low BB, med BB and high BB) for the initial bark beetle population (pop_{BB}) at the time of the wind exposure ($t_w=44$): 1) 10 000, 2) 25 000 and

3) 40 000 beetles ha⁻¹, respectively. Therefore, altogether 9 different scenarios (3 root rot scenarios * 3 bark beetle scenarios) were simulated in stand scale.

All the disturbance models are mechanistic models with stochastic features such as tree location within the simulated area and wind speed. Therefore, the simulation error should be stabilized. The number of replicated simulations required in the model in stand scale was studied by running the model with various amounts of replications (2–400). Previously, the inclusion of HWIND in the simulation framework increased the required number of replications to 200 (Honkaniemi et al., 2017a). In this study, the simulation error for the number of trees killed by bark beetles was considered sufficiently small (<0.5 tree/ha) with 200 replications in all risk scenarios over the 10-year simulation period and within one year with largest variation in the output. Therefore, 200 replications were used in the subsequent simulations. Annual and 10-year simulation period averages were calculated based on the output of these 200 replications.

We compared the model predictions against field data including wind and bark beetle disturbances (Eriksson et al., 2007, 2005) (Table 3). This data was collected from Southern Finland including 60 windthrow areas (some omitted due to various reasons, see Eriksson et al. 2005, 2007) and corresponds quite well to our simulated stand conditions and environmental conditions for bark beetle dynamics. It includes data of number of wind damaged trees, dead standing trees prior to the wind event (proxy for bark beetle presence), size of the windthrow area, share of attacked windthrown trees, number of trees killed by bark beetles in the adjacent 4 years after the major wind disturbance event as well as the total number of egg galleries in the windthrown trees in those areas in the year after wind disturbance. These were compared against simulation output from WINDROT framework.

Unfortunately, the field data did not include records on root rot nor population levels for the initial bark beetle population.

3 Results

3.1 Model evaluation

3.1.1 Tree level sensitivity analysis

The tree level sensitivity analysis showed that the reproduction of bark beetles (number of offspring from one tree, N_{fl}) in all the three trees was sensitive to the changes in the maximum bark thickness (b_{max}), but not for the minimum bark thickness (b_{min}) (Fig. 2). The effect of maximum bark thickness in N_{fl} increased with increasing tree size. By default there was no limit for the maximum bark thickness for bark beetle reproduction. Reducing the b_{max} to 4.0 mm decreased the reproduction in 40 cm tree 72 870 beetles from the scenario where b_{max} was not limited (Fig. 2). The reduction in 30 cm tree was 45 670 beetles and in 20 cm tree 23 280 beetles. The reduction of the minimum bark thickness b_{min} from parameter value 2.5 mm to 2.0 mm increased the number of offspring from the tree at maximum 330 beetles, and increase of the b_{min} from 2.5 to 3.0 mm decreased the reproduction at maximum by 480 beetles. Respectively, the changes in 30 cm tree were 450 and 630 and in 40 cm tree 580 and 770 beetles. The maximum number of offspring per tree with the default parameter values $b_{min}=2.5$ and $b_{max}=no\ limit$ mm were 26 370, 48 550 and 76 000 from trees with dbh 20, 30 and 40 cm, respectively.

3.1.2 Colonizable bark area on stand level

The colonizable bark areas for bark beetle reproduction (A_{bark}) of infested trees from all scenarios were compared against the results by Weslien and Regnander (1990) (Fig. 3). The simulation output shows that the model's colonizable bark areas with b_{min} of 2.5 mm for bark beetle suitability was in line with the field data (Weslien and Regnander, 1990). Similar patterns are reported in other field studies as well where *I. typographus* beetles occupied almost the whole stems with decrease in density of egg galleries in the last 20% of the relative height (Schlyter and Anderbrant, 1993). The maternal gallery density per BB scenario (average over *Heterobasidion* scenarios) was 755, 895, and 842 m⁻² for low, medium and high BB risk scenarios, respectively.

3.1.3 Stand level output against field data

Stand level output was compared against field data by (Eriksson et al., 2007, 2005). The total number of egg galleries in the wind damaged trees of first year after exposure was in many replicates overestimated compared to the field data in low and medium BB scenarios (Fig. 4A and 4D). The share of bark beetle attacked wind damaged trees out of all wind attacked trees was overestimated slightly by the model in both scenarios (Fig. 4B and 4E). The number of first year wind damaged trees was compared against the number of trees killed by bark beetles in the consecutive four years (Fig. 4C and 4F). The low risk scenario was in line with the field observations with no previous bark beetle damages (Fig. 4C). Both the model output and field data show low levels of spruce mortality. However, the medium BB risk scenario overestimated the spruce mortality when compared against the field data with recent spruce mortality prior to the study period suggesting a higher initial population (Fig. 4F).

3.2 Stand level results

Comparison of all the disturbances together at the stand level showed that the root rot risk level increased both the overall number of infections in the stand and the number of infections where decay had reached the stem (Fig. 5). In all nine scenarios the number of root rot infected trees was significantly higher than the number of wind or bark beetle disturbed trees. In high root rot risk scenario, the overall number of infections reached an asymptote where almost all of the trees in the stand had an infection in some part of their root system.

The stand level results of the nine different scenarios indicate that mortality due to bark beetles occurred only in few simulated replications when the initial bark beetle population *popBB* was low (initially 10 000 beetles ha⁻¹) indicating that the initial population *popBB* was too low to cause any damages (Fig. 6). Therefore, the bark beetle disturbances are not visible at all in Fig. 5 which includes average values over the 200 iterations. Increase in the initial bark beetle population significantly increased the number of trees dying due to bark beetle attack. In both medium and high BB risk scenario (initially 25 000 beetles ha⁻¹ and 40 000 beetles ha⁻¹, respectively) the number of trees killed by the bark beetles continued throughout the simulated 10 year period. The annual maximum number of dead trees due to bark beetles was below 1 tree ha⁻¹ in low BB scenario and below 14 and 40 trees ha⁻¹ in medium and high BB scenarios, respectively. The mean annual mortality rate over the 10 year simulation period was 0.07, 8.97 and 19.04 trees ha⁻¹ in the low, med and high BB scenarios (over the *Heterobasidion* scenarios), respectively.

The wind damages increased with the increasing root rot risk (Fig. 7). Majority of the wind damages occurred during the first year after the stand was exposed for wind in all scenarios

(year 45). This was seen also in the number of wind damaged trees colonized and used for bark beetle reproduction during the first years of the simulation period (Fig. 8). However, trees were damaged by wind throughout the simulation period and those trees were used by bark beetles for reproduction. The number of infested wind damaged trees was below 21 trees per year in low BB risk scenario and the bark beetle population decreased over time with most of the replicates having bark beetle population only on the initial year. The overall share of colonized wind damaged trees out of all bark beetle infested trees over the 10-year simulation period was close to 50 % in all nine scenarios (Fig. 6 and 8). However, in both medium and high BB risk scenarios, the effect of increasing wind damages with increasing root rot incidence actually started to decrease the bark beetle effect as there were less trees to attack and kill for such a large population of bark beetles.

We also compared the tree vigor index (*tvig*) of healthy trees and trees with root rot infection but found no significant difference and therefore no significant differences in the resistance threshold against bark beetles. This was due to the only small decreases in the relative growth due to decay in sapwood in the simulated scenarios. The lowest relative annual growth levels were 0.96, 0.98 and 0.93 in low, medium and high risk scenarios. In addition we didn't find any significant effect of bark beetle caused mortality on subsequent root rot infection rates.

The number of attacking males per tree in the successfully infested trees varied from 56 to 11560 beetles in all of the simulated scenarios. The average numbers of attacks per tree were significantly lower in wind damaged trees compared to standing trees. Average number of males attacking wind damaged trees was 140, 370 and 510 in the low, medium and high BB risk scenarios, respectively. The corresponding numbers for healthy trees were 700, 1350 and 1400 males per tree. However, the wind damaged trees were also smaller and slender in

dimensions and therefore had smaller colonizable bark areas, partly explaining the difference (Fig. A2). Other factors explaining the difference were lower threshold for producing anti-aggregation and the fact that most the trees were wind damaged earlier in the rotation thus leaving them smaller than the healthy trees attacked later during the outbreak.

4 Discussion

The main objective in the development of the BBDYN model described in this study was to simulate interactions between different disturbance agents in Norway spruce stands with the WINDROT framework. The key findings from the model performance analysis were that bark beetle induced mortality of trees occurred only quite infrequently when the initial bark beetle population was low ($< 10\,000$ bark beetles ha^{-1}). Mortality due to bark beetles over 10-year simulation period occurred in medium and high bark beetle risk scenarios. Root rot increased the wind disturbances, which further played a significant role in the bark beetle dynamics as the increasing amount of wind damaged trees increased the number of wind damaged trees colonized by bark beetles. However, the wind damages also reduced the number of living trees and thus decreased the number of living trees colonized by bark beetles especially in the high root rot risk scenario (Fig. 6 & 7).

The key feature of the BBDYN model is the bark beetle dynamics to be tree-size dependent. To our knowledge there are no models incorporating the colonizable bark area for bark beetle reproduction, although many parameter values, such as attacks, number of egg galleries or reproduction rate, are commonly measured from the field as a number per bark area. The bark offers protection and food during the life stages under the bark. Therefore, the bark has to be thick enough to cover an adult bark beetle and provide food during the larval stage. The

inclusion of colonizable bark area and tree vigor index enables the BBDYN to use such field results and further enhance the parametrization of the model in the future. It also creates the possibility to better simulate the interspecific interactions between different bark beetle species. Bark beetles share similar dynamics of reproduction, but different species are often segregated within a tree to different parts of the stem (Grünwald, 1986).

The tree level results showed that the simulated reproduction is sensitive to the changes of the maximum colonizable bark thickness for bark beetle reproduction (Fig. 2). The maximum bark thickness was significant for all trees, whereas minimum bark thickness was not significant for any trees. The colonizable bark area was evaluated against results by Weslien and Regnander (1990). They measured the colonized bark area in pheromone-baited and non-baited trees with different tree height. The colonizable bark areas from stand scale simulation results were well in line with the field data by Weslien and Regnander (1990) (Fig. 3). Weslien and Regnander (1990) had egg galleries from stem base to tree top without any significant vertical gradient, whereas our modelling limited out the tree tops with thinnest bark. The suggestion of minimum bark thickness by Grünwald (1986) is based on the body size of the adults and interspecific competition with other smaller bark beetle species, such as *Pityogenes chalcographus* L. Schlyter and Anderbrant (1993) showed that the gallery density of *I. typographus* started to decrease in the last third of the stem and significantly decreased for the final sixth of the stem. Meanwhile, the gallery density of a competing species *I. duplicatus* (Sahlb.) increased in the top part. Recent study by Grodzki and Gąsienica Fronek (2017) studying infestation rates and reproduction success under several bark thicknesses reported very minor effects on both variables. However, the study was conducted only until 2mm bark thickness and do not therefore offer information whether colonization and reproduction is successful under bark thickness of less than 2mm. These field results and our

sensitivity analysis indicate that even though there is uncertainty on the minimum bark thickness for the *I. typographus* reproduction, the effect of tree tops for the overall reproduction success are small as the bark area contribution is relatively small.

Validation and evaluation of complex models such as the one presented in this manuscript is difficult due to the number of variables and complexity of the system. In the previous manuscripts describing other models of the WINDROT framework (Honkaniemi et al., 2017a, 2017b, 2014), the models have been partially evaluated, meaning that parts of the model output have been evaluated against available field data. We have tried to follow the steps of pattern-oriented modelling (POM) (Grimm and Railsback, 2012) and “evaluation” (Augusiak et al., 2014) while developing this simulation framework. The structure of the individual models as well as the whole framework was evaluated with several iterations and the quality of data was assessed while developing the submodels. In addition, we evaluated some parameters and submodels by following the POM principles (see Table 3).

Comparison of the whole model against field data has been impossible as such data does not exist in large enough extent mainly for two reasons. First, varying forest stand conditions, the stochastic nature of disturbances and the time span for root rot damages (over tree generations) would require a massive amount of field data to cover all of these various conditions and it would also need to span preferably over decades to catch the slow spread of root rot fungi. In this study, we compared the simulation output against interaction data for wind and bark beetles (Eriksson et al., 2007, 2005) to detect if the model can produce patterns observed in the field data. The data is limited to low initial population levels (no record of real population levels in the field data, but recently dead standing trees were used as a proxy for this), but the comparison of the number of egg galleries, share of attacked wind

damaged trees, and spruce mortality by bark beetles suggests that the simulation results are the same order of magnitude when our low BB scenario was compared against stands with no recent dead trees (Fig. 4A-C) and medium BB scenario against stands where Eriksson et al. (2007) detected recently dead trees (Fig. 4D-F). The number of egg galleries after the wind event were slightly higher in our model compared to the field data (Fig. 4A and D) suggesting that it either overestimates the number of egg galleries or that the initial population numbers were higher in our simulations. In both scenarios, the wind damaged trees were colonized as in the field data. However, the field data was lacking many sites with large wind disturbance (Fig. 4B and E). In addition, we calculated all attacked trees whether they were successfully colonized or not. If only successfully colonized trees were calculated, the values were little bit lower, but still in line with the field data (data not shown). Spruce mortality was well in line with the field data in low BB risk scenario (Fig. 4C), but overestimated in medium BB risk scenario (Fig. 4F). This could be an issue of discrepancies in the initial conditions or interpretation of the field data. Recently, the bark beetle monitoring in Finland has shown that the populations vary roughly between the low and medium BB risk scenarios' initial populations (Neuvonen et al., 2017, 2016). In addition, it is important to remember that we used only one scenario for the antagonists whereas Fahse and Heurich (2011) show that the model can be sensitive to the parameters of that submodel. All in all, we consider that the model was able to produce similar patterns observed in the field data. However, we have noted the limits of the field data and further data is needed to cover a more broad range of initial states and interaction scenarios (i.e. different bark beetle populations and intensities of wind damage).

Stand level results showed that there were interaction effects between root and wind disturbance intensity as well as with the subsequent bark beetle damages, although the wind

717 damaged trees were not preferred by any assumptions within the model during the dispersal
718 of the beetles. The beetles only benefitted from the weakened trees through the lowered
719 resistance threshold. In our study the root rot incidence increased the wind disturbance
720 intensity and aided the bark beetle population as well as the beetles were able to reproduce in
721 the wind damaged trees. However, the increasing wind damages also decreased the mortality
722 of standing trees by bark beetles. The interaction may be counterintuitive compared to the
723 common idea on the interaction between wind disturbance and bark beetles (e.g. Komonen et
724 al., 2011). However, this effect is most likely due to the small size of our simulation area. The
725 wind damages decreased the number of trees in the stand especially in the high root rot risk
726 scenario and less living trees were left in the stand to be attacked by bark beetles. A negative
727 correlation was seen especially in the medium and high BB risk scenario with the increasing
728 root rot and wind disturbance incidence (Fig. 6 & 7). Simulations over larger area or
729 landscape level could show better the interaction between wind damages and subsequent bark
730 beetle damages. In larger scale, the bark beetle population would have also more space to
731 disperse. Landscape level analysis would also reveal patterns of stand replacing disturbances
732 (e.g. expansion of disturbed areas in time), which could be further used for model evaluation
733 by comparing the model results against remote sensing data. In all scenarios, wind damaged
734 trees increased the bark beetle population and the intensity of wind damages prolonged the
735 bark beetle population suppression (Fig. 6 & 7). Eriksson et al. (2007, 2005) showed that the
736 number of wind damaged trees increased the mortality due to bark beetles. They also found
737 that the diameter of the wind damaged trees was the most significant variable explaining the
738 mortality. Therefore, it is crucial to run large scale simulations with BBDYN and WINDROT
739 framework in the future to study and analyze the effect of timing of the exposure of the stand
740 to winds and thus the effect of stand mean diameter on wind damages and subsequent bark
741 beetle induced mortality.

742

743 Direct interaction effect between the root rot and bark beetle damages (i.e. root decay
744 weakening the tree significantly and lowering the tree resistance threshold against bark beetle
745 attack) was not significant in our simulations. The growth reduction due to the root rot was
746 low in all scenarios and therefore there were only minor changes in the tree resistance
747 threshold against bark beetles. However, the intensity of decay rate clearly increases the stand
748 vulnerability to wind damages (Honkaniemi et al., 2017a; Oliva et al., 2008; Whitney et al.,
749 2002) and therefore increases the risk for subsequent bark beetle attacks. We didn't notice
750 any significant effect on the root rot infection rates after wind and bark beetle disturbances
751 (Fig. 5) where the dead trees infected by the root rot would have speeded up the disease
752 dynamics (threefold increase in the fungal spread rate in the root system of dead trees and
753 stumps compared to living trees). It is most likely that the effects are not visible over short
754 time span and would need either longer rotation length or simulation of an adjacent tree
755 generation.

756

757 When the effect of all three disturbances are compared together in terms of affected stem
758 numbers (Fig. 5), it is clear that the root rot affects far more trees than even wind and bark
759 beetle disturbed trees combined. However, it is important to keep in mind that the root rot
760 causes mortality on Norway spruce only in few cases whereas all wind and bark beetle
761 disturbed trees are dying affecting the stand dynamics more dramatically. The effect of the
762 pathogen infections are seen over a long period and would accumulate over tree generations.

763

764 Weslien et al. (1989) found that a limit value for bark beetle induced tree mortality would be
765 around 15 000 beetles per baiting trap group corresponding loosely to our initial bark beetle
766 population values. In their study, traps were placed 300m from each other and therefore

“catchment” area for a trap group would have been roughly 7.1 ha (radius of 150 m). Assuming that capture rate of traps would be 10% (Wermelinger, 2004) of the whole population within this area, the population per hectare with 15 000 beetle catch would have been 8 800 beetles. In the stand level simulations, there were only few dead trees when the initial bark beetle population was low ($pop_{BB}=10\ 000$) and even the increasing wind damage intensity did not increase the mortality rate of trees by bark beetles. However, in medium and high bark beetle risk scenarios ($pop_{BB}=25\ 000$ and $40\ 000$, respectively) the bark beetle related mortality was higher and mortality rates increased suggesting that the simulation study results were in line with the field data (Weslien et al., 1989). In addition, the number of attacking males per tree as well as the number of offspring produced per tree was well in line with field studies (Eriksson et al., 2005; Gonzalez et al., 1996; Louis et al., 2014).

The dispersal submodel was adopted from SAMBIA with parametrization. In addition, due to the rather small simulation area in WINDROT framework for bark beetle dynamics (one hectare with 8 m buffer zone), the dispersal flight pattern and distance were not considered to affect results significantly. During the dispersal in the model, 95 % of the groups “strong”, “average” and “weak” are distributed over areas of 2.5, 1.1 and 0.3 ha, respectively. Due to this and the assumption that a random coordinates within the simulation area are assigned for every single bark beetle leaving the area (i.e. mimicking the spread from the surrounding areas), the dispersal in BBDYN can be considered almost random. Franklin and Grégoire (1999) reported that only 1 % of the emerging beetles disperse within one hectare area around the reproduction tree in a pheromone-free environment. It is significantly less than the dispersal areas in BBDYN, where almost all of the dispersing beetles stay within few hectares. However, we didn’t consider this an issue due to the small simulation area. In case

791 WINDROT is used in landscape level, the bark beetle dispersal should be considered in more
792 detail.

793

794 Redistribution of the bark beetles is regulated with the production of aggregation and anti-
795 aggregation pheromones. That occurs in much smaller scale than the initial flight dispersal
796 and was thus given more weight in the development of BBDYN. We also modified the
797 response of different flight cohorts to pheromones from SAMBIA. In BBDYN “strong” bark
798 beetles are not considered to respond to aggregation at all although the very first of them start
799 to produce them. Only “average” and “weak” flight cohorts with lower body weight and fat
800 content respond to the aggregation pheromones. On the other hand, only “strong” beetles
801 respond to the repelling anti-aggregation pheromones. The aggregation pheromones are
802 produced until the tree resistance threshold is achieved and from there on the pheromone
803 production changes to anti-aggregation. However, due to the different responses to the
804 pheromones, the threshold may be exceeded greatly and the overpopulation of the tree may
805 lead to a reduced reproduction rate. For colonized trees the overpopulation happened in our
806 simulations for each tree, but only in few cases in that extent that it would have affected the
807 reproduction significantly. It is important to note that tree resistance threshold and density for
808 overpopulation do not go hand in hand. Tree resistance threshold may be low especially in
809 weakened trees, but the optimal reproduction is usually reached with higher densities.

810

811 There are two major points of concern in the BBDYN model. First, we don’t take into
812 account sister broods, re-emerging of the adults due to the density of attacks or the effects of
813 the density of the offspring to future reproduction, flight abilities or pheromone production
814 (Anderbrant et al., 1985). We considered the effect of these minor to the dynamics in the
815 model, but the inclusion of them should be considered especially in the landscape level

simulations as all of them affect the dispersal and further the reproduction. Second limitation is the lack of phenology in the model which has an effect on the bark beetle development and on the number of bark beetle generations per year. Climate data and the bark beetle phenology were excluded from the BBDYN during the development as the temporal resolution of the WINDROT framework is in minimum one year and dynamics within one year are not simulated in detail. In addition, other models of the framework do not take into account climate data yet. However, it is essential in the future to include climate response into all models incorporated in the framework. Stand microclimate should perhaps also be taken into account as it would direct the bark beetle dispersal within stand from random to favor more the stand edges (Peltonen, 1999).

5 Conclusions

The BBDYN mechanistic model incorporated in the WINDROT simulation framework provides novel approach to assess the interactions of three most significant disturbance agents of Norway spruce and to analyze the effects of the risks posed by these disturbances to the forest management. The flexible structure of the model and especially the use of the new bark area model enables the BBDYN to be used for other bark beetle species in the future with parameterization. Model was able to produce similar patterns as the limited field data available for model evaluation. Although *Ips typographus* is one of best studied bark beetle species, the study revealed that further experimental research is still needed. Especially data is needed related to the potential interactions between weakened trees and bark beetles during the dispersal stage. Also the tree resistance and the underlying mechanisms of interactions between disturbance agents need to be studied more profoundly in the future together with field data and simulation modeling.

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842

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1083 Figure 1.

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1085 Figure 2.

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1087 Figure 3.

Figure 4.

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1095 Figure 7.

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1097 Figure 8.

Fig. 1. Conceptual diagram of BBDYN model structure during one simulation step (*i.e.* default of one year) and the linkage with data from other models of the WINDROT framework. (two columns wide)

Fig. 2. Sensitivity of the number of bark beetle offspring from a single tree to minimum (b_{min}) and maximum bark thickness (b_{max}) in three different trees. Left column graphs represent changes in b_{min} with constant b_{max} and right column graphs represent changes in b_{max} with constant b_{min} . (!1.5 columns wide!)

Fig. 3. The colonizable bark areas of infested trees from our simulations as a function of tree diameter at breast height. The line represents the model by Weslien and Regnander (1990) based on field data. (!one column wide!)

Fig 4. Comparison of stand level simulation output against field data by Eriksson et al. (2005, 2007). Figures on same rows are for same initial states: Figures A-C include low BB risk scenario output and data from Eriksson et al. with no previous bark beetle mortality in area and figures D-F include medium BB risk scenario output and data from Eriksson et al. with previous bark beetle mortality in area. Every figure in columns present same comparison of output: relation between the number of first year wind damaged trees and (A and D) total number of egg galleries in them; (B and E) share of attacked wind damaged trees out of all wind damaged trees; and (C and F) total number of trees killed by bark beetles during 4 years after the main wind disturbance event. (!two columns wide!)

Fig. 5. Number of living trees, number of *Heterobasidion* infected trees, number of trees with decay in stem, number of trees disturbed by wind (broken or fallen) and number of trees

1123 killed by bark beetles. (!1.5columns wide!, colours for the e-version, B&W version provided
 1124 for print)

1125

1126 **Fig. 6.** The cumulative number of trees killed by bark beetles over the 10-year simulation
 1127 period in the 200 replications in nine different bark beetle – root rot scenarios. In the
 1128 boxplots, median value is the line within the box and the box represents 25th and 75th
 1129 percentiles. Whisker length is 1.5*box length and values beyond that are presented with open
 1130 dots. (!1.5columns wide!)

1131

1132 **Fig. 7.** The cumulative number of wind damaged trees over the 10-year simulation period in
 1133 the 200 replications in nine different bark beetle – root rot scenarios. Note the different scale
 1134 on y-axis compared to the Fig. 6 & 8. In the boxplots, median value is the line within the box
 1135 and the box represents 25th and 75th percentiles. Whisker length is 1.5*box length and values
 1136 beyond that are presented with open dots. (!1.5columns wide!)

1137

1138 **Fig. 8.** The cumulative number of wind damaged trees successfully colonized by bark beetles
 1139 over the 10-year simulation period in the 200 replications in nine different bark beetle – root
 1140 rot scenarios. In the boxplots, median value is the line within the box and the box represents
 1141 25th and 75th percentiles. Whisker length is 1.5*box length and values beyond that are
 1142 presented with open dots. (!1.5columns wide)

1143

1144

Abbreviation	Explanation	Value	Unit	Source
User defined input variables				
t_W	Starting time of the wind damage and bark beetle simulations		years	
pop_{BB}	Initial bark beetle population		ha ⁻¹	
Model parameters				
Dispersal				
D	Diffusion coefficient	644, 286 and 72 (strong, average and weak, respectively)	m ² season ⁻¹	Transformed from Fahse and Heurich (2011)
t_D	Time of dispersal	1	season	
r_{agg}	Aggregation catchment area radius	13.5	m	Transformed from Fahse and Heurich (2011)
R_{antagg}	Anti-aggregation catchment area radius	4.5	m	Transformed from Fahse and Heurich (2011)
Reproduction				
B_{min}	Minimum bark thickness	2.5	mm	Grünwald (1986)

	for bark beetles			
B_{max}	Maximum bark thickness	-	mm	Grünwald (1986)
	for bark beetles			
Mortality of bark beetles				
$p_{find}(1)$	Probability for the trees to be found by antagonists when all trees in the vicinity ($dist < r_{pfind}$) are infested or dead due to bark beetles (< 1 year)	0.999		Fahse and Heurich (2011)
$p_{find}(0)$	As above, but when no infested trees or dead trees in the vicinity	0.03		Fahse and Heurich (2011)
r_{pfind}	Effective radius for the antagonists	28.2	m	Transformed from Fahse and Heurich (2011)
$p_{survival}$	Survival probability for bark beetles in a tree found by antagonists	0.05		Fahse and Heurich (2011)

Model variables

Colonization

N_{def}	Tree resistance threshold	tree ⁻¹
$tvig$	Tree vigor index	%
BA_i	Basal area of the latest	cm ²

	annual growth	
SA	Sapwood area	cm^2
i_{dbh}	Annual growth at dbh	cm
dbh	Tree diameter at breast height	cm
Reproduction		
D_{fl}	Density of offspring	100 cm^{-2}
D_{male}	Density of males in tree	100 cm^{-2}
D_{fem}	Density of females in tree $2 * D_{male}$	100 cm^{-2}
N_{male}	Number of males per tree	tree^{-1}
N_{fem}	Number of females per tree	tree^{-1}
N_{fl}	Number of offspring	tree^{-1}
A_{bark}	Colonizable bark area	100 cm^2
B	Bark thickness	mm
x	Relative tree height	
h	Tree height	m
l	Height within tree	m
l_{Bmin}	Height at B_{min}	m
l_{Bmax}	Height at B_{max}	m
h_{Abark}	Colonizable bark area length	m

1145 **Table 1.** Model parameters and variables, their abbreviations and explanations as well as
1146 literature sources for parameter value.

1147

Parameter	Value	Std. error
a_1	19.98	0.84
a_2	0.19	0.01
a_3	-40.70	5.47
a_4	13.17	10.04
a_5	41.37	9.85
a_6	-54.48	6.04
a_7	26.91	1.61
u_j	0.88 mm	
ε_{lj}	1.08 mm	
φ	0.99	

1148 **Table 2.** Parameter values for the bark taper curve.

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Parameter or submodel to be calibrated	Pattern used	Field data source	Scale	Major observations
Minimum and maximum bark thickness for bark beetles (b_{min} and b_{max})	Sensitivity to parameter changes		Tree	Model sensitive to maximum bark thickness (Fig. 2)
Reproduction	Colonizable bark area	Weslien and Regnander (1990)	Tree	Colonizable bark area with $b_{min}=2.5$ mm matches the field data (Fig. 3)
Reproduction	Number of egg galleries	Eriksson et al. (2005,2007)	Stand	Number of egg galleries slightly overestimated, but could be due to initial population (Fig. 4A, 4D)
Colonization and mortality of trees	Capability to attack wind damaged trees	Eriksson et al. (2005,2007)	Stand	Wind damaged trees colonized with similar rate as in field data (Fig. 4B, 4E)
Colonization and mortality of trees	Norway spruce mortality during 4 years after major wind event	Eriksson et al. (2005,2007)	Stand	Low risk scenario predicts well the spruce mortality, but medium risk scenario overestimates (Fig. 4C, 4F)
Initial bark beetle population level (input value, pop_{BB})	Outbreak capability/spruce mortality	Weslien et al (1989)	Stand	Spruce mortality due to bark beetles occurs only above the threshold of 15 000 beetles per trap as suggested by field data (Fig. 6)

Table 3. Model evaluation following the principles of pattern-oriented modelling and listing the used patterns as well as the data sources and the operational scale

1153

Variable	Value		
	<i>Low</i>	<i>Medium</i>	<i>High</i>
Number of previous generation stumps (N_{stump} , ha ⁻¹)	590	590	590
Spore density (D_{spore} , m ⁻² hr ⁻¹)	200	400	750
Number of infected previous generation stumps ($N_{infstump}$, ha ⁻¹)	0	118 (20 %)	295 (50 %)
Mean diameter of previous generation stumps ($d_{prestump}$, cm)	37	37	37
Share of <i>Heterobasidion parviporum</i> infections on previous generation stumps (P_{Hp})	0.9	0.9	0.9
Minimum distance between planted trees ($dist_{min}$, m)	1.0	1.0	1.0

1154 **Table 3.** Hmodel inputs with different root rot risk scenarios.

1155

APPENDIX 1.

1 General description of the models in WINDROT framework

1.1 MOTTI

The stand-level decision support system MOTTI (Hynynen et al., 2015, 2014; Salminen et al., 2005) is responsible for the host tree and stand dynamics in the WINDROT simulation framework. MOTTI simulates tree growth and stand dynamics in even-aged stands taking into account forest management operations during the rotation as well as the environmental conditions such as temperature sum, elevation or distance to sea. Climate is not included in the model. MOTTI divides the stand dynamics into two stages; young and old stand. First, the young stand dynamics from regeneration to dominant height of 8m are simulated with stand-level variables. Tree height and diameter are based on distribution models providing a link to the individual-tree-level models applied for the old stand (Siipilehto et al., 2014). The old stand models are spatially implicit simulating the stand development based on sample trees each representing a certain number of trees within one hectare (Hynynen et al., 2014).

The main assumption in WINDROT simulation framework is that every simulation starts from bare ground after a clearcut of a previous tree generation. Simulations are run for a one full rotation length defined by the user. MOTTI inputs include stand characteristics such as location, soil and site type as well as description of forest management operations. These forest management regime options include the intensity, number and timing of thinnings as well as the rotation length. In addition, potential soil preparation prior to regeneration can be defined as well as the type of regeneration (natural vs planting).

1.2 Hmodel

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1186 Hmodel (Honkaniemi et al., 2017b, 2014) is a mechanistic model with stochastic features to
 1187 simulate the dynamics of root and butt rot causing fungal agent *Heterobasidion* species.
 1188 Creating the spatial layout for WINDROT framework is part of Hmodel as MOTTI is spatially
 1189 implicit. Hmodel consists of several submodels each responsible for one significant part of
 1190 the fungal dynamics (e.g. spore infection, secondary spread). The primary infection process
 1191 is a function of stump surface area, the spore density landing on the stump surface and the
 1192 survival probabilities of heterokaryotic mycelia (two homokaryotic spores paired together
 1193 forming a heterokaryotic structure) in stumps. If the mycelia survive and colonize a stump,
 1194 the secondary spread will occur through the root system (roots simulated as a circle until
 1195 root diameter of 2mm). Probability matrix and the overlap area between root systems of
 1196 two trees or tree and stump are used to determine whether the fungus can infect a new
 1197 host. If a secondary infection occurs, the mycelia will grow towards the stem base of the
 1198 newly infected host tree with a given growth rate.

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1200 The fungus enters the host tree stem base at the border of heartwood and sapwood. Once
 1201 the fungus enters the stem base, it starts to decay the wood into all directions. However,
 1202 the tree defence mechanisms decrease the fungal growth rates, which are also dependent
 1203 on the tracheid size (ie. growth is mediated by the number of cell walls that need to be
 1204 degraded). Decay will progress upwards in the stem right after it enters the stem base, but
 1205 will proceed to other parts of the root system only after 50% of the heartwood area in the
 1206 stem base is decayed. Growth losses due to the disease are a function of the ratio between
 1207 decayed sapwood area and healthy sapwood area. Disease causes mortality if the decay
 1208 cover the whole cross-sectional area at stem base or if the decay area covered the cross-
 1209 sectional area in 85% of the main roots at the root collar. Fungal survival in the degrading
 1210 stump roots and roots of dead trees is a function of the diminishing amount of acid
 1211 hydrolysable components (e.g. cellulose, hemicellulose and lignin).

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The root rot also affects the tree mechanical stability against wind in two ways (Honkaniemi et al., 2017a). First, the decay column within the stem (decay height and width at the stem base based on the decay progress at time t) decreases the modulus of rupture of the stem. The decayed part is considered to offer no supportive strength and therefore the stem is considered as a hollow cylinder with only the outer rim of healthy wood offering mechanical stability for the tree. Second effect of root rot is in the root system, where the tree roots decrease their mechanical stability due to decay. The decay is assumed to proceed from the cross-sectional root centre outwards and if the cross-sectional area of healthy root at root diameter rd is less than the minimum cross sectional area offering mechanical strength against wind in a healthy tree, the root is considered to fail at that rd and reduce therefore the root-soil plate weight and diameter. This further decreases the tree stability against uprooting.

1.3 HWIND

HWIND (Peltola et al., 1999) is a mechanistic model to simulate wind disturbance effects on trees. It calculates the effect of static wind load on trees outputting critical wind speeds for each tree of the stand. HWIND predicts the critical wind speeds (given at a height of 10m at the edge of an upwind gap) for uprooting and stem breakage based on tree dimensions and stand characteristics. The tree dimensions include tree height and diameter at breast height as well as rooting depth, root-soil plate weight and modulus of rupture for tree species. HWIND can also include the effect of snow loading and combine that with wind disturbance. Critical wind speeds can be compared against local wind data and used to predict the wind disturbance.

2 Spatial layout of WINDROT framework

Disturbance dynamics are highly dependent on the stand spatial structure. Especially *Heterobasidion* dynamics depend on the tree locations due to the short distance secondary spread. As mentioned above, MOTTI is spatially implicit and therefore Hmodel was designed to include a module for setting up a spatially explicit stand structure (Honkaniemi et al., 2017b, 2014). In this module, the tree and stump locations are created randomly with a minimum distances specified for young trees, adult trees as well as for previous generation stumps. All of them are located within the 1 hectare (100m x 100m rectangle) stand (Fig. A1). Stand is surrounded by a buffer zone of 8 m with similar stand characteristics and forest management.

At the time of the wind exposure (t_w), a neighboring stand is cut from one of the bordering sides of the simulated area forming an upwind gap (Fig. A1). This gap is assumed to be a length of 10 times the height of the tallest tree in the stand as required by HWIND (Peltola et al., 1999).

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1258 **Fig. A1.** Spatial layout of the simulation. Simulated area is a size of 1 hectare with a buffer
 1259 zone of 8 m around it. This buffer zone is similar to the simulated stand and treated with
 1260 same forest management regime with the exception of one bordering side which at the
 1261 time of wind exposure t_w is cut down along with the neighboring stand forming a large
 1262 upwind gap required by HWIND.

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3 Stem form and wind damages

Wind damaged trees in our simulations tended to be slender as they are more prone to wind effects (see also Honkaniemi et al. 2017a). The *height/dbh* ratio of all the simulated trees was higher especially for wind fallen trees compared to healthy trees. This affected the colonizable bark area and further the number of attacking beetles as the threshold for emitting anti-aggregation pheromones was also lower. Even though healthy trees are attacked later in the simulation period and could thus be larger than the wind damaged trees falling or breaking mostly during the first years of the simulation, the similar pattern can be seen from the Fig. A2 with trees of only one year.

Fig. A2. Height/dbh ratio of all simulated trees under bark beetle attack against the number of attacking beetles in them during the whole simulation period or during one year. Trees are further classified by their wind damage status.

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