



Master Thesis

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Competition and facilitation in an individual-based model of forest dynamics for Norway spruce

by

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Osweiler, 29 February 2020

Science pledge

By my signature below, I certify that my thesis is entirely the result of my own work. I have cited all sources I have used in my thesis and I have always indicated their origin.

Oswailer, 29 February 2020

Place, Date

Signature

Preface

After achieving a degree in geography at the university of Bonn, I wanted to further specialize in the field of data collection, visualization and processing. Therefore, I chose to pursue this master's degree in geoinformatics. During the studies my interests grew towards modelling and applying these methods and technologies in an ecological context, especially in the context of trees and forests, which I already knew quite well from my previous studies in geography and the corresponding diploma thesis. These were the main reasons, why I applied to work on the subject proposed by Prof. Dr. Wallentin on expanding on her TREELIM model.

As in most scientific work, changes have been made through the development of this new model. At the beginning, it was planned to compare the expanded model to the TREELIM model using the same, real world, observations. Interestingly, the resulting model and the necessary input data, led to the real-world base data not being detailed enough. Furthermore, simulation runs proved to be time consuming due to the complexity of the model. In a wider perspective this seems to become more and more apparent, with models becoming more and more complex, but the input data, at least for ecological questions, scarcer and scarcer.

All of this resulted in the work you are about to read. I think, even though this model is far from perfect, it gives an ideal base to expand and test different concepts for different species under changing conditions. I hope this work is of a sufficient relevance to qualify for a publication in a scientific journal. Ecological Modelling seems to be an obvious choice. The journal focuses on research of ecological processes and the use of models in the study of these processes. And some of the key papers that this work relates to were published in the journal.

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Manuscript: Competition and facilitation in an individual-based model of forest dynamics for Norway spruce

1. Abstract

Individual-based models (IBM) offer an approach to scaling from the individual to higher level organisational units and have been widely used to model forest ecosystems. The forest IBM presented in this paper is a neighbourhood model of spatial and temporal dynamics within a subalpine spruce forest. The simulation of tree interactions within the model is based on the concept of the zone of influence. The model attempts to improve the representation of competition by the introduction of 3-dimensional tree crowns. Moreover, it is expanded to include a basic concept of facilitation and the presence of coarse woody debris (CWD) as a control of recruitment. The model is tested by analysing the effects of the submodels describing facilitation and CWD on long term temporal and spatial dynamics of tree populations. Further analyses relate to the effects of elevation on the tree population, the character of the initial tree population and the type of symmetry in competition on model results. Facilitation clearly affects population size and structure, but CWD seems to have no effect on tree populations. Comparing numbers of trees/ha between simulations of tree populations at 1400 m, 1600 m, and 1800 m a.s.l. numbers of saplings and adult trees strongly decrease with higher elevation. Modelling symmetric and asymmetric competition, numbers of trees/ha slowly increase for about 200 model cycles indifferent to the type of symmetry, but tree numbers settle to a higher mean under symmetric competition for all life stage classes except for seedlings.

Keywords: Individual-based model, interaction neighbourhood, symmetric and asymmetric competition, facilitation, Norway spruce

2. Introduction

Bottom-up approaches in modelling ecosystems allow for the simulation of population dynamics that emerge from processes at the individual level. Individual-based models (IBMs) offer an approach to scaling from the individual to higher level organisational units (Huston et al. 1988, Railsback 2001) and are closely related to the concept of pattern-oriented modelling (Grimm 1994, Grimm et al. 1996). IBMs have been widely used to model forest ecosystems (Pacala et al. 1996, Berger and Hildenbrandt 2000, Caplat et al. 2008, Wallentin et al. 2008, Seidl et al. 2012). A key component of these models has to be the simulation of competition. As competition is assumed to be a primary factor in determining plant performance (Stoll and Weiner 2000), it can be expected to be a central driver in the establishment of community structure and the dynamics of plant communities. Various indices have been developed to quantify competition between trees. While distance-independent measures of competition describe competition based on stand variables such as basal area (e.g. Peltoniemi and Mäkipää 2011), distance-dependent or spatially explicit measures of competition include distances between trees to determine the intensity of competition (Larocque et al. 2013). To identify competing trees and quantify competition different approaches have been proposed, that include indices weighing distances and size of competitors in relation to a subject tree, the delimitation of the growing space available for each individual or tessellation of space, and the definition of zones of influence (ZOIs) around trees and the description of overlapping areas between these zones (Biging and Dobbertin 1992, Larocque et al. 2013). Emphasising the distance between individuals as an important factor in the quantification of competition has led to a concentration on the tree neighbourhood as

the spatial unit on which competition between plants should be analysed (Berger and Hildenbrandt 2000, Stoll and Weiner 2000).

An important aspect in exploring plant competition is the concept of symmetry and asymmetry of competition (Weiner 1990), that is closely linked to the distinction between above- and belowground competition. Aboveground competition, inherently competition for light, is assumed to be asymmetric and favouring taller individuals disproportionately while belowground competition for nutrients and water seems to be symmetric (Weiner 1986, Weiner and Thomas 1986). However, it has been stressed that plants may be able to reduce the degree of asymmetry in competition through plasticity (Stoll and Weiner 2000). Also, the type of competition may be variable in space and time as asymmetric competition could be more typical on fertile sites where light is the competed resource while symmetric competition could prevail on poor sites and in unfavourable years (Pretzsch and Biber 2010).

It has long been established that interactions between plants are not exclusively competitive but may as well be beneficial and that positive and negative interactions occur simultaneously within plant communities (Callaway and Walker 1997). The importance of facilitation increases along gradients of environmental stress (Maestre et al. 2003, García-Cervigón et al. 2013). In alpine environments facilitation becomes more prominent with increasing elevation (Callaway 1998, Choler et al. 2001, Callaway et al. 2002). In addition to spatial gradients in the outcome of plant interactions, facilitation between plants is similarly not static in time (Kikvidze et al. 2006) and the outcome of an interaction may be subject to ontogenetic shifts (Miriti 2006, Roux et al. 2013).

As models of plant communities are usually still confined to modelling competitive interactions and mainly focus on competition for light (but see Lin et al. 2012), Berger et al. (2008) urge for the inclusion of facilitation and belowground competition.

When focusing on subalpine environments an important factor in the regeneration of Norway spruce forests seems to be the presence of decaying wood. While dense cover of the ground especially by grasses (Hunziker and Brang 2005, Kupferschmid and Bugmann 2005, Dovčiak et al. 2008) or shrubs like *Vaccinium myrtillus* (Jäderlund et al. 1997, Dovčiak et al. 2008) constitutes adverse conditions for the early establishment of Norway spruce, coarse woody debris (CWD) creates particularly favourable microhabitats (Hofgaard 1993a, b, c, Zielonka and Niklasson 2001, Motta et al. 2006, Zielonka 2006, Svoboda et al. 2010, Bače et al. 2011). As the share of seedlings emerging on CWD increases with elevation (Vorčák et al. 2006), it is assumed that the relevance of CWD as a seedbed is particularly prominent in subalpine environments.

The presented model is an individual-based neighbourhood model of Norway spruce in subalpine environments. The model simulates intra-specific interactions based on the concept of overlapping ZOIs (Biging and Dobbertin 1992, Berger et al. 2008, Larocque et al. 2013) but extends this concept by describing the intensity of competitive interactions based on 3-dimensional tree crowns. The model explicitly includes the simulation of intra-specific, facilitative interactions.

3. Materials and Methods

The model is described in detail in an ODD protocol (Overview, Designs concepts, Details) (Grimm et al. 2006, Grimm et al. 2010) that is available as supplementary material to this paper. In this section the model description is limited to the main model concepts, key elements of the model's structure, and entities.

The model was implemented using the GAMA platform (Taillandier et al. 2019), that was developed as a tool for building spatially explicit, individual-based models and allows for the integration of spatial data, e.g. GIS-data.

The model's open structure allows for the addition of further submodels to simulate additional processes and the integration of a range of spatial data. In its current version the model offers the option to load a digital elevation model to simulate population dynamics on sloped terrain. Further raster-based data, e.g. on land use, slope or aspect, can easily be integrated into the model to simulate their effect on stand dynamics.

The aim of the presented model is to simulate spatial and temporal dynamics of monospecific spruce stands in the subalpine regions of the European Alps as the result of intraspecific interactions. Parameters of core ecological processes represented in the model are adopted from empirical studies on Norway spruce in subalpine environments. In its current version the model simulates either symmetric or asymmetric, aboveground competition, it includes submodels to implement facilitation and CWD, and it incorporates the influence of elevation on key ecological processes. The model evolves the concept of the ZOI to delimit the interaction neighbourhood and quantify competition to a 3-dimensional representation of the tree crown.

3.1. Entities, state variables, and scales

The size of the model world is 1 ha and time is modelled in discrete, annual steps. The main entity of the model is the species *tree*. Tree agents are generally represented via their crowns and ZOIs. Individual interaction neighbourhoods include those trees that overlap the subject tree's ZOI with their own ZOIs. For competitive interactions the intensity of competition is determined based on a 3-dimensional representation of the tree crown. Tree crowns are mathematically represented as cylindrical bodies based on the height and the width of their crown. To quantify competition volumes of overlapping parts of tree crowns are determined instead of overlapping areas in the classical ZOI approach. This approach presents two advantages: (1) differences in the size of competing trees are better represented in a 3-dimensional than a 2-dimensional tree crown and (2) the influence of a sloped terrain on size relations between trees is directly represented in the overlapping crown volume. Tree agents are defined by the following state variables: unique identifier, location, elevation, age, and height. Life stages are distinguished by age and size thresholds as seedlings, saplings, and adults.

The second entity of the model is the species *CWD*. Agents of the species are created as successors of tree agents that exceed a certain size threshold. CWD agents represent logs of fallen trees that are a source of CWD on the forest floor. Shape and size of CWD agents are an approximation of fallen logs. CWD agents are defined by the state variables unique identifier, location (centre of the log base), the time since the creation of the agent and three attributes that describe the position and the size of the agent.

3.2. Process overview and scheduling

Within each model cycle three core ecological processes affect the tree population: growth, reproduction, and death. Every tree completes the growth process, mature trees produce seeds and disperse them, and an individual probability of death is calculated for each tree. These processes are influenced to a certain degree by intraspecific interactions as an expression of the individual neighbourhood configuration of each tree. Therefore, the interaction neighbourhood and if applicable the intensity of competition or the occurrence of facilitation are updated during each model cycle. Seeds germinate within the cycle of dispersal and new tree agents are created after successful germination.

The model calls agents in the order of their creation. Attributes are updated synchronously after the execution of each submodel.

3.3. Submodels

3.3.1. Mast year

The seed crop of Norway spruce shows distinct differences between normal seed years and mast years. The occurrence of mast years is a highly synchronised phenomenon on local as well as regional scales (Ascoli et al. 2017, Hackett-Pain et al. 2019). Through the creation of large cohorts of even aged trees, the occurrence of mast years substantially influences the population structure of high elevation spruce forests (Hofgaard 1993b, Hanssen 2003, Zielonka 2006). Within the model the occurrence of mast years is described as a probability (Eq. 1), that increases with the number of years since the last mast year. The maximum period between two consecutive mast years is 15 years.

$$mast_year_{prob} = mast_period_{max} * \left((1 - e^{(-0.035 * mast_period_{current})}) \right)^3 \quad (1)$$

where

$$mast_period_{max} = 15$$

$$mast_period_{current} = \text{number of years since the last mast year}$$

3.3.2. Neighbourhood and competition

Individual interaction neighbourhoods include those trees that overlap the subject tree's ZOI with their own ZOIs. For competitive interactions the intensity of competition is determined based on a 3-dimensional representation of the tree crown. Tree crowns are mathematically represented as cylindrical bodies based on the height and the width of their crown. To quantify competition volumes of overlapping parts of tree crowns are determined instead of overlapping areas in the classical ZOI approach. This approach offers two advantages: (1) differences in the size of competing trees become an inherent characteristic of the model (2) the influence of a sloped terrain on relative size relations between trees is directly represented in the overlapping crown volume.

The intensity of competitive interactions is described by $comp$, $comp_{crown}$, and $comp_{mort}$ for height growth, growth of the crown diameter and mortality, respectively. The competition factors are an expression of the total volume of intersections between the ZOI of a subject tree and the ZOIs of its neighbours in relation to the subject tree's ZOI volume (Eq. 2 - 4).

$$comp = 1 - \frac{intersection_{total}}{ZOI_{volume}}, \text{ if } comp < 0.01 \text{ then } comp = 0.01 \quad (2)$$

$$comp_{crown} = 1 - \frac{intersection_{total}}{ZOI_{volume}} * 2, \text{ if } comp_{crown} < 0.01 \text{ then } comp_{crown} = 0.01 \quad (3)$$

$$comp_{mort} = 1 - \frac{intersection_{total}}{ZOI_{volume}}, \text{ if } comp_{mort} < 0.0 \text{ then } comp_{mort} = 0.0 \quad (4)$$

To simulated size symmetric competition overlapping crown volumes are allocated equally to the competitors. If competition is size asymmetric, overlapping crown volumes are allocated according to the size ratio (Eq. 5) between the competitors. The competitor with the bigger crown retains a larger share of the overlapping crown volume (Fig. 1).

$$size\ ratio = \frac{crown_{volumeN}}{crown_{volumeT} + crown_{volumeN}} \quad (5)$$

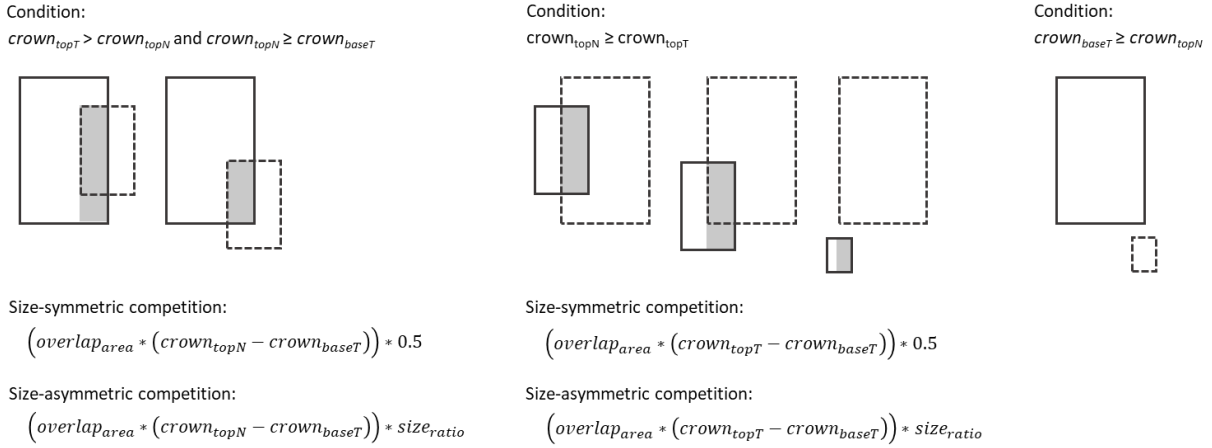


Fig. 1: Schematic depiction of possible ZOI intersections and calculation of intersecting crown volumes for symmetric and asymmetric competition. Solid lines indicate the subject tree (T), dashed lines a neighbour (N). Light grey areas indicate intersecting ZOI volumes.

3.3.3. Growth

The growth simulation is separated into height growth and growth of crown diameter as it is assumed that crown growth is more sensitive to competition than height growth. Height growth modelling is based on the Bertalanffy growth equation that was adapted by Rammig et al. (2007) to simulate growth of Norway spruce in a subalpine environment (Eq. 6). With this equation tree height of the current year is calculated from tree height of the previous year. The factor g determines the shape of the function, i.e. the dynamics of the growth with height. A range of g was determined empirically for Norway spruce on subalpine sites with a maximum of $0.035\ year^{-1}$ by Rammig et al. (2007). This maximum value is taken as an approximation of the growth dynamics of open-grown trees and provides the default value for g in the growth model. To simulate reduced growth as a consequence of competition, g is modified by $comp$.

$$height = height_{max} * \left(1 - \left(1 - \left(\frac{height}{height_{max}}\right)^{\frac{1}{3}}\right) * e^{(-g*comp)}\right)^3 \quad (6)$$

Juvenile trees with a favourable neighbourhood configuration may benefit from facilitation that increases growth. For these trees $comp$ is replaced by a constant (Eq. 7).

$$height = height_{max} * \left(1 - \left(1 - \left(\frac{height}{height_{max}}\right)^{\frac{1}{3}}\right) * e^{(-g*1.3)}\right)^3 \quad (7)$$

The diameter of the crown is an empirical function of tree height (Hasenauer 1997) (Eq. 8). A theoretical tree height ($height_{crown}$) is calculated to simulate crown growth, that allows for the simulation of a distinct influence of competition on crown growth (Eq. 9). In this equation the factor $comp_{crown}$, that is specific to the effect of competition on the growth of the tree crown, replaces $comp$. The growth function for trees with increased growth due to facilitation is adjusted, respectively (Eq. 10).

$$crown_{dia} = a + b * \ln(height_{crown}) * 2 * e \quad (8)$$

$$height_{crown} = height_{max} * \left(1 - \left(1 - \left(\frac{height}{height_{max}}\right)^{\frac{1}{3}}\right)\right) * e^{(-g * comp_{crown})^3} \quad (9)$$

$$height_{crown} = height_{max} * \left(1 - \left(1 - \left(\frac{height}{height_{max}}\right)^{\frac{1}{3}}\right)\right) * e^{(-g * 1.3)^3} \quad (10)$$

3.3.4. Recruitment

The process of reproduction is divided into the submodels seed production and seed dispersal. Both processes are simulated for the individual. Seed production is restricted to mature trees. The number of seeds that a tree produces increases with tree height (Dovčiak et al. 2008), decreases with elevation (Mencuccini et al. 1995) and is highly variable between individuals with a small number of trees that consistently produce a significant amount of seeds (Piotti et al. 2009, Minor and Kobe 2017, Hackett-Pain et al. 2019). Dominant seed trees were identified as larger, faster growing individuals (Hackett-Pain et al. 2019) or individuals with a wider basal diameter (Piotti et al. 2009) and may be individuals with a more favourable configuration of their neighbourhood in terms of a smaller number of competitors (Minor and Kobe 2017). The number of seeds produced by a mature tree is therefore modelled as a function of the tree's height, the elevation at which it grows, and its competitive situation (Eq. 11).

$$seeds_{nb} = (2.75 * height - 25.5) * \left(1 - \left(\frac{(elev - 1300)}{1000}\right)\right) * comp \quad (11)$$

During most years the number of seeds produced by a tree is multiplied by a factor of 18 (Hofgaard 1993b). To reduce the number of seeds within the model, only viable seeds are modelled.

Dispersal of spruce seeds around the maternal tree can be described by a leptokurtic function with an extended tail of long-distance dispersal (Nathan and Muller-Landau 2000). To simulate seed dispersal within the model a function by Dovčiak et al. (2008) was chosen that creates an isotropic and lognormal distribution of seeds and gives the number of seeds at a certain distance from the maternal tree. Seed dispersal is random regarding the direction of dispersal.

$$seeds_{nb} = \frac{seeds_{total}}{\sqrt{2 * \pi * \sigma * i}} * e^{-\frac{\ln(i) - m^2}{2 * \sigma^2}} \quad (12)$$

where

$$\sigma = 1.028$$

i = distance from maternal tree (m)

The factor m is a function of the release height, that can be approximated as $\frac{5}{6}$ of tree height (Dovčiak et al. 2008).

$$m = \ln(0.484 * height_{release}) \quad (13)$$

After dispersal new tree agents are created as seedlings. Initial height is assigned to agents according to a gaussian function (mean = 3 cm, sd = 1 cm with a minimum of 1 cm), to create seedlings within a height range of 1 – 5 cm, reported by Rammig et al. (2007) for Norway spruce regenerating on subalpine blowdown areas. Initial crown diameter of seedlings is defined as being equal to height. Initial age of seedlings is 0.

3.3.5. Germination

Seed germination is modelled as a probability that results from microhabitat characteristics related to neighbourhood configuration and presence of CWD. The model assumes a default germination probability of 30 % (Wallentin et al. 2008). Within the ZOI of a dominant neighbour germination probability increases to 50 %. Microhabitats within the ZOI of tall trees are supposed to be more favourable for germination than open microhabitats. Dense ground vegetation strongly inhibits germination of Norway spruce seeds (Hunziker and Brang 2005, Kupferschmid and Bugmann 2005, Tasser et al. 2007, Dovčiak et al. 2008). Tall trees are assumed to reduce the density and thickness of the groundcover within their ZOI thereby increasing chances for germination. A higher proportion of bare ground and a sparser ground vegetation reduce the risk that seeds get entangled within vegetation without reaching the ground resulting in desiccation before making contact with a suitable seed bed. On coarse woody debris (CWD) germination probability is assumed to be 90 %. CWD has been shown to provide favourable microsites for the establishment of Norway spruce seedlings, thus being an important factor in the recruitment process on subalpine forests (Hofgaard 1993c, Zielonka and Niklasson 2001, Vorčák et al. 2006, Zielonka 2006). Seeds germinate in the year of seed dispersal.

3.3.6. Death

Within each model cycle the probability to die is determined for every tree individually. Seedlings and saplings are subject to age-related mortality. The particular causes for this component of mortality are not simulated. Seedling mortality during the first growing seasons is generally high (Leemans 1991, Hofgaard 1993b, Nilsson and Gemmel 1993, Brang 1998, Hanssen 2003, Juntunen and Neuvonen 2006, Fløistad et al. 2018) with a range of processes causing the death of individuals (Brang 1998).

In agreement with these empirical data a function was fitted to simulate age-related mortality ($mort_{base}$) that defines the mortality of seedlings at age = 1 at 70 % and produces a strong decline of mortality during the following years (Eq. 14).

$$mort_{base} = 0.7/age^{1.4} \quad (14)$$

For adult trees age may not be the decisive factor in mortality but could be replaced by size (Vieilledent et al. 2010). The tallest trees of a population may be subject to an increased risk of windthrow (Canham et al. 2001). Therefore, a constant base mortality of 0.5 % (Vieilledent et al. 2010) is assumed for trees that have reached at least 80 % of their maximum height.

A significant impact on mortality in Norway spruce forests can be attributed to competition (Eid and Tuhus 2001, Castagneri et al. 2010, Svoboda et al. 2010, Vieilledent et al. 2010, Peltoniemi and Mäkipää 2011). It is assumed that mortality increases with the intensity (Eid and Tuhus 2001) and the duration of competition (Bigler and Bugmann 2003). Competition related mortality is therefore modelled as a function of the duration of competition (Eq. 15). As Norway spruce can tolerate competition over prolonged periods (Cherubini et al. 1996, Cherubini et al. 2002, Bigler and Bugmann 2003) it is assumed that mortality increases slowly after the onset of competition but increases faster if competition is more intense (Eq. 16). The model postulates a stronger increase of sapling mortality as a reaction to competition (Eq. 16 and 17) as it is assumed that saplings are more sensitive to competition due to increasing light demands (Modrzynski 2007).

$$mort_{comp} = (1 - e^{-0.01*|comp_{mort}-1|*comp_{dur}})^2 \quad (15)$$

$$mort_{comp} = (1 - e^{-0.02*|comp_{mort}-1|*comp_{dur}})^2 \quad (16)$$

if $comp \leq 0.3$ or if $sapling = true$ and $0.3 \leq comp \leq 1.0$

$$mort_{comp} = 0.035 + (1 - e^{-0.08*|comp_{mort}-1|*comp_{dur}})^2 \quad (17)$$

if $comp \leq 0.3$ and $sapling = true$

Intra-specific competition is assumed to be a minor cause of seedling mortality. Main causes for seedling mortality include insufficient water availability and stability of the ground in addition to infection with pathogenic fungi and clipping by animals (Cui and Smith 1991, Brang 1998). Seedlings are therefore excluded from the simulation of competition related mortality.

Facilitation is assumed to reduce mortality by 50 %.

3.4. Model analysis

3.4.1. Initialization

The model can be initialized with any data describing individual trees with their location and further state variables. For this study the initial tree population is either a nucleus population of 15 trees with tree heights ranging between 4 – 15 m and crown diameter and age defined to be consistent with trees growing with their maximum growth rate. The nucleus population represents a loose group of trees at the centre of the model area of 1 ha. An alternative initialization creates a tree population of 1764 saplings that covers the whole model area. Height of all saplings is 16 cm with a corresponding crown diameter and an age of 3 years. Saplings are regularly spaced at distances of 2.4 m.

3.4.2. Sensitivity analysis

To determine the effect of different model components on spatial and temporal dynamics of the simulated tree population, simulation runs were performed for different scenarios. The baseline scenario starts with a nucleus population at an elevation of 1600 m a.s.l. and simulates competition as asymmetric. The effect of the type of competition was tested by comparing results of the baseline scenario to a scenario of symmetric competition. To assess the model's sensitivity to different elevations simulation runs were performed for additional tree populations at 1400 m and 1800 m a.s.l. For further simulation runs either the submodel creating CWD or the submodel causing facilitation were excluded from the model. Finally, the impact of the initial tree population was tested by comparing results of the baseline model to those of populations developing from a plantation. As the baseline scenario this scenario was run with asymmetric and symmetric competition.

All simulations were run for a time span of 600 years to enable the analysis of long-term population dynamics. All analyses are based on mean results created from 5 simulations with identical configurations of the model.

4. Results

4.1. Asymmetric vs. symmetric competition and types of initial population

The effect of asymmetric and symmetric competition was compared between different initializations of the model either as a small nucleus population at the centre of the model area or as a regular-spaced and even-aged plantation covering the whole model area.

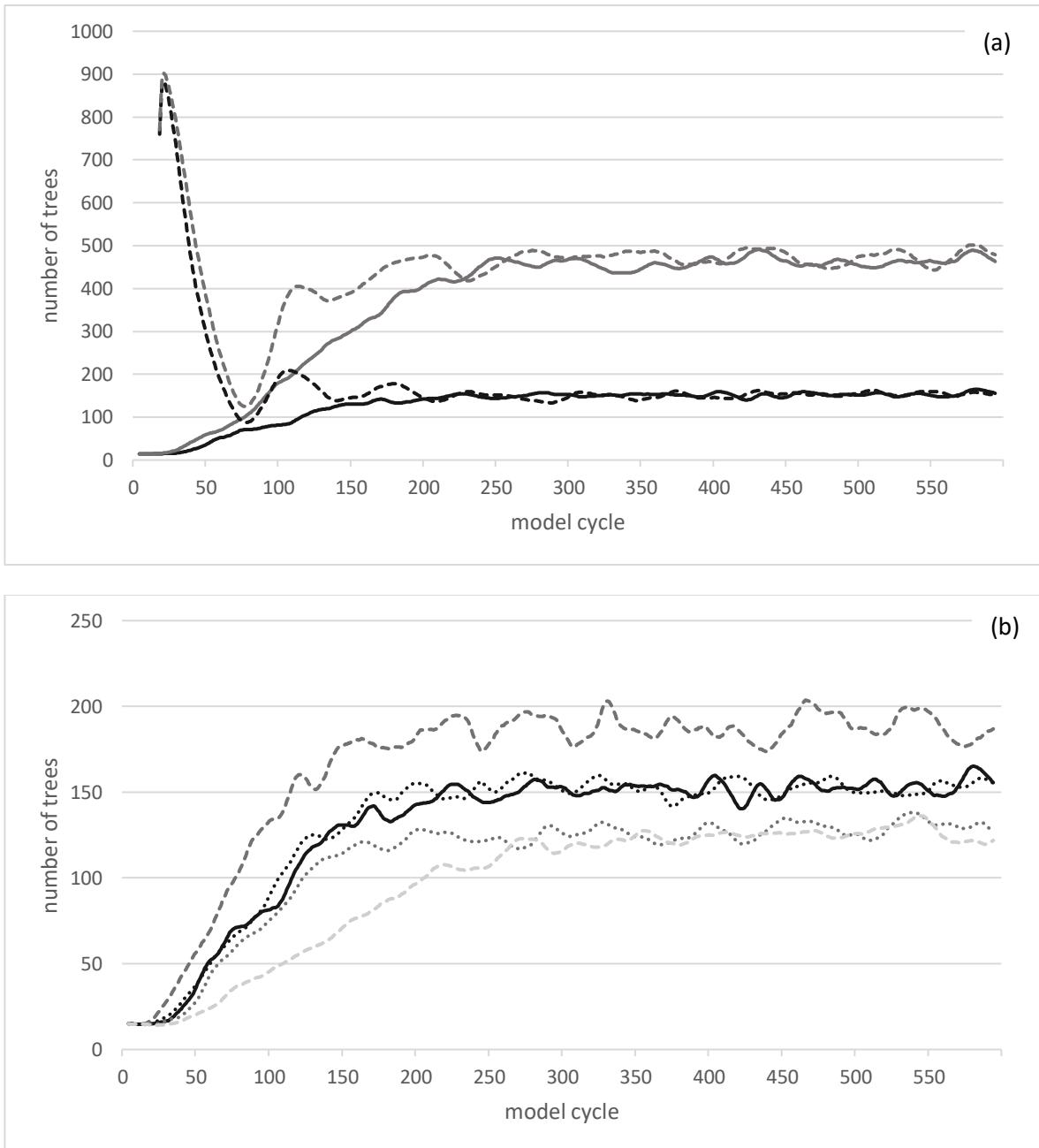


Fig. 2: Development of the adult population over a 600 years time series. (a) different types of competition and initial population. Solid black line: asymmetric competition in a nucleus population, dashed black line: asymmetric competition in a plantation, solid grey line: symmetric competition in a nucleus population, dashed grey line: asymmetric competition in a plantation. (b) populations at different elevations and model without CWD and facilitation, respectively. Solid black line: population at 1600 m a.s.l., dashed grey line: population at 1400 m a.s.l., dashed light grey line: population at 1800 m a.s.l., dotted grey line: population without CWD, dotted light grey line: population without facilitation. Numbers of trees are shown as 10-year moving averages.

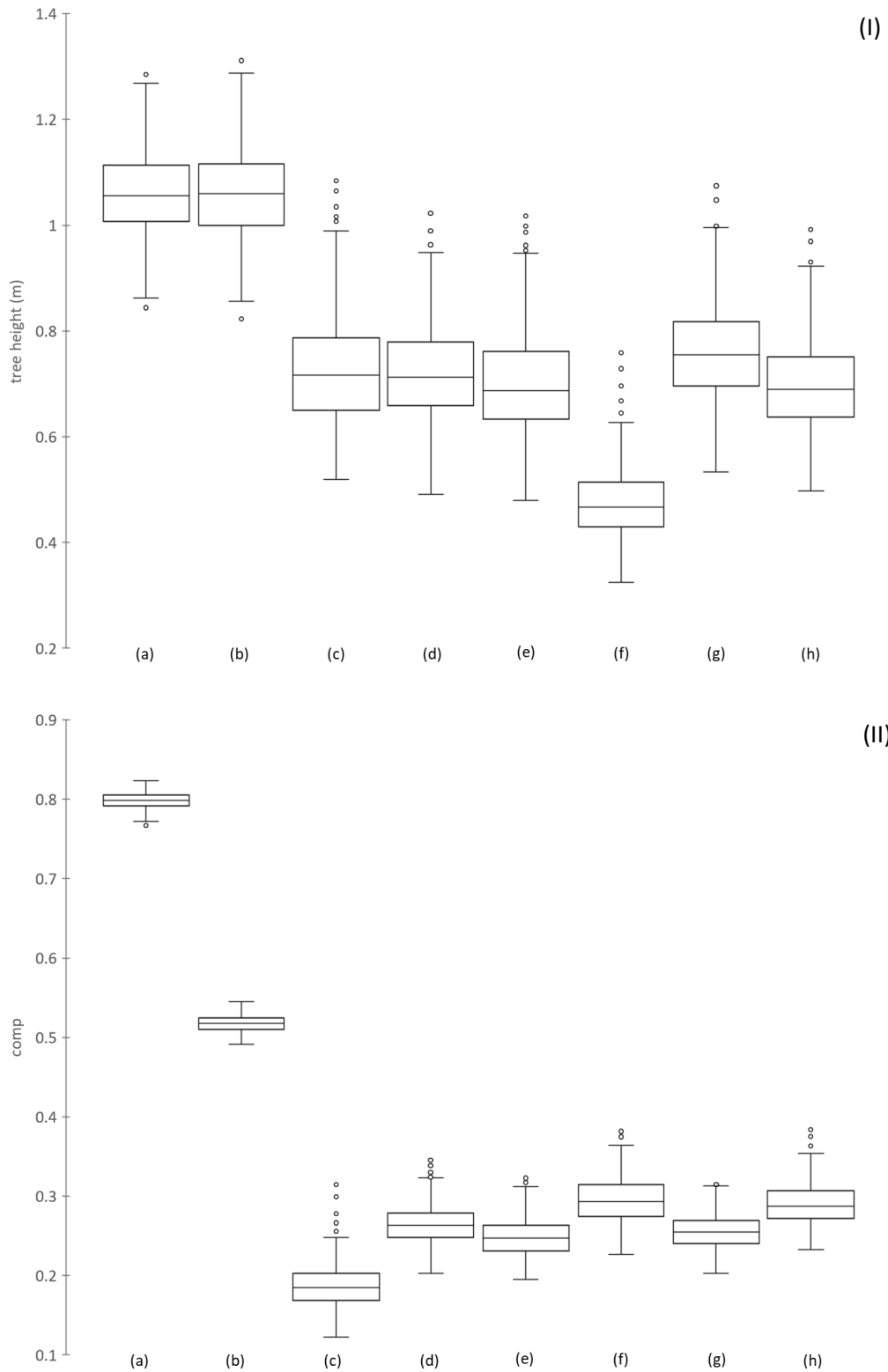


Fig. 3: Comparison of mean sapling (I) height and (II) intensity of competition between populations modelled under different scenarios. (a) symmetric competition in a plantation, (b) symmetric competition in a nucleus population, (c) asymmetric competition in a plantation, (d) asymmetric competition in a nucleus population, (e) asymmetric competition without CWD, (f) asymmetric competition without facilitation, (g) asymmetric competition at 1400 m a.s.l., (h) asymmetric competition at 1800 m a.s.l. (Calculated for model cycles ≥ 200 .)

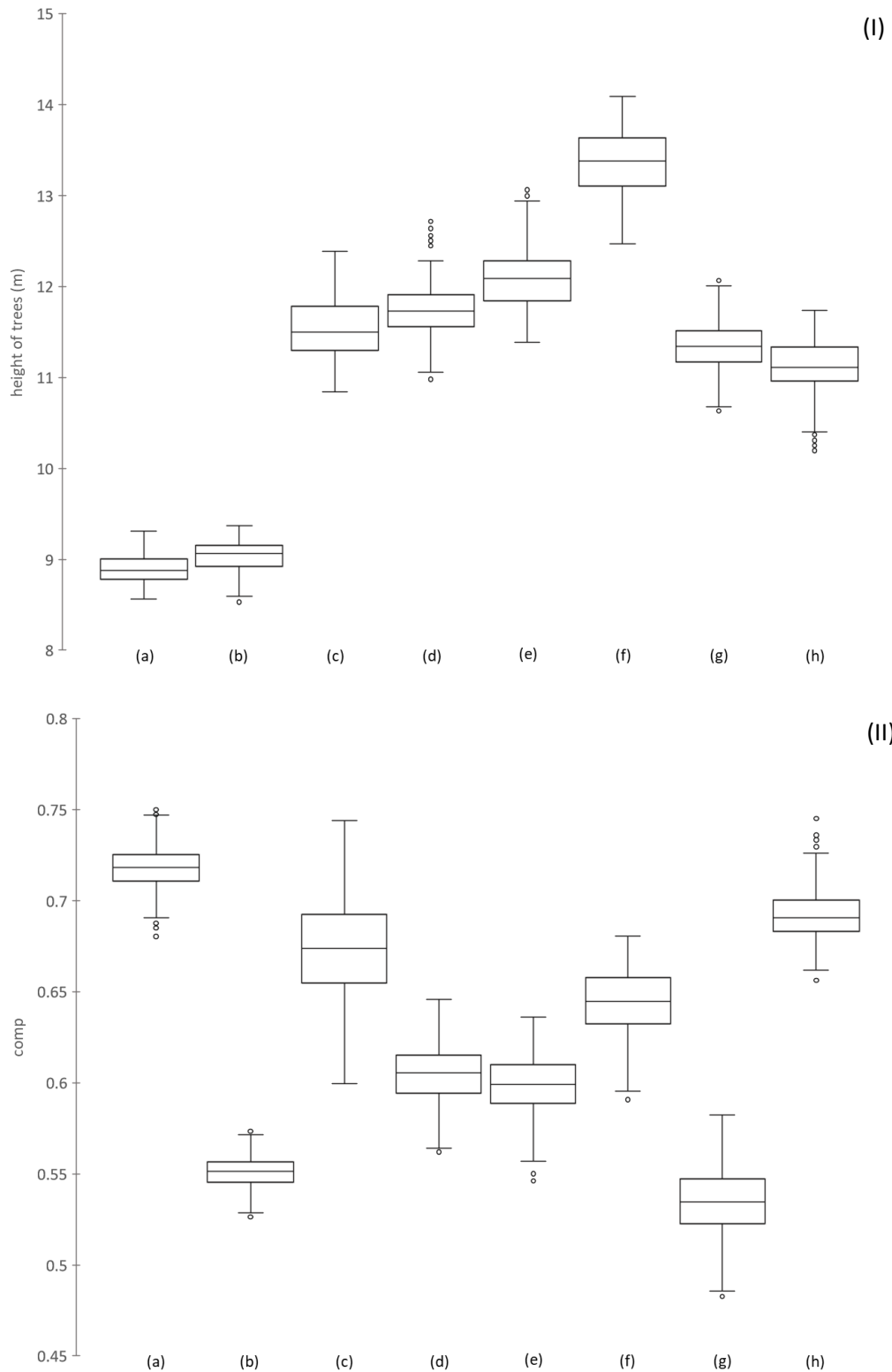


Fig. 4: Comparison of mean adult (I) height and (II) intensity of competition between populations modelled under different scenarios. (a) symmetric competition in a plantation, (b) symmetric competition in a nucleus population, (c) asymmetric competition in a plantation, (d) asymmetric competition in a nucleus population, (e) asymmetric competition without CWD, (f) asymmetric competition without facilitation, (g) asymmetric competition at 1400 m a.s.l., (h) asymmetric competition at 1800 m a.s.l. (Calculated for model cycles ≥ 200 .)

4.1.1. Initialization of nucleus population: symmetric vs. asymmetric competition

If simulations start from a nucleus population of trees, numbers of trees/ha slowly increase for about 200 model cycles indifferent to the type of symmetry, but tree numbers settle to a higher mean under symmetric competition for all life stage classes except for seedlings (Fig. 2, results only shown for the adult population). The sapling population is taller, and competition is more moderate under symmetric competition (Fig. 3). Within the adult population asymmetric competition results in larger mean tree heights that again correspond to more moderate competition (Fig. 4). The population of mature trees reacts similarly to symmetric competition but differences in mean height are less pronounced than for adult trees.

4.1.2. Initialization of plantation: symmetric vs. asymmetric competition

For tree populations that originate from plantations the number of trees/ha again is higher under symmetric than asymmetric competition for all life stage classes except for seedlings (Fig. 2, results only shown for the adult population). Especially the adult population is characterized by an initial period of strong fluctuations of the population size. This period lasts for about 150 model cycles under asymmetric competition and for about 200 model cycles under symmetric competition. After a first peak of adult tree numbers at around 920 trees/ha in model cycle 19, tree numbers strongly decrease to lows of 86 trees/ha under asymmetric and 120 trees/ha under symmetric competition in model cycle 78. A second peak of tree numbers is reached under asymmetric competition at around 214 trees/ha in model cycle 106 and under symmetric competition at around 410 trees/ha 10 model cycles later. After these initial fluctuations tree numbers approach a steady-state with limited fluctuations of population size around a constant mean (Fig. 2). Competition is less intense under symmetric competition (Fig. 3 and 4). For saplings this difference is especially pronounced. Their larger mean population height corresponds to the more moderate competition (Fig. 3), while adult trees are distinctly taller under asymmetric competition (Fig. 4). For mature trees the difference in mean population height is smaller but favours trees under symmetric competition.

4.1.3. Asymmetric competition: types of initialization

Under asymmetric competition simulations starting from plantations produce larger numbers of saplings and mature trees compared to simulations starting from a nucleus population. The size of the adult population is unaffected by the type of the initial population (Fig. 2). Competition is more intense in plantation populations for saplings (Fig. 3) while for adult trees these populations result in less intense competition (Fig. 4). Mean population heights do not differ between types of initialization (Fig. 3 and 4).

4.1.4. Symmetric competition: types of initialization

Tree numbers are equally affected by the type of initialization under symmetric and asymmetric competition with denser populations resulting from plantation populations for saplings and mature trees but not for adult trees (Fig. 2, results only shown for the adult population). For both sapling and adult populations competition is distinctly less intense if they originate from plantations (Fig. 3 and 4). Mean tree height of populations is unaffected by the type of the initial population as it is under asymmetric competition (Fig. 3 and 4).

4.2. Elevation

The effect of elevation on population structure was analysed by comparing populations resulting from simulations along an elevational gradient. Comparing numbers of trees/ha between simulations of tree populations at 1400 m, 1600 m, and 1800 m a.s.l. numbers of saplings and adult trees (Fig. 2, results only shown for the adult population) strongly decrease. For seedling numbers a decreasing trend with elevation can be observed (data not shown), although variability in the number of seedlings is high between model cycles. The number of mature trees increases with elevation. In line with a sparser

adult population the intensity of competition becomes distinctly more moderate for adult trees with increasing elevation (Fig. 4). For saplings this effect is less clear, but competition is still more moderate at 1800 m compared to 1400 m a.s.l. (Fig. 3). While height of the sapling population is not affected by elevation (Fig. 3), mean population height of adult and mature trees is. Adult trees are slightly taller at 1600 m than at 1400 m and 1800 m a.s.l. (Fig. 4). For mature trees there is a clear trend that tree height decreases with elevation.

4.3. Facilitation and CWD

The model simulates the effects of intra-specific facilitation as increased growth and reduced mortality, that affect seedlings and saplings. Seeds that are dispersed to areas of CWD have a higher germination rate and seedlings growing on CWD benefit from the same increased growth rate and reduced mortality that characterize facilitation. The effect of facilitation on population structure was analysed by comparing results of simulations that included both the facilitation and the CWD submodel to simulations that either excluded the CWD or the facilitation submodel. If facilitation is excluded from the model populations of saplings and adult trees are less dense (Fig. 2, results only shown for the adult population). And while saplings are smaller despite a slightly more moderate intensity of competition (Fig. 3), for adult trees competition is markedly more moderate and they are taller without facilitation (Fig. 4).

The simulation of CWD had no significant effects on population structure (Fig. 2 and Fig. 3) or competition (Fig. 4) for any of the life stage classes.

4.4. Effect of facilitation and CWD on seedlings and saplings

Under asymmetric competition about 28 % of seedlings and 31 % of saplings are facilitated and under symmetric competition about 21 % of seedlings and 12.5 % of saplings. The share of seedlings that germinated of CWD is about 5 % under asymmetric and about 6 % under symmetric competition.

Here the combined effects of facilitation and the type of competition symmetry within the model on seedlings and saplings are presented by comparing mean height for all seedlings and mean height and competition for saplings under asymmetric and symmetric competition. Under asymmetric competition seedlings benefiting from facilitation are significantly taller than seedlings without facilitation (Fig. 5).

If competition is asymmetric, facilitated saplings are taller than all saplings, but not taller than saplings without facilitation. For these a much wider range of heights was observed (Fig. 6). However, competition is distinctly more intense for facilitated saplings than for saplings without facilitation, and these have less competition than all saplings (Fig. 7).

If competition is symmetric, facilitated saplings are significantly smaller than all saplings and saplings without facilitation. Under symmetric competition saplings are generally taller than under asymmetric competition (Fig. 6). Although they are smaller competition is significantly less strong for facilitated saplings than for all saplings and saplings without facilitation. Under symmetric competition facilitation for saplings is generally less intense than under asymmetric competition (Fig. 7).

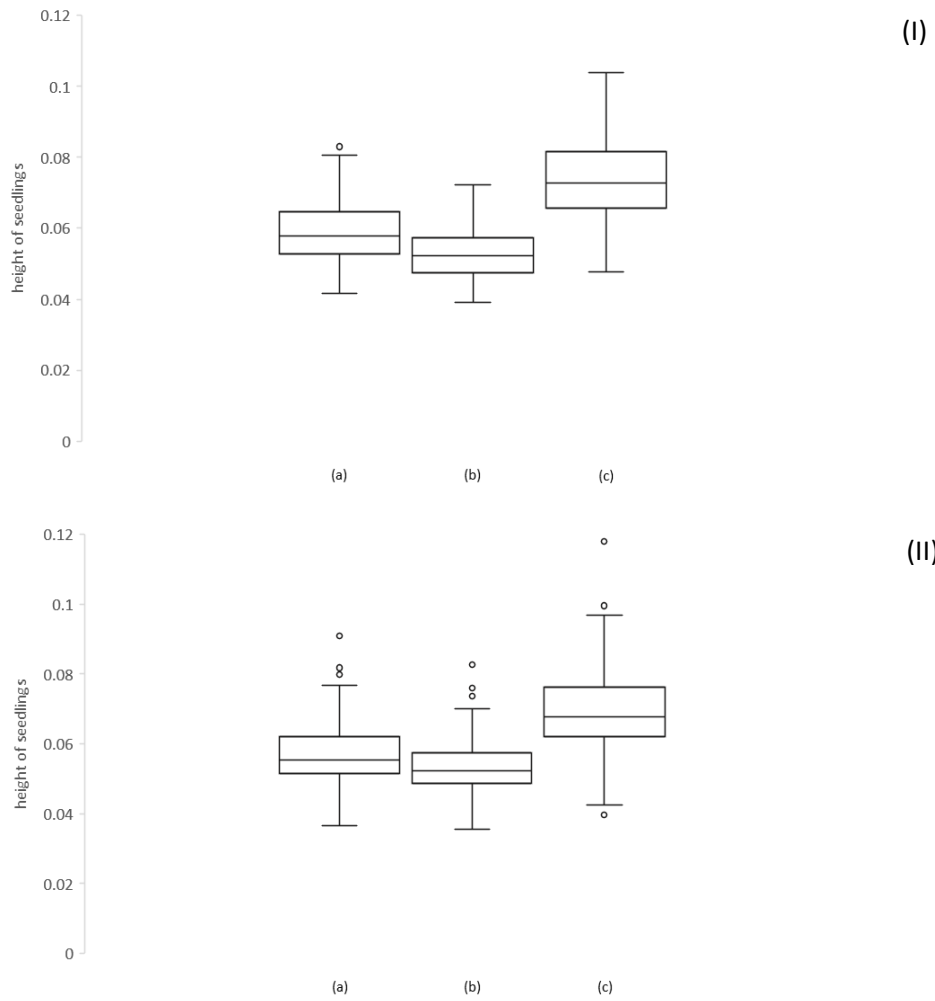


Fig. 5: Height of seedlings under (I) asymmetric and (II) symmetric competition. (a) all seedlings, (b) seedlings without facilitation, (c) facilitated seedlings (Calculated for model cycles ≥ 200 .)

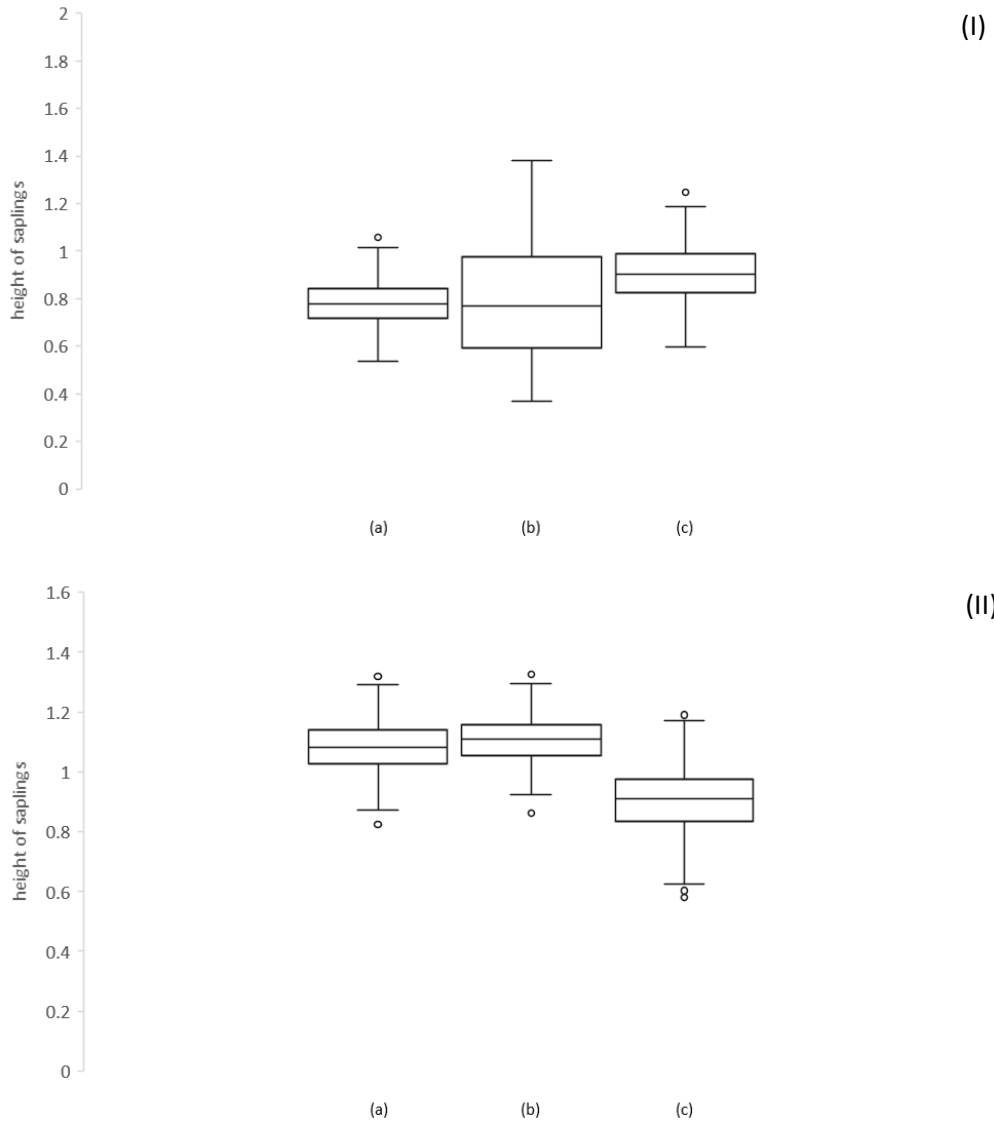


Fig. 6: Height of saplings under (I) asymmetric and (II) symmetric competition. (a) all saplings, (b) saplings without facilitation, (c) facilitated saplings (Calculated for model cycles ≥ 200 .)

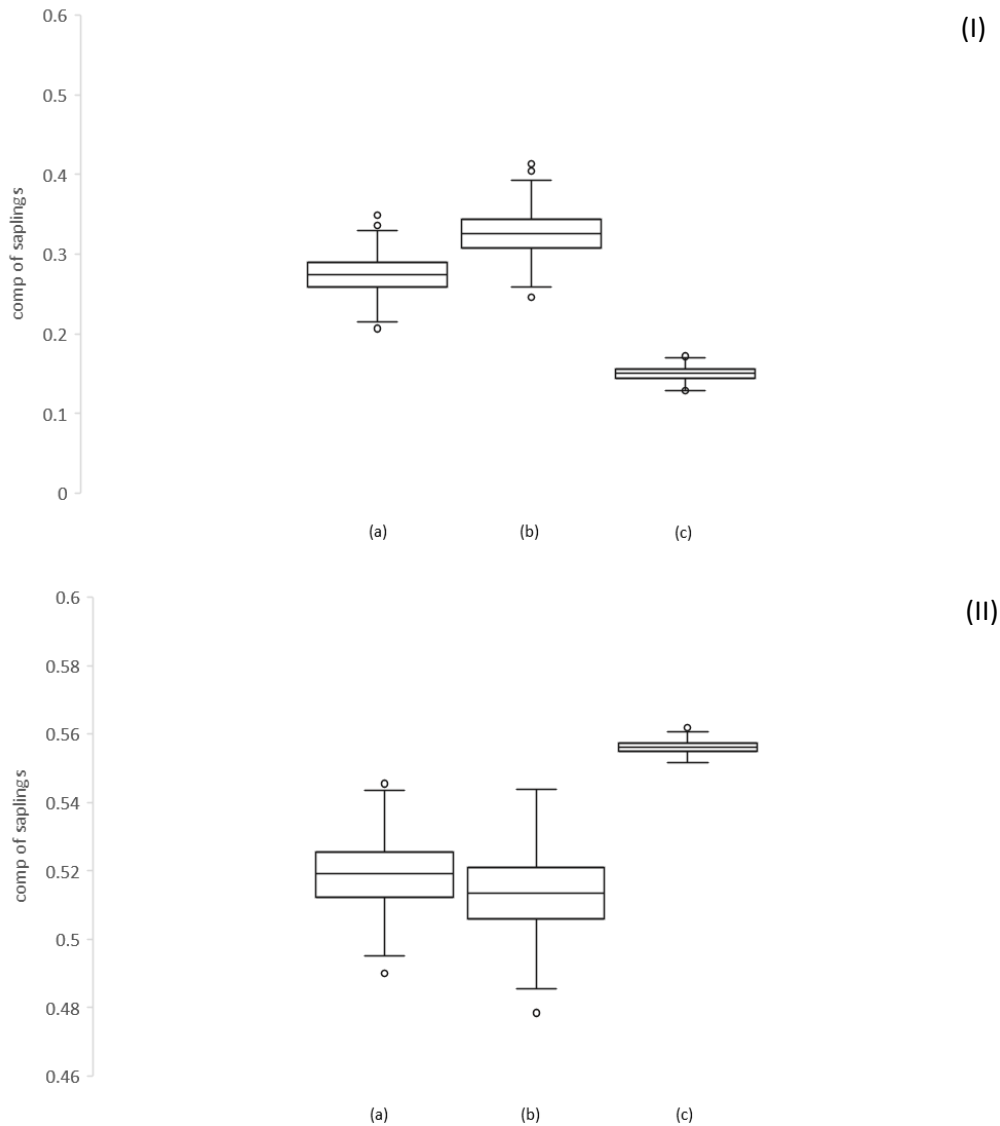


Fig. 7: Competition of saplings under (I) asymmetric and (II) symmetric competition. (a) all saplings, (b) saplings without facilitation, (c) facilitated saplings (Calculated for model cycles ≥ 200 .)

5. Discussion

The presented individual-based neighbourhood model of Norway spruce in subalpine environments was analysed by comparing tree populations under asymmetric or symmetric competition, and populations developing from small nucleus populations or from regular-spaced and even-aged plantations. Populations were simulated along an elevational gradient and the effect of facilitation and CWD on population dynamics were analysed.

5.1. Asymmetric and symmetric competition in nucleus population and plantation

Within the model, symmetric competition increases the density of populations (Fig. 2) as is expected due to symmetric competition favouring smaller trees compared to asymmetric competition. Saplings benefit from less intense competition (Fig. 3). This reduces mortality and results in more densely populated tree stands.

While adult tree numbers converge to a steady state after an initial period of strong fluctuations for both types of initialization (Fig. 2), the number of mature trees remains at a higher level in populations

originating from plantations compared to populations originating from nucleus tree groups. This behaviour could be a result of the initially regular spacing of trees. The higher number of mature trees in turn causes higher numbers of seedlings and saplings.

5.2. Elevation

Tree height is expected to decrease with elevation as maximum tree height is implemented in the model as a function of elevation. While results for mature trees are in line with expectations, for the adult tree population differences in mean height between elevations are small and trees are tallest at 1600 m a.s.l. (Fig. 4). Tree growth at 1400 m a.s.l. seems to be restricted due to intense competition in a dense population, while the tree population at 1800 m a.s.l. is sparser and competition is more moderate. Therefore, at the highest elevation tree heights are more effected by maximum tree height than by interactions with neighbours.

5.3. Facilitation

Facilitation clearly affects population size (Fig. 2) and structure (Fig. 3 and 4) and its effects are most strong in the adult population although it does not affect this life stage class directly. Due to its effect on mortality, seedling and sapling facilitation increases the number of saplings and adults respectively. This is the case even though general competition is higher in the denser, facilitated populations.

CWD seems to have no effect on tree populations due to the small number of seedlings germinating on CWD.

5.4. Effect of facilitation and CWD on seedlings and saplings

Under asymmetric competition saplings are taller if they are facilitated as can be expected due to increased growth that is associated with facilitation (Fig. 6). However, competition is distinctly more intense for facilitated saplings (Fig. 7). As mortality is reduced for these saplings, they can survive longer under more intense competition leading to a higher mean value. Symmetry of competition eases the intensity of competition for saplings, causing competition to be generally more moderate and allowing saplings to grow taller. Under symmetric competition facilitated saplings have slightly less competition but are smaller than saplings without facilitation (Fig. 6 and 7). It is assumed that due to the more relaxed competitive conditions of symmetric competition saplings generally survive longer causing especially the faster growing, facilitated saplings to lose facilitation due to interacting with new neighbours.

5.5. Model limitations and perspectives

An aspect that should be included in the development of future models when simulating interactions between plants is below-ground competition (Berger et al. 2008). Although the presented model is restricted in its current version to the simulation of above-ground competition for light, its flexible structure allows for the integration of below-ground competition that could be implemented as a parallel process alongside above-ground competition.

As noted by Berger and Hildenbrandt (2000) a shortcoming of the ZOI approach in the simulation of competition is that the actual position of a tree within the ZOI of the neighbour is no longer decisive, if the ZOI of a juvenile tree or suppressed tree is completely overlapped by the ZOI of a neighbour. Berger and Hildenbrandt (2000) proposed the field of neighbourhood (FON) approach to enhance the simulation of competition within the ZOI. The FON concept assumes that the strength of competition decreases within the ZOI with increasing distance from the centre of the tree.

Facilitation is an important aspect of interactions between plants with an increasing impact along environmental gradients of stress (Callaway and Walker 1997, Callaway 1998, Maestre et al. 2003).

The presented model includes a basic simulation of facilitation. Facilitation is described as a benefit for seedlings and saplings that arises from an interaction with a dominant tree. This approach restricts the occurrence of facilitation to a very specific spatial configuration of the interaction neighbourhood and simplifies facilitation to a binary phenomenon within space. A further development of the model should focus on enhancing the facilitation submodel by describing the intensity of facilitation within space. The aim of this development should be a simulation of intra-specific interactions within tree neighbourhoods that include competition and facilitation as two forces that coexist within space (Brooker et al. 2008) and prove as competition if negative interactions prevail and as facilitation if positive interactions prevail as a result of the spatial configuration of the interaction neighbourhood. Key challenges in the simulation of interactions in plant communities besides spatial heterogeneity are temporal changes in abiotic conditions (Kikvidze et al. 2006) and ontogenetic shifts in the involved individuals (Miriti 2006, Roux et al. 2013) that affect the outcome of interactions.

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Report

1. Model development

An individual-based model was implemented in the GAMA platform (Taillandier et al. 2019). The model simulates either symmetric or asymmetric, aboveground competition, it includes submodels to implement facilitation and CWD, and it incorporates the influence of elevation on key ecological processes. The model evolves the concept of the zone of influence (ZOI) (Biging and Dobbertin 1992, Berger et al. 2008) to delimit the interaction neighbourhood and quantify competition to a 3-dimensional representation of the tree crown. As detailed description of the model covering its concepts, structure, and processes an ODD protocol is included as part of this report that was proposed by Grimm et al. (2006) as a standard to describe and communicate individual-based models. The functions and their parameters describing ecological processes were selected to fit the model to Norway spruce in subalpine environments.

2. ODD protocol for an individual based model

The model description follows the ODD (Overview, Design concepts, Details) protocol for describing individual- and agent-based models (Grimm et al. 2006, Grimm et al. 2010).

2.1. Purpose

The presented individual-based model is aimed at simulating spatiotemporal dynamics of subalpine mono-specific spruce forests. Three core ecological processes determine the dynamics of plant communities: growth, reproduction, and mortality. The design of the model is based on the notion that intra-specific interactions between individuals are at the basis of spatiotemporal changes of the stand structure of forests by shaping the dynamics of growth, propagation, and mortality. The model aims at simulating these dynamics with a bottom-up approach that is focused on the interactions between trees on a neighbourhood scale. The basic hypothesis of this approach is that spatiotemporal dynamics of a forest can be simulated from the fate of individuals that is determined on the scale of the interaction neighbourhood. The neighbourhood definition of the model is based on identifying interacting trees. The model draws on the concept of the zone of influence (ZOI) (Biging and Dobbertin 1992, Berger et al. 2008) that delimits an area within which a tree interacts with neighbouring trees. Thus, an individual interaction neighbourhood exists for each tree and is formed by all trees that overlap the ZOI of the subject tree with their own ZOI.

Interactions with a net negative outcome are perceived as competitive interactions as they can reduce growth, impede reproductive success, and increase mortality for the individual. Trees compete for essential resources as light, water, and nutrients. The model is restricted to the simulation of above-ground competition that is the competition for light. When simulating competition between plants interactions can be conceptualised as symmetric or asymmetric. Under conditions of symmetric competition all plants acquire a share of the resources that is proportionate to their size and their competitive effects on each other are also a direct expression of differences in size. If competition is asymmetric taller plants acquire more resources than their size advantage would suggest, and they have a disproportionate competitive effect on smaller neighbours.

Interactions with a net positive outcome are described as facilitative. Facilitation requires that at least one of the interacting individuals benefits from the interaction. Facilitation between plants is assumed to have important effects on the dynamics of plant communities especially under conditions of increasing environmental stress (Callaway 1998, Callaway et al. 2002, Eränen and Kozlov 2008, Lingua

et al. 2008, García-Cervigón et al. 2013). An important factor in the recruitment of juvenile trees in subalpine spruce forests is the presence of coarse woody debris (CWD) on the forest floor. Decomposing wood from fallen trees provides important microhabitats for the germination and the establishment juvenile trees (Hofgaard 1993a, b, c, Zielonka and Niklasson 2001, Motta et al. 2006, Zielonka 2006, Svoboda et al. 2010, Bače et al. 2011).

2.2. Entities, state variables, and scales

The model world represents a square of 1 ha. Locations within the model world are indicated based on a coordinate system with its origin in the upper left corner of the model world. Space is measured in metres. Time is modelled as discrete steps and each model cycle represents one year.

Four entities are represented in the model. The species *tree* represents individual Norway spruce trees. The model simulates a monospecific population of trees. All different life stages of a spruce tree are modelled within the same entity. *Tree* agents are characterized by four state variables (Tab. 1).

Tab. 1: State variables of agents of the species *tree*

State variable	Description	Unit
<i>location</i>	The location of <i>tree</i> agents is indicated as x-/y-coordinates via the internal coordinate system of the model. The location is defined at the centre of a tree.	
<i>elevation</i>	Elevation at the location of an agent. Information on elevation is either obtained from a DEM that is included in the model as grid and represents a real-world terrain or agents are assigned a hypothetical elevation. If a DEM is used, agents are assigned the values of the grid cell in which they are located.	m a.s.l.
<i>age</i>	Age of an agent at the current model cycle	years
<i>height</i>	Vertical height of an agent from its stem base to the top of its crown.	m

The second entity of the model is the species *CWD*. Agents of the species are created when agents of the species *tree* die, that exceed a certain size threshold. *CWD* agents represent substantial amounts of decomposing wood from fallen trees that plays an essential part in the recruitment of Norway spruce in subalpine environments. *CWD* agents inherit some of their attribute values from the *tree* agent that is their predecessor. They are characterized by five state variables (Tab. 2).

Tab. 2: State variables of agents of the species CWD

State variable	Description	Unit
<i>location</i>	The location of <i>CWD</i> agents is indicated as x-/y-coordinates via the internal coordinate system of the model. The location is defined at the centre of the log base. The location is inherited from the preceding tree agent.	
<i>log_tip</i>	Random point at a distance from the location of the <i>CWD</i> agent that is equal to the last value of the <i>height</i> attribute recorded for the preceding <i>tree</i> agent.	
<i>log_width</i>	The attribute value is inherited from the <i>tree</i> agent preceding the <i>CWD</i> agent and is equal to the last value of the <i>DBH</i> attribute recorded for the former.	m
<i>log_length</i>	The attribute value is inherited from the <i>tree</i> agent preceding the <i>CWD</i> agent and is equal to the last value of the <i>height</i> attribute recorded for the former.	m
<i>decomp_duration</i>	Time since the creation of the <i>CWD</i> agent i.e. the death of the preceding <i>tree</i> agent.	years

If a digital elevation model (DEM) is integrated into the model to simulate stand dynamics within a specific study area, the DEM constitutes a third entity. *Tree* agents then retrieve the value of their *elevation* attribute from the *elevation_model* grid. The resolution of the DEM is adopted as the cell size of the grid species.

The final entity of the model is the environment. Environmental forcing affects the temporal variability of the seed crop. The seed crop of Norway spruce shows distinct differences between normal seed years and mast years with a strongly increased production of seeds. As the occurrence of mast years is a highly synchronised phenomenon on local as well as regional scales (Ascoli et al. 2017, Hackett-Pain et al. 2019) it is modelled as an environmental forcing that affects all *tree* agents in the same way.

Tab. 3: State variables of the environment, i.e. the world agent

State variable	Description	Unit
<i>mast_year</i>	Boolean variable that is true when the current model cycle is simulated as a mast year.	
<i>mast_year_prob</i>	Probability that the current model cycle is a mast year.	
<i>max_mast_period</i>	Maximum number of years between two consecutive mast years.	years
<i>current_mast_period</i>	Number of years since the last mast year.	years

2.3. Process overview and scheduling

At the beginning of a simulation run the model executes a first sequence of actions as part of the initialization of the starting population of *tree* agents.

- a) *get_elevation*
set_height
- b) *check_lifestage*
- c) *init_areas*
- d) *find_neighbours*
- e) *comp_calculation*

Each model cycle starts with the execution of a global action that determines if the current cycle is a mast year.

- a) *check_mast_year*

After that *tree* agents execute their actions. Some of these are only executed by a subgroup of *tree* agents.

- a) *get_older*
check_lifestage
grow_height
grow_areas
- b) *create_seeds*
This action is only executed by agents that are characterized as mature trees.
- c) *disperse_seeds*
This action is only executed by agents that are characterized as mature trees.
- d) *die_outside_world*
- e) *die_germination*
die_germination_stem_base
These actions are only executed if the value of the age attribute of an agent equals 0.
- f) *set_height*
init_areas
These actions are only executed if the value of the age attribute of an agent equals 0.
- g) *find_neighbours*
- h) *comp_calculation*
- i) *check_facilitation*
- j) *die_tree*

CWD agents execute their actions at the end of a model cycle. Some of these are only executed by a subgroup of the agents.

a) *init_log*

count_decomp

CWD_gone

strike_trees

The action init_log is only executed if the value of the duration_decomp attribute of an agent equals -1. The action strike_trees is only executed if the value of the duration_decomp attribute of an agent equals 0.

The grid entity does not execute any actions of its own. Instead it is addressed by *tree* agents during the *get_elevation* action and provides them with an elevation information on their location.

Actions are executed per species. The first action to be executed during model cycles is the global action, followed by actions of the species *tree* and the species *CWD*. Actions are either grouped to be executed in parallel or are called individually to be executed successively. On the level of individual agents, the execution order matches the order of the creation of agents or the order in which agents are read from an input file, respectively. After the execution of a single action or a set of actions attributes involved are updated synchronously.

2.4. Design concepts

The model does not include any adaptive traits or decision making. Instead growth, reproduction, and mortality of the individual are a direct consequence of the configuration of its neighbourhood.

2.4.1. Basic Principles

This individual-based model simulates the spatiotemporal dynamics of monospecific, subalpine spruce stands. The main hypothesis is that intraspecific interactions are a main factor in determining stand dynamics. Stand dynamics are perceived within the model as the result of only the basic ecological processes growth, reproduction, and mortality. External influences that can have massive effects on stand dynamics, e.g. storms, avalanches, landslides, or insect outbreaks, are not considered. The model therefore simulates growth, reproduction, and mortality of the individual as processes that directly emerge from interactions between neighbouring trees.

While interactions are negative for the involved individuals in the majority of cases, it is possible that individuals benefit from an interaction. Interactions with net-negative outcome, i.e. competitive interactions, reduce growth and reproductive success and can result in the death of the individual. Competitive interactions are often disadvantageous to both individuals. Net-positive interactions, i.e. facilitative interactions, are restricted to the juvenile life stages of a tree. Facilitation increases growth and reduces mortality and always includes a juvenile tree that benefits from the presence of a dominant tree. Thus, facilitation can only be a one-sided interaction, while competition is often two-sided.

Different versions of the model are designed to explore the effects of asymmetric compared to symmetric competition (Weiner 1990) on stand dynamics.

2.4.2. Interaction

Interactions between *tree* agents are modelled in the form of competition and facilitation. Interactions between sessile organisms are subject to distance between them and their size. And when they occur interactions cannot be ended by evasion but only by the death of an interacting individual. Aboveground interactions between trees are assumed to occur whenever the influence zones of individuals overlap. All interactions with a net-negative outcome for an individual are assumed to be

competitive while interactions with a net-positive outcome are recognized as facilitative. The outcome is not necessarily the same for all individuals involved and some individuals might also be unaffected by an interaction. It is assumed that only seedlings and saplings can benefit from facilitation while interactions between established trees are always competitive. Intraspecific interactions affect growth, mortality, and seed production.

An underlying interaction between seeds and ground vegetation during germination is assumed by simulating a germination probability of 30% for seeds beyond the influence zone of neighbouring trees above a certain size threshold and a germination probability of 50% for those within the influence zone of such a tree. This distinction is based on the assumption that dominant trees compete with ground vegetation and reduce its density and thickness. A sparser ground vegetation in turn increases the chances of seeds to get in contact with a suitable seedbed during germination thereby increasing the chances of successful germination.

2.4.3. Stochasticity

Elements of stochasticity affect different processes of the model regarding the timing or the entry of events or the determination of attribute values. Mast year occurrence is periodical with irregular intervals. The model simulates this natural variability. For each model cycle the probability for the occurrence of a mast year is determined based on the time passed since the last mast year. The probability of the current model cycle to be a mast year increases over time until the maximum interval between consecutive mast years is reached.

The simulation of seed dispersal has a random component as the travel distance of seeds is determined according to a non-stochastic function, but the direction of dispersal from the maternal tree is random for each seed.

The initial height of a seedling after germination is not fixed but follows a gaussian distribution around a mean of 3 cm with a standard deviation of 1 cm and a minimum of 1 cm. Initial seedling heights vary due to differences in the timing of germination between seeds, differences between microhabitats regarding their suitability for germination and seedling growth, and differences in seed quality. As processes related to these factors are not simulated, randomness in initial seedling heights is used to reproduce the resulting variability.

Seed germination and tree mortality are modelled as partly random processes. Germination success is determined by probabilities related to habitat. Survival is controlled by individual mortality probabilities that result from age, size, and competition of the *tree* agent.

Logs of dead trees above a certain size threshold are modelled as a source for CWD on the forest floor. While slope and wind directions cause trees to fall non-randomly regarding direction, within the scope of the model trees are simulated to fall in random directions. The actual spatial distribution of CWD within a tree stand is assumed to be of minor relevance for the spatiotemporal dynamics of the stand.

2.4.4. Observation

Data on the two species *tree* and *CWD* are collected after updating attribute values during each model cycle. Values of attributes essential to characterize the current status of the simulated tree stand are collected from each *tree* and *CWD* agent. The data include information on age, life stage, size, competitive status, and mortality of trees as well as area and decomposition time of *CWD* agents. Corresponding data are also collected on *tree* agents that die during the current model cycle to describe their state at the time of death. These data are collected within the submodel *die_tree* for trees that die because of age, size, or competition and within the submodel *strike_trees* for trees that are struck by a falling neighbour. Collected data are written to separate CSV-files for the two model species and the two simulations of tree death.

2.5. Initialization

The model allows for different initializations. An initial tree population with any number of trees can be loaded into the model e.g. in CSV or SHAPE format. Agents must be characterized by their state variables *location*, *height*, *age*, and *elevation*. For the present project a theoretical tree population representing a loose group of trees was created to initialize the model. The population includes 15 trees that are characterized by their location, diameter of their crown, height, age, and elevation (Tab. 4). For the initial population tree heights were chosen between 4 m and 15 m. Age and crown width of agents were chosen according to their height and as applicable for open-grown trees. So, all trees of the initial population are established. Seeds, seedlings, or saplings are not initialized. Agents of the species *CWD* are not created when the model is initialized. Initialization is always the same.

Tab. 4: Data describing the initial tree population

tree	location (x/y coordinates)	crown diameter (m)	height (m)	age (years)
01	63/42	4.7	4	16
02	50/37	8.3	9	26
03	31/64	9.6	12	32
04	38/50	7.2	7	22
05	65/50	8.8	10	28
06	35/55	6.5	6	20
07	50/47	7.8	8	24
08	37/34	10	13	33
09	33/41	4.7	4	16
10	50/53	10.6	15	37
11	60/60	8.3	9	26
12	45/32	9.2	11	30
13	58/50	8.8	10	28
14	55/55	7.8	8	24
15	46/70	10	13	33

2.6. Input data

The model does not use input data to represent time-varying processes.

2.7. Submodels

Submodels are presented in the following paragraphs separately for the two species *trees* and *dead_wood*, and a paragraph that introduces submodels on the global level of the model. The grid species *elevation_model* is not addressed because the species has a purely informing function for the species *trees* in transmitting the elevation at the location of a tree.

Time-related attributes are always given in years, sizes in m, areas in m² and volumes in m³.

2.7.1. Global submodels

Global submodels include processes that are not performed by one of the model species but are triggered on a higher model level. Conditions that originate from processes on the global level are consistent for all agents of a species. In contrast, submodels that are executed on the species level generate individual results for each agent.

2.7.1.1. Action: check_mast_year

The submodel determines the probability that the current model cycle is a mast year with an increased seed production of the tree population compared to a normal seed year.

$$mast_year_{prob} = mast_period_{max} * \left((1 - e^{(-0.035 * mast_period_{current})}) \right)^3 \quad (1)$$

where

$mast_period_{max} = 15$ = maximum number of years between consecutive mast years

$mast_period_{current}$ = number of years since the last mast year

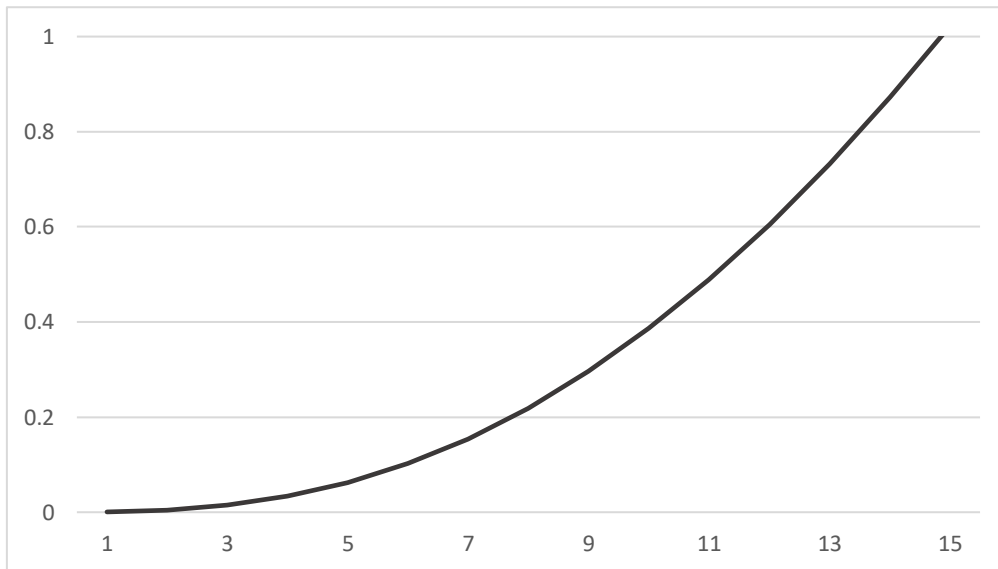


Fig. 8: Trend of the mast year probability with time since the previous mast year

2.7.2. Species “trees”

The species includes all life stages of a tree that are represented in the model. Due to restrictions in the application of spatial operators on 3-dimensional bodies within the GAMA modelling platform trees are simulated as 2-dimensional geometries. The basic geometry in the simulation of a tree is a circle representing the tree crown. The circle is equivalent to a vertical projection of the crown area on the forest floor. It therefore represents the maximum diameter of the crown. Further circles represent the influence zone of a tree and zones within the crowns of trees with a certain minimum size. These are the inner competition zone and the outer facilitation zone that are used in the simulation of interactions between dominant trees and seedlings as well as saplings (Fig. 2).

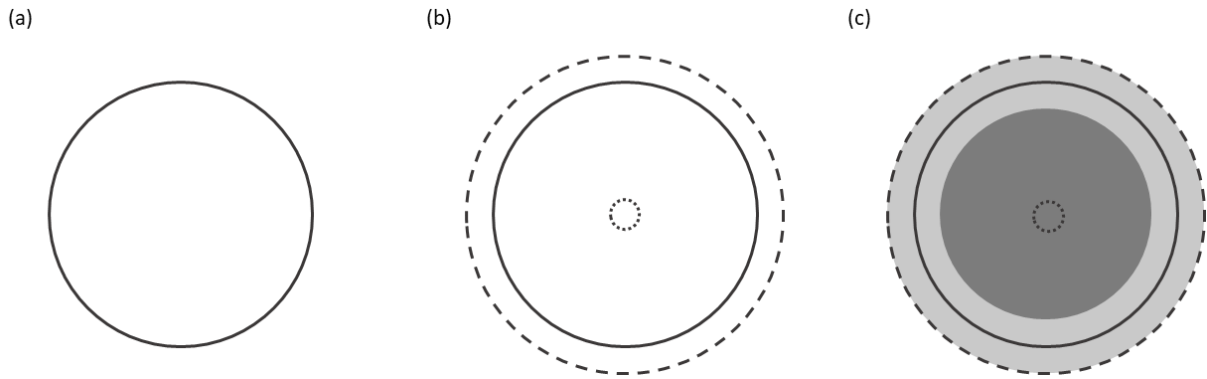


Fig. 9: Tree agents as represented in the model: (a) seedlings, (b) saplings and established trees, (c) dominant trees. Solid lines mark the outer limit of the crown, dotted lines the stem base, dashed lines the outer limit of the ZOI. The dark grey area indicates the competition zone and the light grey area the facilitation zone.

All submodels of the species trees are triggered once during each model cycle.

The simulation of tree growth is based on separate submodels for height growth and for diameter growth of the crown to allow for a different weighing of competition. Diameter growth of the crown is assumed to be more sensitive to competition than height growth.

2.7.2.1. Action: get_older

The submodel increases the value of the *age* attribute by 1 during each model cycle.

2.7.2.2. Action: set_height

The submodel sets the maximum height to which a tree can grow depending on elevation once either during initialization of the model for trees of the initial tree population or after germination for trees created during a simulation.

$$height_{max} = -0.04 * elevation + 90 \quad (2)$$

The relation between maximum tree height and elevation that underlies Eq. 2 is adopted from Holeksa et al. (2007) but was slightly adapted to the elevational range of upper montane and subalpine Norway spruce in the European Alps. As the equation describes an infinite straight line a lower and an upper limit to maximum tree height are set at 10 m and respectively 60 m. The resulting correlation between maximum tree height and elevation is supposed to be valid for Norway spruce of sub-alpine forests.

The initial values of the attributes $crown_{top}$, $crown_{base}$, and $crown_{height}$ are determined. For details on these attributes cf. section 7.2.3.

2.7.2.3. Action: grow_height

Height growth modelling is based on the Bertalanffy growth equation that was adapted by (Rammig et al. 2007) to simulate growth of subalpine spruce trees (Eq. 3). In order to be able to simulate changes in growth due to competition, a competition factor (*comp*) is added to the equation that reduces growth for trees in competitive neighbourhoods in correspondence with the intensity of competition affecting these trees. The maximum value of the growth constant *g* was determined by Rammig et al. (2007) on a site with natural spruce regeneration after a blowdown event at 0.035. This maximum value is used as an approximation of the growth dynamics of open-grown trees and provides the default value for the constant *g* in the growth simulation.

$$height = height_{max} * \left(1 - \left(1 - \left(\frac{height}{height_{max}}\right)^{\frac{1}{3}}\right) * e^{(-g*comp)}\right)^3 \quad (3)$$

While competition reduces growth, intra-specific interactions may also enhance growth. Height growth of trees that are benefiting from facilitation is constantly increased by a factor of 1.3.

$$height = height_{max} * \left(1 - \left(1 - \left(\frac{height}{height_{max}}\right)^{\frac{1}{3}}\right) * e^{(-g*1.3)}\right)^3 \quad (4)$$

When the submodel is triggered the variables $height_{release}$, $crown_{top}$, $crown_{base}$, and $crown_{height}$ are updated according to current tree height.

$$height_{release} = \frac{5}{6} * height \quad (5)$$

$$crown_{top} = elevation + height \quad (6)$$

$$crown_{base} = elevation + (height * 0.1) \quad (7)$$

$$crown_{height} = crown_{top} - crown_{base} \quad (8)$$

2.7.2.4. Action: grow_areas

Crown width (Eq. 9) and DBH (Eq. 10) are calculated from tree height according to empirical relations between these measures determined for open-grown spruce trees in Austria (Hasenauer 1997).

$$crown_{dia} = a + b * \ln(height_{crown}) * 2 * e \quad (9)$$

$$DBH = (1.2263132 * height^{1.2413})/100 \quad (10)$$

It is assumed that height and crown growth are differently affected by interactions with neighbouring trees. Crown growth may be more sensitive to competition than height growth and show a stronger growth reduction. To take this into account the variable $height_{crown}$ is introduced. It is a theoretical tree height that is used to calculate crown width. The calculation is based on the same equation used to determine tree height but employs a different competition variable ($comp_{crown}$) (Eq. 11) that allows to simulate a reaction of crown growth to competition that differs from the reaction of height growth. For trees benefiting from facilitation growth of the crown increases by a factor of 1.3 (Eq. 12) as does growth of tree height.

$$height_{crown} = height_{max} * \left(1 - \left(1 - \left(\frac{height}{height_{max}}\right)^{\frac{1}{3}}\right) * e^{(-g*comp_{crown})}\right)^3 \quad (11)$$

$$height_{crown} = height_{max} * \left(1 - \left(1 - \left(\frac{height}{height_{max}}\right)^{\frac{1}{3}}\right) * e^{(-g*1.3)}\right)^3 \quad (12)$$

An alternative equation is used to determine crown width of trees with crowns smaller than 1.5 m (Eq. 13) The relation between tree height and crown width as adopted from Hasenauer (1997) is only applicable for trees with a minimum height of 2.4 m and crown widths in excess of 1.6 m. Crown widths of smaller trees are clearly overestimated.

$$crown_{dia} = height_{crown} * 1.15 \quad (13)$$

The factor of 1.15 by which crown width is estimated to exceed height of small trees is chosen to allow a smooth transition between the application of eq. 13 and eq. 9. When switching from one equation to the other reductions of crown width can still occur due to individual growth trajectories resulting from competition and facilitation. To prevent shrinking of crown size current crown width is compared to previous crown width and in case of a smaller current crown width $crown_{dia}$ remains constant during the respective model cycle.

When the submodel is triggered the geometries $crown$, ZOI , $competition_{zone}$, $facilitation_{zone}$, and $stem_{base}$ and the variable ZOI_{vol} are updated according to current tree height or diameter of the crown respectively.

2.7.2.5. Action: create_seeds

Seed production is restricted to mature trees. The number of seeds that a tree produces is determined by the tree's height, the elevation at which it grows, and its competitive situation.

$$seeds_{nb} = (2.75 * height - 25.5) * \left(1 - \left(\frac{elev - 1300}{1000} \right) \right) * comp \quad (14)$$

The number of seeds increases with tree height (Dovčiak et al. 2008) and decreases with elevation (Mencuccini and Piussi 1995).

Seed production is subject to significant temporal changes that occur synchronized in large areas and dramatically increase seed production during mast years (Hackett-Pain et al. 2019). If the current model cycle was determined to be a mast year, for each tree the number of seeds is multiplied by a factor of 18 (Hofgaard 1993b).

To reduce the number of seeds within the model, only viable seeds are modelled, that are able to germinate given they are dispersed to a suitable microhabitat.

2.7.2.6. Action: disperse_seeds

Dispersal of spruce seeds around the maternal tree can be described by a leptokurtic function with an extended tail of long-distance dispersal (Nathan and Muller-Landau 2000). To simulate seed dispersal within the model a function by Dovčiak et al. (2008) was chosen that creates an isotropic and lognormal distribution of seeds and gives the number of seeds at a certain distance from the maternal tree.

$$seeds_{nb} = \frac{seeds_{total}}{\sqrt{2 * \pi * \sigma * i}} * e^{-\frac{\ln(i) - m^2}{2 * \sigma^2}} \quad (15)$$

where

$$\sigma = 1.028$$

i = distance from maternal tree (m)

The factor m is a function of the release height, that can be approximated as $\frac{5}{6}$ of tree height (Dovčiak et al. 2008).

$$m = \ln(0.484 * height_{release}) \quad (16)$$

Dispersal is realized within the model by creating circles at regular distances of 1 m around seed trees up to a maximum dispersal distance of 500 m. The maximum dispersal distance of 500 m guaranties

that more than 99 % of seeds are dispersed. The circles are then used as centre lines for rings with a width of 1 m that serve as geometries within which seeds are randomly spread. As all dispersed seeds are assumed to be viable new tree agents are created at each seed location during the same model cycle as seed dispersal takes place. Initial attributes and their values as assigned to the new tree agents are shown in Tab. 5. Initial seedling heights are determined randomly by a gaussian function (mean = 3 cm, sd = 1 cm). The minimum seedling height is set to be 1 cm. Thus, initial heights of seedlings correspond to a range of 1-5 cm (Rammig et al. 2007). The initial crown width of the seedlings is assumed to equal their height, their initial age is 0 and they are assigned the elevation of the grid cell in which they are located from the digital elevation model.

Tab. 5: Initial attributes and their values for tree agents created during seed dispersal

Attribute	Description
<i>location</i>	x-/y-coordinates at the location of the corresponding seed
<i>elevation</i>	Cell value of the grid species at the location of the tree Initial tree height
<i>height</i>	Random gaussian value, $mean = 0.03\ m$, $sd = 0.01\ m$ If $height \leq 0$, $height = 0.01\ m$
<i>crown_{dia}</i>	Initial diameter of the crown $crown_{dia} = height$
<i>age</i>	Initial age $age = 0$

2.7.2.7. Action: die_outside_world

All seeds that are dispersed outside the study area are deleted from the model.

2.7.2.8. Action: die_germination_stem_base

All seeds that are dispersed within the stem base area of a sapling or an established tree are deleted from the model. The stem base is a circular area around the location of a tree. The diameter of the stem base equals *DBH*.

2.7.2.9. Action: die_germination

The germination probability of a seed is determined by the environmental conditions of the microhabitat to which it has been dispersed. Although the model only simulates viable seeds not every seed eventually germinates. The model assumes a general germination probability of 30 % (Wallentin et al. 2008). Within the ZOI of a dominant neighbour germination probability increases to 50 %. On coarse woody debris (CWD) germination probability is 90 %. CWD has been shown to be a very favourable seed bed for spruce in subalpine forests (Zielonka and Niklasson 2001, Zielonka 2006). Microhabitats within the ZOI of tall trees are supposed to be more favourable for germination than open microhabitats. Dense ground vegetation strongly inhibits germination of Norway spruce seeds (Hunziker and Brang 2005, Kupferschmid and Bugmann 2005, Tasser et al. 2007, Dovčiak et al. 2008). Tall trees are assumed to reduce the density and thickness of the groundcover within their influence zones thereby increasing chances for germination. A higher proportion of bare ground and a sparser ground vegetation reduce the risk that seeds get entangled within vegetation without reaching the ground resulting in desiccation before making contact with a suitable seed bed.

2.7.2.10. Action: check_lifestage

Three basic life stages (*seedling*, *sapling*, *established*) are distinguished in the model based on an agent's age and height. Trees with a crown width above a minimum threshold 8.8 m are additionally marked as *dominant*. This crown width is equivalent to a height of 10 m of an open grown tree. This size threshold is used to identify trees with a substantial effect on their immediate environment. These trees are assumed to significantly change the environmental conditions within their influence zones particularly through intense shading, thereby causing changes in ground vegetation and creating microhabitats with conditions that differ substantially from corresponding open patches.

Tab. 6: Definition of life stages

Life stage	Description
<i>seedling</i>	$age \leq 2$
<i>sapling</i>	$age > 2$ and $height \leq 3$
<i>established</i>	$height > 3$

Mature trees ensure the survival of a forest through the production and dispersal of trees. But the number of seed trees within a forest is relatively small (Piotti et al. 2009, Hacket-Pain et al. 2019). It is assumed that a combination of factors including age, size, and competitive state are crucial to determine maturity. While trees only start to produce seeds at a certain age, open grown trees start to produce seeds at a younger age than trees in competitive neighbourhoods (Modrzyński 2007). As competition can have a significant effect on the growth of a tree, the correlation between age and size of a tree can be misleading. Therefore, model trees have to fulfil the same size requirement to become mature as to be characterized as dominant. It is assumed that trees under intense competition ($comp \leq 0.3$) do not become mature.

$maturity = true$

$$\begin{aligned}
 & \text{if } ((age \geq 30) \text{ and } (comp = 1.0) \text{ and } (crown_{dia} \geq 8.8)) = true \\
 & \text{else if } ((age \geq 40) \text{ and } (0.8 \leq comp \leq 1.0) \text{ and } (crown_{dia} \geq 8.8)) = true \\
 & \text{else if } ((age \geq 60) \text{ and } (0.3 < comp < 0.8) \text{ and } (crown_{dia} \geq 8.8)) = true
 \end{aligned} \tag{17}$$

2.7.2.11. Action: check_facilitation

This submodel only identifies those individuals that benefit from facilitation while the effect of the facilitation is determined within the submodels simulating growth and mortality. Facilitation occurs when the net outcome of the interactions with con-specific neighbours are positive. Plants can benefit from facilitation through increased growth or reduced mortality. It is assumed that in a tree community only seedlings and saplings can benefit from facilitation while interactions between established individuals generally have a net negative outcome.

Two situations are considered within the model that induce facilitation. Seedlings and saplings benefit from a low competitive neighbourhood constellation. These are created by dominant trees that suppress ground vegetation (Jäderlund et al. 1997, Hunziker and Brang 2005, Kupferschmid and Bugmann 2005, Dovčiak et al. 2008) but also imply low intra-specific competition (Hofgaard 1993c, Hunziker and Brang 2005, Zielonka 2006, Scotti et al. 2008, Svoboda et al. 2010). Therefore, microhabitats with net-positive interactions are those that are located within the facilitation zone (outer are of the influence zone) of only one dominant neighbour. Facilitated individuals are selected

based on their location within a facilitative microhabitat. It is not necessary that the crown of the benefiting tree is completely located within a facilitative microhabitat (Fig. 3).

In addition to low competitive neighbourhoods the presence of CWD induces facilitation for individuals that germinate on this type of substrate (Hofgaard 1993c, Hunziker and Brang 2005, Zielonka 2006, Holeksa et al. 2007). The facilitative effect for individuals growing on CWD is restricted to the seedling stage.

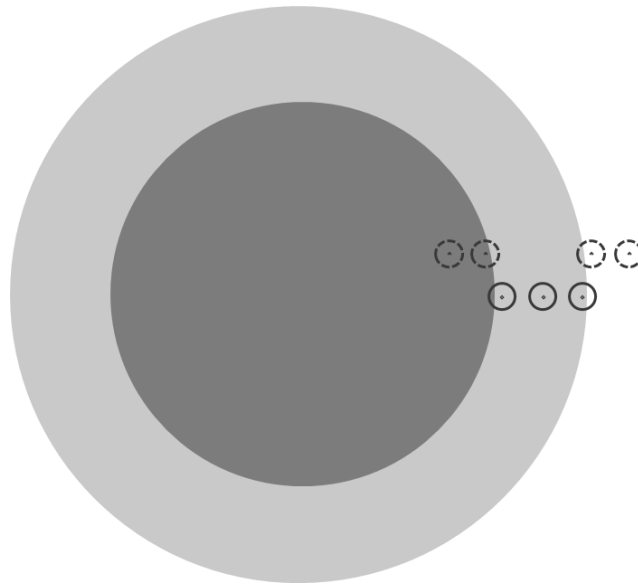


Fig. 10: Schematic illustration of the positioning of seedlings and saplings that benefit from facilitation with respect to the facilitator. The light grey area represents the facilitation zone, the dark grey area the competition zone of a dominant tree. Small circles indicate crown areas of seedlings or saplings. Dots mark their locations. Solid lines indicate seedlings or saplings that benefit from facilitation, dashed lines indicate those without facilitation. The presence of only one neighbour is a prerequisite for facilitation.

2.7.2.12. Action: find_neighbours

Competition is assumed to be either symmetric or asymmetric. Relative size symmetry implies that the competitive effect of a tree is proportional to its size, while in the case of asymmetric competition larger competitors have a disproportionate advantage over smaller competitors (Weiner 1990). It is often assumed that competition for light is the most important aspect of above-ground competition and that this competition is asymmetric, because light interception of a larger neighbour can result in a pre-emption of the resource (Weiner and Thomas 1986, Thomas and Weiner 1989, Weiner 1990, Schwinning and Weiner 1998). Within the model symmetric and asymmetric types of competition can be simulated through the rules determining the allocation of contested volumes of the lfs between the contestants. Size-symmetric competition is simulated as the equal allocation of the intersecting ZOI volume to both competitors (Weiner et al. 2001) while under size asymmetry parts of the intersecting ZOI volumes are assigned to competitors in accordance with their size relation (Eq. 18 and Fig. 4).

The purpose of this submodel is to define the interaction neighbourhood of each tree. Within the model trees are defined as interacting neighbours if their ZOIs intersect. Interactions between neighbours affect the main ecological processes growth, reproduction, and mortality. The net outcome of interactions between trees can be negative or positive. A tree either competes with its neighbours or it is facilitated. In addition to delimiting the interaction neighbourhood of each tree based on intersections of ZOIs the volume of ZOI intersections is determined for individual trees. Starting from 2-dimensional ZOIs cylindrical bodies are calculated as an approximation of the 3-dimensional tree

crown. Working with intersecting volumes instead of areas brings the advantage of a realistic representation of height differences between neighbouring trees. The height of interacting trees is a major influence on the outcome of the interaction for all individuals. Competition is either simulated as symmetric or as asymmetric (Weiner 1990). To simulate symmetric competition, it is assumed that both competing trees lose 50 % of the volume of intersecting ZOIs. Under this premise, trees with larger crowns have a competitive advantage over smaller trees since the lost part of the crown accounts for a greater share of the crown of the smaller competitor compared to its larger neighbour. But competition is size-symmetric since both competitors lose the same volume of their crown. The idea of asymmetric competition is based on the assumption that larger competitors have a disproportionate advantage over smaller competitors. To simulate this type of competition the share of the intersecting ZOI volume that each competitor loses is proportionate to their size relation (Eq. 18). Thus, the intersecting ZOI volume is lost to a greater share to the smaller competitor (Fig. 4).

$$size\ ratio = \frac{CROWN_{volumeN}}{CROWN_{volumeT} + CROWN_{volumeN}} \quad (18)$$

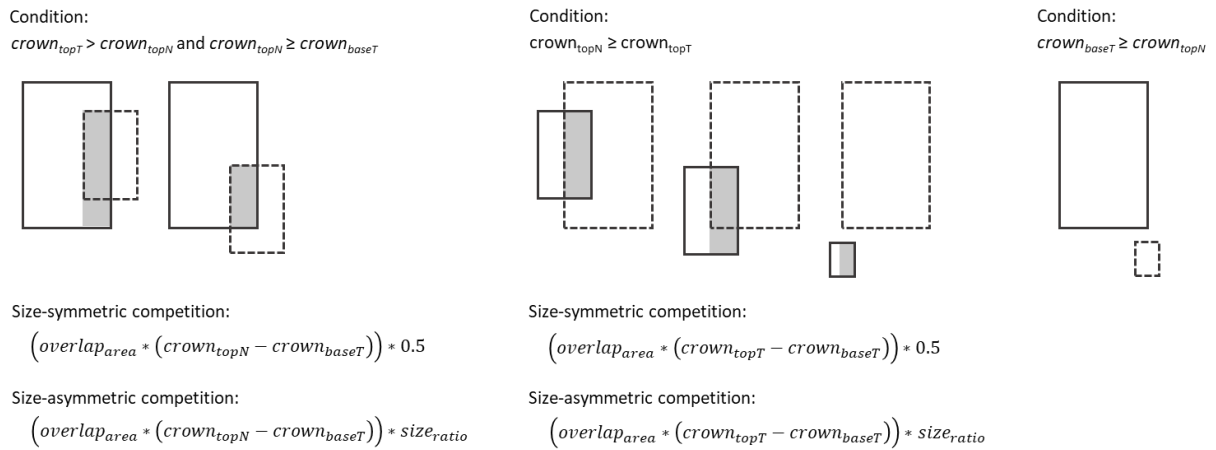


Fig. 11: Schematic depiction of possible ZOI intersections and calculation of intersecting crown volumes for symmetric and asymmetric competition. Solid lines indicate the subject tree (T), dashed lines a neighbour (N). Light grey areas indicate intersecting ZOI volumes.

Calculations are done separately for each neighbouring tree. The volume of ZOI intersections per tree is used to determine the intensity of competition for individual trees in the submodel *comp_calculation*. For seedlings only the number of neighbours and the position of the seedling within the ZOI zones of its dominant neighbours are recorded. A more detailed assessment of the neighbourhood configuration, as described above, is assumed to offer no additional value to the simulation of growth and mortality of seedlings. Also, seedlings are not considered in the simulation of neighbourhood configurations as they are assumed to have no relevant effect on other trees.

2.7.2.13. Action: comp_calculation

The submodel calculates competition factors that are specific to height growth (*comp*), growth of the tree crown (*comp_{crown}*) and mortality (*comp_{mort}*) and applied in the submodels simulating growth, reproduction, and mortality as processes linked to competition. In the absence of competition competition factors retain a value of 1.0 that does not change the results of growth calculations. Thus, maximum growth is maintained and only subject to current tree height. For a competition factor of 1.0 competition-related mortality generally gives out 0.0, independent of the duration of competition. Competition factors decrease with increasing competition and approach 0.0 if competition is intense.

The minimum value for competition factors related to growth is set at 0.01 as living trees are assumed to retain a minimum growth even under intense competition. For the competition factor specific to mortality the minimum value is 0.0. Competition factors are calculated as the inversed ratio of all intersecting volumes of the ZOI between a tree and its neighbours and the total volume of the ZOI of that tree. The ratio is 0.0 for trees growing without any neighbours and increases with a rising volume of intersecting ZOI. If more than one neighbour intertwines into or overshadows the same part of the crown of a tree the ratio can attain values > 1.0 .

$$comp = 1 - \frac{intersection_{total}}{ZOI_{volume}}, \text{ if } comp < 0.01 \text{ then } comp = 0.01 \quad (19)$$

$$comp_{crown} = 1 - \frac{intersection_{total}}{ZOI_{volume}} * 2, \text{ if } comp_{crown} < 0.01 \text{ then } comp_{crown} = 0.01 \quad (20)$$

$$comp_{mort} = 1 - \frac{intersection_{total}}{ZOI_{volume}}, \text{ if } comp_{mort} < 0.0 \text{ then } comp_{mort} = 0.0 \quad (21)$$

In general, the model assumes a proportional relation between the ratio of intertwined or overshadowed ZOI volume and the reduction in height growth. However, this relation is modified if parts of a tree's ZOI volume are occupied by more than one neighbour. As the diameter growth of a tree's crown is assumed to be more affected by competition than the tree's height growth, $crown_{intersection_ratio}$ is multiplied by a factor of 2 to simulate a more distinct effect of competition.

For trees that are impacted by competition, the duration of the competitive stress is recorded in years. The duration during which a tree is affected by competition is reset to 0, if the competition factor increases considerably between the last and the current year (Eq. 22). A higher competition factor indicates lower competitive pressure. Resetting the duration of competitive stress is important to account for sudden releases from competition that occur when neighbouring trees are lost due to e.g. windthrow or insect attacks or intrinsic processes. Trees can react to releases from competition with considerable increases in growth (Cherubini et al. 1996). Such growth dynamics and the existence of a class of suppressed saplings, also referred to as advance regeneration, seem to be common in subalpine spruce forests (Mencuccini et al. 1995, Szwagrzyk and Szewczyk 2001, Svoboda et al. 2010).

$$\frac{(1 - comp)}{(1 - comp_{(t-1)})} \leq 0.5 \quad (22)$$

2.7.2.14. Action: die_tree

Mortality is simulated representing different life stages and accounting for competition as well as facilitation. Mortality is calculated annually as the probability of a tree to die during that year. In the model mortality is broken up into an age/size-related and a competition-related component to allow for an explicit simulation of mortality as a result of competition of individual trees. The two components of mortality are added to obtain total mortality.

Age-related mortality of seedlings and saplings is modelled with a power function. This function induces a seedling mortality during the first growing season of 70 %, that strongly decreases during the following years (Cui and Smith 1991, Brang 1998, Nilson and Lundqvist 2001, Hanssen 2003).

$$mort_{base} = 0.7/age^{1.4} \quad (23)$$

For established trees base mortality is not strictly age-related but rather size related as the tallest trees of a stand are subject to an increased risk of windthrow (Canham et al. 2001). Therefore, a constant base mortality of 0.5 % (Vieilledent et al. 2010) is assumed for trees that have reached at least 80 % of their maximum height.

Adding to age-related mortality the model also simulates competition-related mortality that is higher, if competition is more intense, and increases with the duration of competition (Eid and Tuhus 2001, Cherubini et al. 2002, Bigler and Bugmann 2003, Castagneri et al. 2010, Vieilledent et al. 2010, Peltoniemi and Mäkipää 2011). For trees that are under intense competition mortality increases faster than for trees with less competition and for saplings mortality increases faster than for established trees (Eq. 24-26).

$$mort_{comp} = (1 - e^{-0.01*|comp_{mort-1}|*comp_{dur}})^2 \quad (24)$$

$$mort_{comp} = (1 - e^{-0.02*|comp_{mort-1}|*comp_{dur}})^2 \quad (25)$$

if $comp \leq 0.3$ or if $sapling = true$ and $0.3 \leq comp \leq 1.0$

$$mort_{comp} = 0.035 + (1 - e^{-0.08*|comp_{mort-1}|*comp_{dur}})^2 \quad (26)$$

if $comp \leq 0.3$ and $sapling = true$

Generally, competition- related mortality increases slowly after the onset of competition as trees can tolerate competition for prolonged periods of time (Cherubini et al. 1996, Cherubini et al. 2002, Bigler and Bugmann 2003). Saplings are assumed to be more sensitive against intense competition ($comp \leq 0.3$) as light requirements of Norway spruce increase with age (Modrzynski 2007).

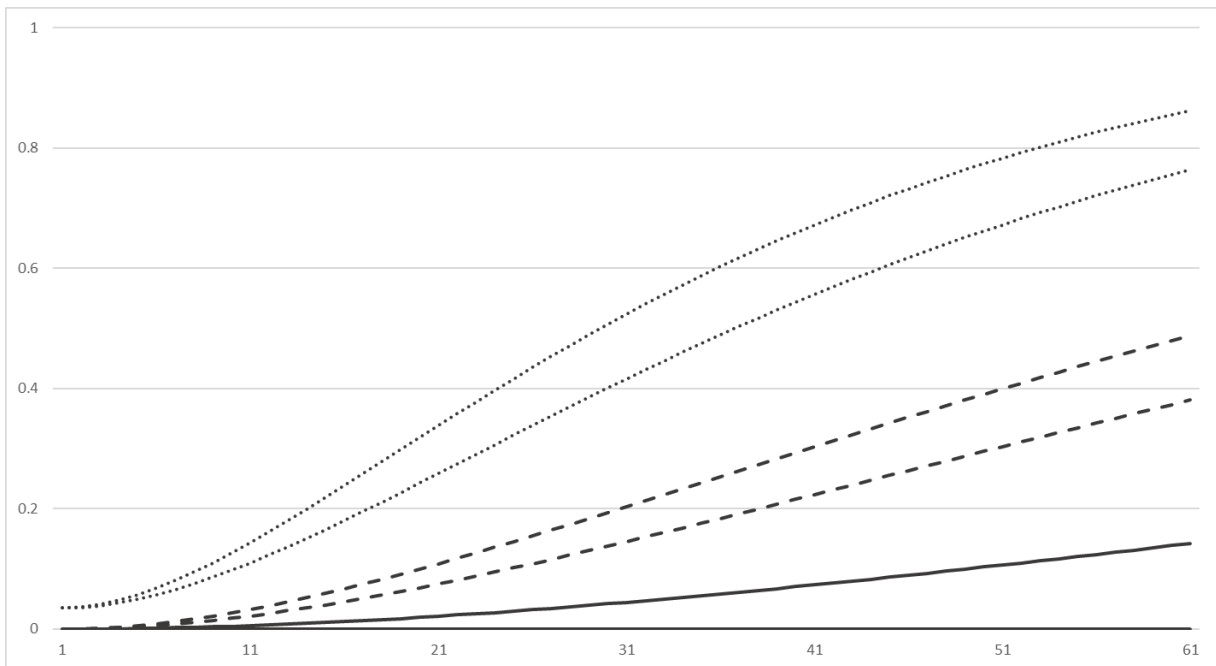


Fig. 12: Changes of competition-related mortality probability with the duration of competition. Solid lines show the range of mortality for trees under light to moderate competition ($0.21 \leq comp \leq 0.99$), dashed lines the range under strong competition ($0.00 \leq comp \leq 0.20$), and dotted lines the range of mortality for saplings under strong competition ($0.00 \leq comp \leq 0.20$).

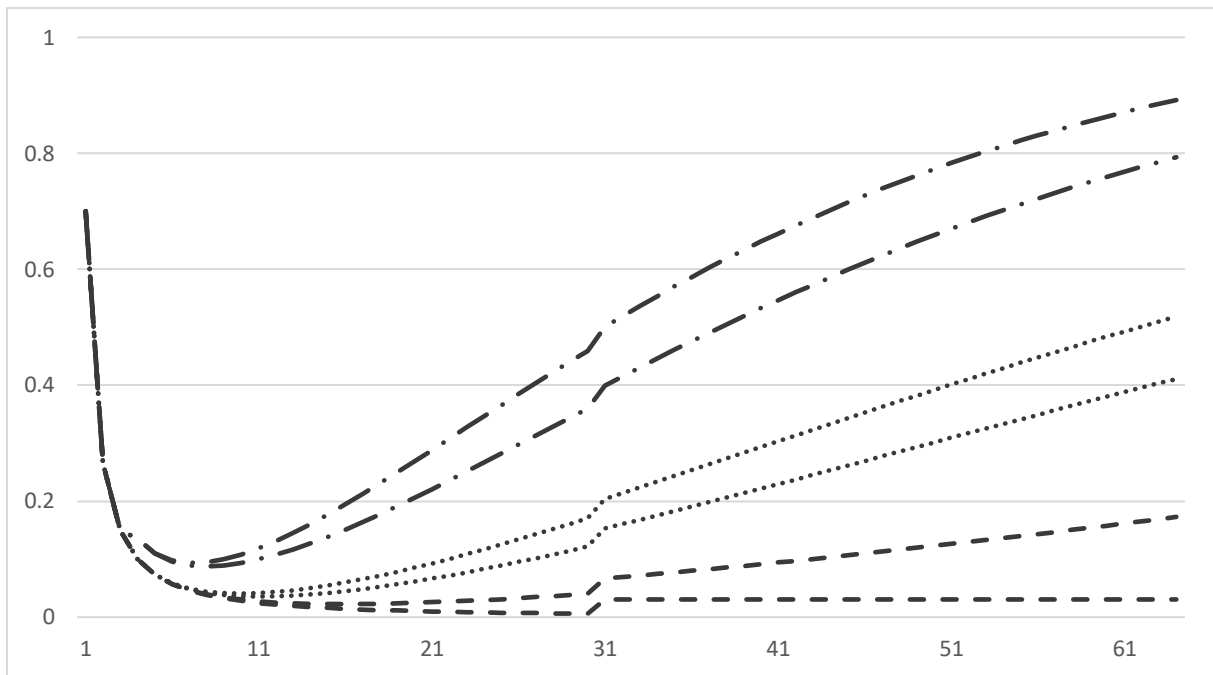


Fig. 13: Total mortality of trees that grow under constant competition from the start of competition calculations. Dashed lines show the range of mortality for trees under light to moderate competition ($0.21 \leq \text{comp} \leq 0.99$), dotted lines the range under strong competition ($0.00 \leq \text{comp} \leq 0.20$), and dash-dotted lines the range of mortality for saplings under strong competition ($0.00 \leq \text{comp} \leq 0.20$).

It is assumed that intra-specific competition has no significant effect on the mortality of seedlings. These are therefore excluded from the simulation of competition related mortality. Instead conditions within the micro-habitat of the seedlings are assumed to be decisive factors for mortality. Especially the rudimentary root system makes seedlings susceptible to fluctuations in habitat conditions and disturbances to their habitat. Main causes for seedling mortality include insufficient water availability and stability of the ground in addition to infection with pathogenic fungi and clipping by animals (Cui and Smith 1991, Brang 1998).

For agents that benefit from facilitation total mortality is reduced by half.

2.7.3. Species “CWD”

The purpose of the species is to simulate decaying wood from fallen trees that creates favourable microsites for seedlings and saplings of Norway spruce in subalpine spruce forests. Decomposing wood from fallen trees or coarse woody debris (CWD) forms an important microhabitat for recruitment of Norway spruce in subalpine forests (Zielonka and Niklasson 2001, Hunziker and Brang 2005, Kupferschmid and Bugmann 2005, Motta et al. 2006, Zielonka 2006, Svoboda et al. 2010). The model simulates only the presence of the logs as the main wood volume and therefore the most important source for stable, long term habitats for recruitment. Complete decomposition of a log may take more than 100 years in a subalpine environment (Holeksa and Cybulski 2001, Zielonka 2011). Logs of small trees are not considered as a source of CWD in the model. They are assumed to be of less importance to spruce recruitment as they do not create such long-term habitats for seedlings and saplings due to their shorter decomposition time.

The creation of agents of the species *dead_wood* is triggered by the death of tree agents that exceed a minimum height requirement ($\text{crown_dia} \geq 8.8$). The *dead_wood* agent is a linear object that represents the log of a tree. When created *dead_wood* agents are assigned three initial attributes, that

they inherit from the corresponding tree agent: location, that is x- and y-coordinates, diameter of the log that equals the tree's DBH, and length of the log that equals the tree's height.

2.7.3.1. Action: `init_log`

Agents of the species *CWD* are created as rectangular geometries that represent an area of CWD on the forest floor. The base of the log is created at the location of the former tree. The top of the log points at a random direction.

2.7.3.2. Action: `count_decomp`

The submodel records time since the creation of an agent. An agent is recognised as a favourable seed bed ten years after its initial creation. At that time the model starts to count the age of the seed bed.

2.7.3.3. Action: `CWD_gone`

Agents are erased from the model when the age of the seed bed is 40.

2.7.3.4. Action: `strike_trees`

Falling trees may knock down other trees in their proximity. If the ZOI of a tree is overlapped by a *dead_wood* agent this tree might be triggered to fall as well, if the *dead_wood* agent is more than 50 % taller than the tree. In this case the tree dies and creates in turn a new *dead_wood* agent if its height is at least 10 m.

2.7.4. Grid species "elevation_model"

The grid species is created from a digital elevation model of the study area with a resolution of 1 m². The digital elevation model is not processed or changed within the model. Its only purpose is to inform tree agents of the elevation corresponding to their location.

3. Model analysis

The model was analysed by comparing results of simulations for different scenarios. The baseline scenario starts with a nucleus tree group at an elevation of 1600 m a.s.l. Competition is modelled as asymmetric and both facilitation and CWD are included as active submodels. Alternative scenarios were chosen to evaluate the model's sensitivity to changes in core elements of the model. The effect of the type of competition was tested by comparing results of the baseline scenario to a scenario of symmetric competition. To assess the model's sensitivity to different elevations simulation runs were performed for additional tree populations at 1400 m and 1800 m a.s.l. For further simulation runs either the submodel creating CWD or the submodel causing facilitation were excluded from the model. Finally, the impact of the initial tree population was tested by comparing results of the baseline model to those of populations developing from a plantation. As the baseline scenario this scenario was run with asymmetric and symmetric competition.

The nucleus population is made up of 15 trees with tree heights ranging between 4 – 15 m and crown diameter and age defined to be consistent with trees growing with their maximum growth rate. The nucleus population represents a loose group of trees at the centre of the model area of 1 ha. An alternative initialization creates a tree population of 1764 saplings that covers the whole model area. Height of all saplings is 16 cm with a corresponding crown diameter and an age of 3 years. Saplings are regularly spaced at distances of 2.4 m. The plantation population was assumed to be particularly sensitive to edge-effects. Therefore, the model area was extended by 16 m on each side for simulations of plantation populations and results were only analysed for the core population.

All simulations were run for a time span of 600 years to enable the analysis of long-term population dynamics. Attribute values for each model agent of the species trees and CWD were written to

separate CSV-files at the end of each model cycle. An additional CSV-file was created, that contained attribute values of trees dying during a model cycle describing their state at the time of death. Microsoft Excel was used to analyse data and create the corresponding figures. All analyses are based on mean results created from 5 simulation runs with identical configurations of the model. Results for simulations of the different scenarios were compared for the number of trees/ha, tree height, and competition and stratified according to the life stage classes seedlings, saplings, and adult trees as well as mature trees.

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