



Plastic tree crowns contribute to small-scale heterogeneity in virgin beech forests—An individual-based modeling approach

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ABSTRACT

Old-growth beech (*Fagus sylvatica* L.) forests in Europe show a structural heterogeneity, which distinguish from managed ones. Recent investigations revealed that facilitative belowground interactions might counteract aboveground competition for light. However, the exact interaction of these mechanisms is unclear. We developed the BEEchPlasticity (BEEP) model to investigate whether the mere focus on the aboveground competition for canopy space with subsequent modeling of the light transmittance through the forest canopy suffices to reproduce the observed structural attributes. The BEEP model is individual-based, and explicitly describes the plasticity of tree crowns in a three-dimensional space through a geometric approach. This conceptual design allows tracing neighborhood effects to the forest stand level.

We ran 10 simulation experiments with 1000 time steps on a simulation area of 0.5öha. We analyzed the emerging spatial point patterns, gap dynamics as well as distributions of tree age, tree height, tree crown projection area, and tree diameter. By applying various indices that revealed the emergent horizontal and vertical forest structure, we were able to show a strong mutual link between beech crown plasticity and forest heterogeneity. The crown plasticity enabled the trees to close small gaps, which resulted in a highly dynamic tree regeneration, which in turn led to a small-scale heterogeneous forest structure. We found that, over long periods, crown centroids of canopy trees taller than 20öm were more regularly distributed than stem foot points. Absolute crown displacements were greater than reported from beech stands in North-Germany and the Sudetes in the Czech Republic. This indicates a need to restrain the model crown growth in order to recognize tree architecture and stability. We could simulate an increasing forest structural heterogeneity. Starting with a structural homogeneous layer of tree saplings, we showed that forest structures similar to those in unmanaged beech forests took several tree generations or approximately 700 time steps to emerge. We recommend enhancing this model approach with spatial explicit modeling of the leaf-area distribution, which has already been done for single beech trees.

1. Introduction

Today, relicts of virgin beech forests (*Fagus sylvatica* L.) in Europe are scattered, and are mostly of small size (Leibundgut, 1993; Smejkal et al., 1997; Tabaku, 2000), while extensive forests are exceptional (Tabaku, 2000; Hobi et al., 2015a). This situation is the result of a human-induced reduction of beech forest, once the most important forest community in central Europe (Peterken, 1996). Consequently, relict beech forests have been listed as a UNESCO world natural heritage (Vološćuk, 2014).

Hobi et al. (2015a) found multi-layered beech forests stands interrupted by mostly small canopy gaps, and a high abundance of old large-

diameter trees in the Ukrainian Carpathians. Less than 2% of the gaps were greater than 200 m² (Hobi et al., 2015b). Similar results have been reported from Slovenian virgin beech forests (Zeibig et al., 2005).

Beech trees are able to adapt their crown shape according to neighborhood crown pressure, and available Photosynthetic Active Radiation (PAR) (Petriřan et al., 2009). This mechanism is known as crown plasticity. Release events in the forest canopy caused by the death of trees lead to an extension of tree crowns into canopy gaps (Muth and Bazzaz, 2001; Fichtner et al., 2013). If the gap is sufficiently small, closure is reached after several years depending on the vitality of the trees that surround the gap edges. Canopy gaps remain if their size is beyond the average shoot growth potential of the canopy trees.

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Trees position their crowns away from neighborhood pressure and shading (Muth and Bazzaz, 2003). Crown displacement can be described by the horizontal distance between the stem foot position and the center of gravity or centroid of the crown projection area (Schröter et al., 2012). Spatial statistics, such as Ripley's K function (Ripley, 1977) or the Clark-Evans-Index (Clark and Evans, 1954), have been successfully applied in revealing different spatial patterns of tree stem foot positions and their crown centroids, leaving the latter more regularly distributed than stem foot positions (Schröter et al., 2012; Bulušek et al., 2016). However, only a few studies directly link the observed patterns to the underlying processes (e.g. Fichtner et al., 2015).

Crown plasticity facilitates the expansion of the tree crown into canopy gaps and, in turn, enhances individual tree growth (Juchheim et al., 2017) demonstrating the importance of plastic tree crowns as a driver of forest dynamics (Fichtner et al., 2013; Glatthorn et al., 2017). This mechanism has already been studied for mixed species forests (Longuetaud et al., 2013; Jucker et al., 2015) and for *Pinus sylvestris* L. forests (Uria-Diez and Pommerening, 2017). The interplay between canopy openings and crown plasticity alters the environmental conditions beneath the forest canopy and impacts the growth of understory trees. However, well-studied are only the influences of gap size on the light regime and microclimatic conditions for beech forests (Ritter et al., 2005; Gálhidy et al., 2006; Bílek et al., 2014; Čátek et al., 2014; Čátek and Kobler, 2017).

The analysis of belowground processes is still hard to handle, and results from the few available studies are contradicting. For example, beech trees seem to compete size-asymmetrically for belowground resources, and this behavior is in contrast to many other species (Beyer et al., 2013). Facilitative effects have been also observed particularly between small- and large-diameter trees. These effects, for example, are attributed to mycorrhizal networks (Beiler et al., 2015; Fichtner et al., 2015). It seems to be established, however, that belowground processes can counteract the aboveground intraspecific competition in old-growth beech forests (Fichtner et al., 2015), which demonstrates the complementarity of both, and the basis for the complexity of the net outcome of tree interactions in near-natural beech forests. Facilitative effects have been observed between small- and large-diameter trees probably caused by mycorrhizal networks (Beiler et al., 2015; Fichtner et al., 2015).

These effects could even increase the resilience of forests against environmental changes, which would be in agreement with the hypotheses that forests with a long ecological continuity are better adapted to global change than others (von Oheimb et al., 2014). Various case studies demonstrated the existence of beech-microbial mutualism (e.g., Cesarz et al., 2013). Beech selectively allocates carbon to specific mycorrhizal species at the root tip level (Valtanen et al., 2014). Mycorrhizal species exert a functional feedback on their hosts in terms of nutrient uptake, transfer, and storage (Seven and Polle, 2014). Klein et al. (2016) revealed a significant carbon exchange in a temperate forest, even between trees of different species. However, empirical studies have not been able to capture the importance of these belowground interactions for stand dynamics so far.

The question arises how above and belowground processes interact, and if focusing on one mechanism alone, namely the aboveground competition for light and crown space, could explain the patterns and structures we observe in beech forests. Individual-based models (e.g. Lin et al., 2012; Grueters et al., 2014) provide an excellent basis to address such questions. However, the focus on the aboveground competition for light needs the explicit description of beech crown plasticity, which has not been achieved yet. The grid-based model BEFORE can reproduce the mosaic pattern of developmental stages of old-growth beech forests (Rademacher et al., 2004), but does not include tree crown plasticity. Individual-based forest models, such as LES, include plastic tree crowns (Liénard and Strigul, 2016), but do not explicitly model beech forests. Beech crown dynamics were accurately

modeled for single trees but not for complete stands, nor from an individual-based perspective (Beyer et al., 2014, 2015, 2017). This led us to the development of the BEEchPlasticity (BEEP) model, which is able to simulate plastic tree crowns from an individual-based perspective for whole forest stands. The plasticity approach used in this model is geometric, and was already applied for modelling crown plasticity of *Hevea brasiliensis* (Willd.) (Vincent and Harja, 2008).

We applied the model to the question if spatial point patterns, crown displacements, gap dynamics and subsequent alteration of the light transmittance through the forest canopy can be reproduced by only focusing on modeling the aboveground competition for crown space.

2. Materials and methods

2.1. The model

The description of our individual-based BEEP model (Grimm and Railsback, 2005) follows the ODD protocol (Grimm et al., 2010).

2.1.1. Purpose

The BEEP model was developed for the description of old-growth forests of European beech (*Fagus sylvatica* L.). The model explicitly considers tree crown plasticity as a response to available radiation, and neighboring tree crowns. The model is used to explore the mutual link between light competition, crown shift, random loss of crown parts, tree growth, and mortality. Particular emphasis is placed on the importance of crown plasticity for structural patterns, such as the vertical heterogeneity in tree heights and horizontal distribution patterns of stem locations and crown centroids.

2.1.2. Entities, state variables, and scales

The BEEP model has only one entity, namely individual beech trees. They are described by a set of simple state variables characterizing the location for the tree and the dimension of the stem

- x, y [m, m] coordinates of the stem foot point.
- dbh [cm] stem diameter at breast height.
- h [m] tree height.

Further state variables specify the crowns dimensions:

- [m] - height of the crown onset point (the x, y – coordinates are equal to the stem foot point of the tree). The crown onset point is the origin of the crown vectors shown in Fig. 1.
- x, y, z [m, m, m] – coordinates of the points spanning the crown surface.
- Vectors connecting the onset point with the various points on the crown surface are referred to as crown vectors.

Considering the photosynthetic active radiation (PAR) as environmental factor, the

- PACL [%] – percentage of above canopy light received is the last state variable of the trees regulating their height growth.

One time step represents one year. Space is described in three dimensions. The typical size of a simulated plot is 0.5 ha in order to keep the simulation time manageable, but can be varied by the experimenter.

2.1.3. Process overview and scheduling

The model describes five processes, namely *regeneration*, *radiation*, *mortality*, as well as *height*, and *crown growth*. The flowchart in Fig. 2 shows the sequence of their execution.

Regeneration assumes a masting rhythm of three time steps. The new tree recruits are established in a minimum distance of 0.3 m of an

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