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An Individual-Based Process Model to Simulate Landscape-Scale Forest Ecosystem Dynamics

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An individual-based process model to simulate landscape-scale forest ecosystem dynamics

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ABSTRACT

Forest ecosystem dynamics emerges from nonlinear interactions between adaptive biotic agents (i.e., individual trees) and their relationship with a spatially and temporally heterogeneous abiotic environment. Understanding and predicting the dynamics resulting from these complex interactions is crucial for the sustainable stewardship of ecosystems, particularly in the context of rapidly changing environmental conditions. Here we present iLand (the individual-based forest landscape and disturbance model), a novel approach to simulating forest dynamics as an emergent property of environmental drivers, ecosystem processes and dynamic interactions across scales. Our specific objectives were (i) to describe the model, in particular its novel approach to simulate spatially explicit individual-tree competition for resources over large scales within a process-based framework of physiological resource use, and (ii) to present a suite of evaluation experiments assessing iLands ability to simulate tree growth and mortality for a wide range of forest ecosystems. Adopting an approach rooted in ecological field theory, iLand calculates a continuous field of light availability over the landscape, with every tree represented by a mechanistically derived, size- and species-dependent pattern of light interference. Within a hierarchical multi-scale framework productivity is derived at stand-level by means of a light-use efficiency approach, and downscaled to individuals via local light availability. Allocation (based on allometric ratios) and mortality (resulting from carbon starvation) are modeled at the individual-tree level, accounting for adaptive behavior of trees in response to their environment. To evaluate the model we conducted simulations over the extended environmental gradient of a longitudinal transect in Oregon, USA, and successfully compared results against independently observed productivity estimates (63.4% of variation explained) and mortality patterns in even-aged stands. This transect experiment was furthermore replicated for a different set of species and ecosystems in the Austrian Alps, documenting the robustness and generality of our approach. Model performance was also successfully evaluated for structurally and compositionally complex old-growth forests in the western Cascades of Oregon. Finally, the ability of our approach to address forest ecosystem dynamics at landscape scales was demonstrated by a computational scaling experiment. In simulating the emergence of ecosystem patterns and dynamics as a result of complex process interactions across scales our approach has the potential to contribute crucial capacities to understanding and fostering forest ecosystem resilience under changing climatic conditions.

1. Introduction

Analyzing ecosystems from a complex systems perspective has yielded considerable advances in our understanding of their dynamics in recent years (e.g., Sierra et al., 2009; Donato et al., 2011). Complexity in ecosystems, i.e., their diversity, nonlinearity, interconnectedness, and spatio-temporal heterogeneity (see Wu and Marceau, 2002; Cadenasso et al., 2006), is also a core component of emerging approaches to managing change in social–ecological systems, such as the resilience concept (Holling and Gunderson, 2002; Chapin, 2009). Consequently, ecological complexity has received increasing attention also in the management of forest ecosystems recently (e.g., Heinimann, 2009; Kuuluvainen, 2009; Puettmann et al., 2009).

Management inherently involves an element of forecasting, and simulation modeling is a powerful tool for making projections about the trajectories of complex systems (Wu and David, 2002;

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Green et al., 2005). To make ecological complexity more operational in the context of modeling, different dimensions can be distinguished, e.g., the functional, structural, and spatial complexity of ecosystems (Loehle, 2004). In traditional forest modeling, these dimensions have generally been addressed separately by different families of forest models. Physiological models (e.g., Running and Coughlan, 1988; Bossel, 1996) have focused on a detailed representation of ecosystem processes such as photosynthesis, respiration, and allocation, and the influence of environmental drivers on these processes, i.e., they primarily address functional complexity. Gap models (e.g., Botkin, 1993; Bugmann, 2001) have been developed to study the structural and compositional dynamics of forest ecosystems as mediated by the environment, and thus deal mainly with structural complexity. Forest landscape models (e.g., He et al., 1999; Scheller and Mladenoff, 2007) have been designed to simulate patterns and processes across forest landscapes, presenting a means to study spatial complexity in ecosystems. From a complex systems perspective traditional forest modeling paradigms have thus largely adopted a reductionist approach (Li, 2000).

However, the expected changes in the climate system are going to affect a variety of processes across a wide range of scales simultaneously (Lindner et al., 2010; Spies et al., 2010). Assessing how climate change might impact the dynamics of complex forest ecosystems and how resilient they are to these impacts thus requires an integrated, multi-scale perspective. Recent advances in forest modeling have thus addressed the challenge of integration: Hybrid approaches have been developed to integrate functional and structural aspects in modeling (e.g., Peng et al., 2002; Seidl et al., 2005), while interactions between spatial and structural aspects have been tackled with modular designs (e.g., Scheller et al., 2007). Advances in computing power and software design have also aided endeavors to model patterns and processes in forest ecosystems more holistically (Scheller et al., 2010; Yang et al., 2011). Yet, unifying fundamental processes of plant physiology with a mechanistic account of vegetation structure while scaling over several levels of organization has remained a major challenge for forest ecosystem modeling to date (Fourcaud et al., 2008; Jeltsch et al., 2008).

Here we address the issue of modeling landscape-scale forest ecosystem dynamics as an emergent property of interactions and feedbacks between the adaptive agents of a complex system, i.e., individual trees, and their environment (see Green and Sadedin, 2005; Grimm et al., 2005). Our specific objectives were (i) to develop a simulation approach that simultaneously satisfies mechanistic realism, structural detail and explicit scalability, and (ii) to evaluate the approach in a suite of simulation experiments against independent empirical data, as well as assess its scaling performance over a range of landscape sizes. Section 2 contains a description of the modeling approach and is amended by Appendices A through F (Online Supplement), which contain a more detailed account of our modeling, a description of model parameters and drivers (indicated in italics throughout the text), and a model sensitivity analysis. Section 3 describes the data and designs used to evaluate our approach, and section 4 presents the results of these evaluation experiments. Sections 5 and 6 contain discussion and conclusions, respectively.

2. A scalable, individual-based process model of forest ecosystem dynamics

2.1. Development goal and design principles

A core question in any model development is to find the appropriate level of detail and process resolution (Green et al., 2005; Jeltsch et al., 2008). Rather than an implicit or *a posteriori* consideration of these aspects (e.g., Astrup et al., 2008; Kimmins et al., 2008) we started out from this central question of detail and resolution, and revisited it throughout our development process. Generally, to achieve the proposed integration over functional, structural and spatial processes, we aimed at addressing individual components with an intermediate level of detail (i.e., the Medawar zone *sensu* Loehle (1990)). This strategy has been proposed as promising approach for individual-based modeling of complex systems, as adding detail beyond a certain level is hypothesized to decrease the overall payoff in model development (Grimm et al., 2005). The goal of our model development was thus not to advance our capacity to model individual processes of ecosystem dynamics in isolation, e.g. by developing a more detailed model of forest production or a higher resolution model of canopy structure, but rather to present an approach coherently integrating functional, structural, and spatial processes and their interactions in a dynamic simulation modeling framework. The novelty of our contribution thus lies in developments allowing to achieve this integration, i.e., a scalable competition modeling approach (Section 2.2) and its coupling with physiology-based resource use modeling (Section 2.3), embedded in a robust scaling framework to address landscape-level dynamics (Section 2.4). With scalability we here refer to the ability to address a variety of scales from the individual tree to the landscape scale, both in conceptual (e.g., not being limited by model-inherent assumptions of resolution or scale) and computational (e.g., not being limited by exponentially increasing computational costs with increasing scope) terms. For modeling many specific, relatively self-contained processes such as e.g., autotrophic respiration, allocation, and phenology we relied on previously presented approaches, and made only moderate adaptations where necessary to achieve consistency within our modeling framework.

Since all models are context-dependent, what constitutes an "intermediate level of detail" depends on the context of the model. We in this regard defined the greater context and objective for our model as serving as a platform to simulate forest ecosystem dynamics under changing climate and disturbance regimes, with a particular focus on modeling the interactions and feedbacks between climate, management, and disturbance regimes. We thus named our approach 'iLand', the individual-based forest Landscape and disturbance model. Specific demands on modeling in this context were surveyed in detail in two literature reviews (Wolfslehner and Seidl, 2010; Seidl et al., 2011a), serving as background and foundation for the development of the model. iLand is conceived as a comprehensive model of ecosystem dynamics at the landscape scale, integrating complex population processes (e.g., the growth, mortality, regeneration, and distribution of individuals) and ecosystem processes (e.g., above- and belowground cycling of carbon, nitrogen, and water). Here we focus on describing the core component of individual-tree competition for and utilization of resources, while regeneration, disturbance, and soil processes will be subject to future contributions. The model software described here was implemented as an open source project using the C++ programming language and the Qt toolkit (http://qt-project.org). Code and software are available under the GPL open source license (GNU general public license) and are – together with extensive technical model documentation – available at the model website http://iland.boku.ac.at.

2.2. Individual trees as agents of forest ecosystem dynamics

2.2.1. General concept: ecological field theory

We recognize the individual tree as primary agent of forest ecosystem dynamics and use an individual-based model (IBM) as the conceptual approach for our simulation framework (Grimm and Railsback, 2005). Our modeling builds on the growing experience with IBMs (see reviews by Bousquet and Le Page, 2004; Busing and Mailly, 2004; Berger et al., 2008; Jeltsch et al., 2008), and particularly focuses on the challenge of integrating an IBM with physiological process modeling and scalability.

The IBM approach of iLand is inspired by ecological field theory (EFT, Wu et al., 1985; Walker et al., 1989) and its adoption by Berger and Hildenbrandt (2000) in their field of neighborhood approach. In EFT a plants' influence on its neighborhood is defined by the domain (i.e., spatial extent, usually dependent on plant size) and intensity (i.e., the strength of interference with other plants in the competition for resources, usually decreasing with distance from the plant) of influence. Integrating these individual influences and accounting for plant interactions a continuous field of resource competition can be deduced. The position of every plant within this field, together with its response to competition gives a process-oriented indicator of an individuals' success in the competition for resources (see Walker et al., 1989). EFT can be applied for both facilitating and suppressing interactions between plants, and separate fields for different resources (e.g., light, nutrients, water) can be conceived (Wu et al., 1985). Here, we start by focusing on light competition among individual trees, and consequently only consider suppression (i.e., resource competition).

2.2.2. *Individual tree light interference*

Previous applications of EFT based influence intensity and domain either on theoretical models (e.g., exponential decrease in intensity from plant position, Berger and Hildenbrandt (2000)) or empirical observations (e.g., Miina and Pukkala, 2002). We here derive these crucial parameters in a process-based manner by means of computational experimentation. We render a tree in silico and calculate the shading potential for locations in its surrounding based on global light index (*GLI*, Canham (1988), see Appendix A in the Online Supplement). We derive $GLI^{x,y,z}$ values (i.e., the annual integral over the relative amount of radiation reaching a certain location *x,y,z*, where a $GLI^{x,y,z}$ of 1 represents unobstructed sky) for a regular three-dimensional grid (with 2 × 2 × 2 m resolution in *x,y* and *z* dimensions) surrounding a tree, and aggregate to a proxy of influence intensity by averaging values over the vertical dimension *z* (Eq. (1)).

$$i^{x,y} = 1 - \frac{\sum_{z \le z^{*x,y}} GLI^{x,y,z}}{z^{*x,y}} \quad \text{with} \quad z^{*x,y} = \max(z^{x,y} \,|\, GLI^{x,y,z} < 1) \quad (1)$$

The domain of influence can subsequently be delineated by setting a marginal influence as cutoff, defining the light interference pattern (*LIP*) for a given tree (see Fig. 1 for an example and Appendix A (Online Supplement) for more details). These *LIPs* are subsequently used as approximations of a trees' field of competitive interference *sensu* EFT, and can also be seen as a meta-model of GLI with regular sampling in 3D space, aggregated at the level of an individual tree.

Berger et al. (2008) found high computational demand to be a major factor limiting EFT applications. More generally, scaling individual tree interactions in modeling is challenging, and most previous attempts have approximated individual trees and their interactions by closed-form equations to achieve computational scalability (e.g., Moorcroft et al., 2001; Garman, 2004; Lischke et al., 2006; but see Sato et al., 2007). Despite their ability to reproduce important aspects of system dynamics, emergence through adaptive behavior of individuals – a crucial characteristic of complex systems (Grimm and Railsback, 2005) – is largely forgone in such approaches. Our aim was thus to simulate individuals explicitly in iLand, and we harnessed modularity and repetitiveness of competition for light to achieve scalability: *LIP*s, as described above, are solely dependent on tree height and crown shape, and thus reoccur throughout the landscape for trees of similar size and species. This repetitiveness of light interference patterns is utilized by rendering a large number of possible tree shapes and sizes in a pre-processing routine, and assigning the respective *LIP* from this library of light interference patterns to individuals at every time step of the dynamic simulation. We thus decouple the detailed calculation of *LIP*s (based on simplified ray tracing) from the actual simulation of ecosystem dynamics to promote computational scalability. In addition, rendering *LIP*s for a 2 × 2 m grid (instead of a continuous calculation, see Berger and Hildenbrandt (2000)) allows the use of efficient grid algorithms in handling a large number of individuals.

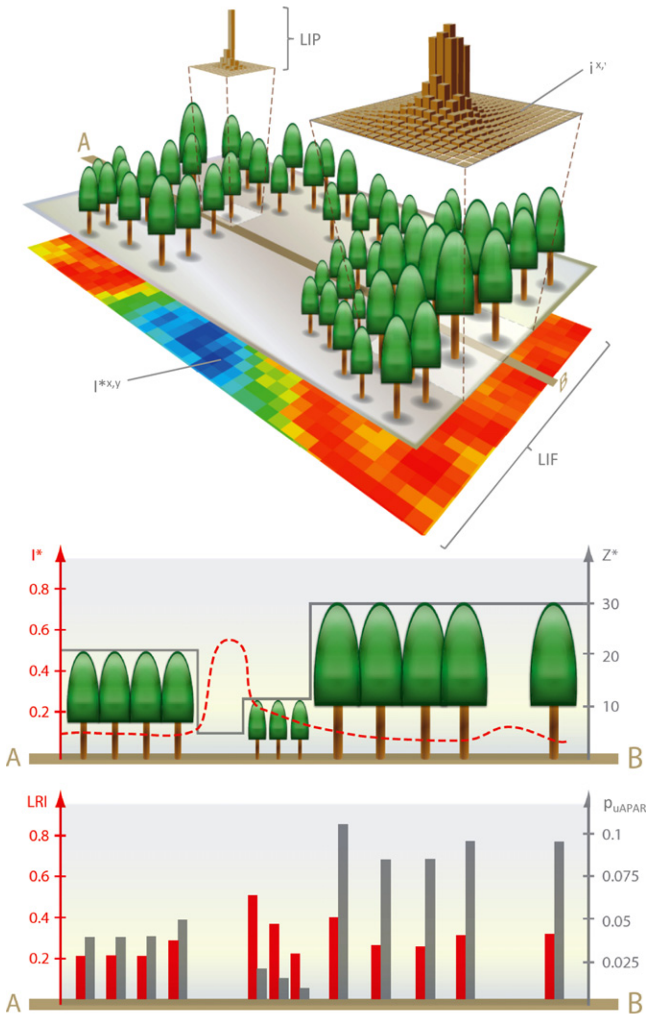

Fig. 1. Schematic illustration of the approach to simulate individual-tree competition for light in iLand. *LIP* = individual tree light interference pattern, displayed here for two individuals of different dimensions for illustration purposes, $i^{x,y}$ = individual tree interference intensity at cell *x,y*, *LIF* = continuous light interference field from interacting individual *LIP*s, $I^{*x,y}$ = aggregated interference intensity at *x,y*, scaled to local canopy height Z^*, *LRI* = a trees' light resource index (representing light availability), derived from an individuals' position in *LIF*, p_{uAPAR} = an individuals' share on overall utilized photosynthetically active radiation, based on *LRI*, leaf area (represented by green crowns in this illustration) and its potential to utilize light. In the lower panels the 3D view is reduced to 2D along the transect A–B for increased clarity. See text for details.

2.2.3. *A continuous field of interference across the landscape*

In a dynamic simulation, the *LIP*s of individual trees are superimposed based on tree positions. We chose a multiplicative interaction of individual tree influences since it preserves a traceable [0,1] interval and results in realistic behavior, i.e., diminishing marginal increases in competition intensity with an increasing number of competitors. To account for the asymmetric resource distribution within a forest canopy (i.e., light availability decreases within the canopy) the intensities of all individuals were scaled to their local canopy height Z^* (approximated as maximum tree height at 10 × 10 m resolution, Eq. (2)) priory to their aggregation (Eq. (3)).

$$i_j^{*x,y} = i_j^{x,y} \cdot \min\left(\frac{Z_j^{*x,y}}{Z^*}, 1\right) \tag{2}$$

$$I^{*x,y} = \prod_j i_j^{*x,y} \tag{3}$$

The result of Eq. (3) is a continuous field of light interference across the simulated landscape (2 × 2 m grain) that accounts for the local configuration and height structure of individuals (Fig. 1). In a dynamic simulation the calculation of the *LIF* is updated on annual time step, accounting for changes in stand structure resulting from the growth and mortality of individuals (see below).

2.2.4. Individual tree light availability

The position of an individual in this continuous landscape of light resource availability determines its relative competitive success with regard to radiation interception. We derive a respective index (light resource index, *LRI*, for tree *j*) by averaging over I^* within a trees crown projection area (A_j,) while factoring out its own contribution to I^* (Eq. (4), see also Berger and Hildenbrandt (2000)).

$$LRI_j = 1 - \sum_{x,y \in A_j} \frac{I^{*x,y}}{i_j^{*x,y}} \cdot p_{Aj}^{x,y} \tag{4}$$

with $p_{Aj}^{x,y}$ the fraction of the crown projection area A_j of individual *j* occupied by a given *LIF* cell *x,y*. In addition, the vertical situation of the focal tree within its neighborhood is accounted for by penalizing individuals of height $h < Z^*$. The resulting *LRI* indicates relative light availability of an individual tree *j* where $LRI_j = 1$ represents no competitors (i.e., full radiation) and $LRI_j \to 0$ signifies high competitive pressure from neighbors.

2.3. Harnessing physiological principles to model tree growth and mortality

2.3.1. General concept: light use efficiency approach

An ecophysiological approach based on light use efficiency (LUE, see Medlyn et al. (2003)) is employed in iLand. We start from the widely tested and used 3-PG model (Landsberg and Waring, 1997), but apply modifications in accordance with recent advances in understanding and make adaptations to account for the particular context of iLand where necessary.

The absorbed photosynthetically active radiation (*APAR*) at stand level (i.e., 100 × 100 m resolution in this study) is derived from Beers law (Eq. (5)) via the leaf area (*LA*) of the stocked area of a stand (*SA*).

$$APAR = PAR \cdot SA \cdot p_{PAR} \quad with \quad p_{PAR} = 1 - e^{-kK \cdot \frac{\sum_{j=1}^{n} LA_j}{SA}} \tag{5}$$

where *PAR* is the above canopy photosynthetically active radiation per unit area and *kK* a dimensionless constant. According to the light use efficiency concept (Eq. (6)), gross primary productivity (*GPP*) is linearly related to the fraction of utilized *APAR* (i.e., *uAPAR*) and the effective light use efficiency (ε_{eff}, see more details below).

$$GPP = uAPAR \cdot \varepsilon_{eff} \tag{6}$$

Since this linear efficiency applies only to time steps greater than approximately two weeks (Medlyn et al., 2003) a monthly time step was used to derive *GPP* according to Eq. (6) (Landsberg and Waring, 1997). An overview of the main physiological processes and their interactions modeled in iLand is given in Fig. 2.

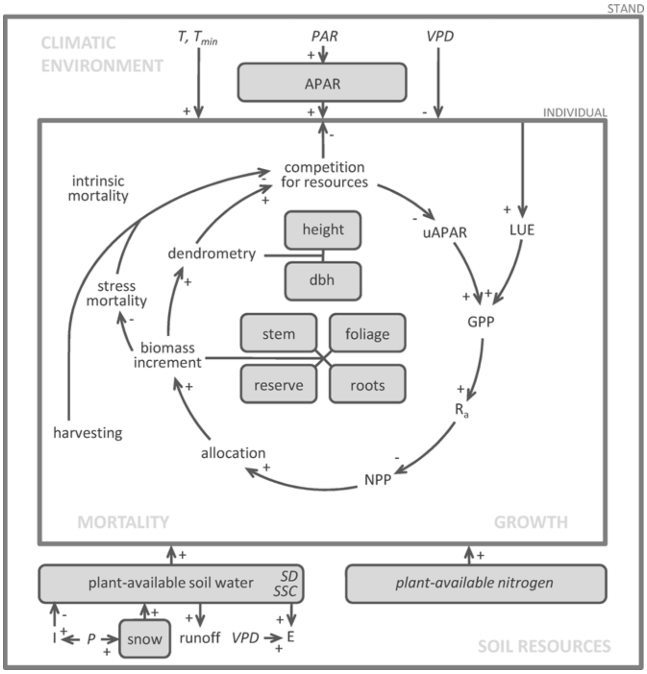

Fig. 2. The principal physiological processes and causal influences modeled in iLand. Individual tree growth and mortality are driven by climate and resource availability modeled at stand level. An individual's competitive success for these resources is determined by a pattern-based ecological field approach (see Fig. 1). Square boxes denote the main levels in a hierarchical multi-scale framework, rounded boxes are state variables or pools. Arrows denote causal influences or relationships between processes (+ indicates a positive or enhancing effect, − a negative or diminishing effect). External environmental drivers are given in italics. *T* = mean temperature, T_{min} = minimum temperature, *PAR* = photosynthetically active radiation, *VPD* = vapor pressure deficit, *P* = precipitation, *SD* = soil depth, *SSC* = soil physical properties, *APAR* = absorbed *PAR*, *uAPAR* = utilizable *APAR*, LUE= light use efficiency, GPP= gross primary production, R_a = autotrophic respiration, NPP = net primary production, I = interception, E = transpiration.

2.3.2. Environmental effects

The utilizable fraction of *APAR* is determined by weather conditions favorable for leaf level gas exchange and photosynthetic activity, represented by scalar response functions (*f*, [0,1]) to daytime air temperature, soil water availability and vapor pressure deficit. In contrast to Landsberg and Waring (1997) we compute these environmental effects on a daily time step (see also Mäkelä et al., 2008), to better represent environmental heterogeneity in general (cf. Jensens inequality in applying nonlinear response functions to average data, Sierra et al. (2009), Medvigy et al. (2010)), and to improve the dynamic simulation of the water cycle in particularly. Temperature response (f_T) is calculated applying a state acclimation approach based on a first order dynamic delay model of plant response to ambient air temperature (Mäkelä et al., 2004). Decreasing radiation use due to closing stomata in response to vapor pressure deficit (f_D) is modeled using the exponentially decreasing response function of Landsberg and Waring (1997).

A daily soil water balance is computed for a single soil layer accounting for precipitation inputs, interception and evaporation from the canopy, snow storage and melting, transpiration demand from the canopy, and runoff of excess water. Interception, accounting for leaf area specific canopy water storage, is modeled following the general scheme of Landsberg and Gower (1997) and its specific rendering by Seidl et al. (2005). Evaporation from the canopy is calculated by the widely used Penman-Monteith equation with conductance set to infinity (Landsberg and Gower, 1997). Snow water storage is implemented following Running and Coughlan (1988), and canopy transpiration is modeled using the Penman-Monteith equation. We follow Landsberg and Waring (1997) in assuming a plateau of maximum canopy conductance for leaf area indices (*LAI*) greater than three (Kelliher et al., 1995). Furthermore, f_D is applied to account for the decrease in conductivity with increasing *VPD* (Oren et al., 1999).

Volumetric soil water content is converted to soil water potential using physical soil properties in conjunction with empirically derived coefficients (Cosby et al., 1984; Schwalm and Ek, 2004). Water content exceeding field capacity is percolated out of the simulated system. A trees' response to soil water stress (f_W) is modeled to decrease linearly between field capacity and a species-specific minimum soil water potential (Hanson et al., 2001; Wullschleger and Hanson, 2003). The most detrimental factor of the environmental responses f_T, f_D and f_W limits daily *APAR* utilization, which is subsequently aggregated to monthly values of *uAPAR* (Eq. (7)).

$$uAPAR = \sum APAR \cdot \min(f_T, f_D, f_W) \tag{7}$$

For deciduous trees radiation absorption is limited to the growing season as calculated by a climate-sensitive growing season index (*GSI*, Jolly et al., 2005). Biome-specific optimum LUE (ε_0) is modified by nutrient availability (f_N) and atmospheric CO_2 concentration (f_C). We use plant-available nitrogen (N_{av}) as an indicator of nutrient limitation and apply the phenomenological species-specific response functions of Pastor and Post (1985) to derive the response scalar f_N (see also Seidl et al., 2005). Although CO_2 is not explicitly considered in a number of LUE approaches (e.g., Landsberg and Waring, 1997; Mäkelä et al., 2008) we include it in our approach to bolster applicability under climate change (cf. model objectives in Section 2.1). Based on a review of modeling approaches (Kicklighter et al., 1999) and the empirical evidence provided by Norby et al. (2005) we adopt a Michaelis-Menten equation of growth response to CO_2 that accounts for increasing CO_2 sensitivity under increased soil water stress, but also limits growth response to increasing CO_2 under nutrient-limited conditions (Friedlingstein et al., 1995; Berthelot et al., 2005). The effective LUE is derived by combining the effects of nutrients and CO_2 on optimum LUE (Eq. (8)).

$$\varepsilon_{eff} = \varepsilon_0 \cdot f_N \cdot f_C \tag{8}$$

A detailed description of the environmental response functions is given in Appendix B in the Online Supplement.

2.3.3. Net primary production

We assume net primary production (*NPP*) to be a constant fraction of *GPP* (Eq. (9)), with an autotrophic respiration rate (R_a) of 0.47 (Waring et al., 1998).

$$NPP = GPP \cdot R_a \tag{9}$$

Notwithstanding the reservations of e.g., Medlyn and Dewar (1999) and Mäkelä and Valentine (2001) the parsimony and robustness of this simplified approach to model R_a (e.g., Coops et al., 2001; Landsberg et al., 2003) warrant its suitability in the context of iLand (see Section 2.1).

Most previous LUE models were developed for single-species, even-aged stands, frequently applying a mean tree approach to represent stand structure. Here we aim at a more general IBM approach also applicable to multi-species and multi-layered stands. Assuming that for a given set of conditions the environmental modifiers *f* only vary between species (but not at the level of individual trees *j*), and given the linearity of Eq. (6) and (9), the latter two can be decomposed to the level of individual trees if every individuals' share on *uAPAR* is known (see below). We can thus re-write Eq. (6) as Eq. (10) and proceed to describe aging effects, allocation, tree growth and mortality at the level of individual trees.

$$GPP = \sum_j uAPAR_j \cdot \varepsilon_{eff} \tag{10}$$

The effect of age-related decline on productivity is modeled as a simple modifier on *NPP* (Eq. (11), Landsberg and Waring (1997)), in which both relative age and relative height (a_{rel} and h_{rel}; both relative to their species-specific maximum attainable value) are employed as aging indicators. Empirical studies point towards a size (i.e., height)-related pattern of growth decline (e.g., Bond et al., 2007) resulting from hydraulic limitations (e.g., Ryan et al., 2006). However, although hydraulic limitations with increasing tree size appear to be common, no universal relationship has been found (Ryan et al., 2006), and factors associated with physical age might also contribute to the observed age-related decline (Munne-Bosch and Alegre, 2002). Niinemets (2002), for instance, found tree height as well as physical age to be related to growth decline. We thus utilize both traits to derive an individual tree aging index (*AI*) as the harmonic mean of relative age and relative height (Eq. (12)). *AI* is based on experimental results showing that under fertile conditions and fast growth a height limitation of *NPP* is necessary to achieve correspondence with observed growth curves, while for slow-growing stands in harsh environments, where a h_{rel} close to 1 might never be reached (e.g., high elevation forests), physical age is a better indicator for aging (data not shown).

$$f_A = \frac{1}{1 + (AI/kA_1)^{kA_2}} \tag{11}$$

$$AI = 1 - \frac{2}{(1 - a_{rel})^{-1} + (1 - h_{rel})^{-1}} \tag{12}$$

where kA_1 and kA_2 are empirical coefficients.

2.3.4. Allocation

Allocation of carbohydrates to tree compartments is modeled based on ratios between compartment-specific allometric equations (Landsberg and Waring, 1997). This approach, originally conceived in the context of a mean tree model, was recently tested successfully also in an IBM context (Seidl et al., 2010). Allocation and dendrometric updates are calculated on annual time step in iLand. Allocation is hierarchical, with highest priority for allocation to roots and foliage, followed by the reserve and stem pools. A harsher environment, as indicated by the environmental modifiers described above, increases allocation of carbohydrates to roots (Landsberg and Waring, 1997). Belowground allocation is partitioned between fine and coarse roots maintaining a functional balance between foliage and fine root biomass. Allocation of above-ground *NPP* (*ANPP*) follows the approach of Duursma et al. (2007), who extended the allometry-based scheme of Landsberg and Waring (1997) to explicitly include turnover rates for biomass compartments. We further modified their approach to include a carbohydrate reserves pool into the allometry-based allocation model. This pool is specified to have a maximum size equaling the sum of the annual maintenance terms for foliage and fine roots (Bossel, 1996), and has priority over allocation to wood increment. The previous years' carbohydrate reserves of an individual tree are added to its current *NPP* prior to allocation (see Appendix C in the Online Supplement for more details on allocation).

2.3.5. Stem increment

Altering the allocation regime between height and diameter increment is a major adaptive response to competition for light in trees. Ecological theory suggests that height growth is favored over diameter increment with decreasing light levels, aiming to improve the competitive status in the canopy (Grime, 2001). This is also supported by empirical findings, documenting a variable allometric relationship between height and diameter growth of individual trees as a result of their competitive status (e.g., Henry and Aarssen, 1999). Niklas (1995), for instance, found the rate of height growth to diameter increment greater for trees growing in closed stands compared to open-grown trees.

To simulate this adaptive behavior as an emergent property of the model we extended the approach of Bossel (1996), who defined two different height–diameter ratios for increment allocation (hd) in trees with and without light competition (see also Peng et al., 2002). Acknowledging the size-dependence of these height–diameter ratios we rendered them diameter-dependent allometric equations and applied LRI_j as a continuous indicator for the light regime experienced by an individual (Eq. (15)).

$$hd = hd_{\min} \cdot LRI_j + hd_{\max} \cdot (1 - LRI_j) \tag{15}$$

For an open-growing tree ($LRI \rightarrow 1$) hd is close to its minimum and allocation to diameter growth is favored over height increment, while a tree under intense competition for light ($LRI \rightarrow 0$) aims at improving its competitive status by investing carbohydrates particularly into height growth. Assuming a constant species-specific wood density and form factor, hd is employed to translate stem wood biomass production to increments in height (h) and diameter at breast height (dbh) at a given stem biomass, h and dbh (see Bossel, 1996; Appendix C in the Online Supplement). Subsequently, the individual tree LIP for the light competition calculations in the next time step is determined from updated h and dbh values (see Appendix A in the Online Supplement).

2.3.6. Mortality

Modeling individual tree mortality, although a crucial process for vegetation dynamics, has received considerably less attention than growth modeling. Our approach combines an intrinsic mortality component (μ_i) based on life history traits of tree species (Keane et al., 2001) with a stress-related mortality component (μ_s) based on C starvation (Güneralp and Gertner, 2007). Annual intrinsic mortality probability is calculated from maximum tree age ($a_{\max}$) assuming that only a certain percentage of individuals ($p_{a\max}$) reach this maximum age (Botkin, 1993; Wunder et al., 2006; Eq. (16))

$$\mu_i = 1 - p_{a\max}^{a_{\max}^{-1}} \tag{16}$$

To model stress-related mortality we use the C balance of a tree as process-based proxy for stress (Hawkes, 2000). Stress occurs in iLand when the minimum requirements to support a trees' structural compartments (i.e., root and foliage turnover) cannot be met by C available from NPP and carbohydrate reserves (see Waring, 1987). A continuous stress index (SI) is derived as ratio between C gain and maintenance demand (Eq. (17)), an approach closely related to the asphyxiation index of Güneralp and Gertner (2007).

$$SI = \max\left(1 - \frac{NPP + w_s}{2 \cdot \left(\gamma_f \cdot W_f + \gamma_r \cdot W_r\right)}, 0\right) \tag{17}$$

with γ_f and γ_r the turnover rates of foliage and fine roots, W_f and W_r the respective biomass compartments derived from allometric equations and functional balance, and w_s the dynamically simulated reserves pool of a tree. Based on the analysis of Hawkes (2000), who reviewed previous experiences in mortality modeling, we used SI in a probabilistic context (rather than as causal deterministic driver of tree death), i.e., mortality probability increases with increasing stress in iLand (Eq. (18)).

$$\mu_s = 1 - e^{-kM \cdot SI} \tag{18}$$

with kM an empirical coefficient. Güneralp and Gertner (2007) recently demonstrated that a structurally similar approach was able to unify Manions (1981) gradual decline hypothesis and Bossels (1986) sudden death hypothesis of tree mortality. Furthermore, extended periods of little stem growth (e.g., in harsh environments) do not necessarily lead to increased mortality probability in this approach, thus remedying a shortcoming of earlier vegetation models basing stress on dbh increment (Loehle and LeBlanc, 1996; Bigler and Bugmann, 2003). Overall, tree mortality occurs in iLand if the combined probability μ (Eq. (19)) exceeds a uniform random number on the interval [0,1].

$$\mu = \min(\mu_i + \mu_s, 1) \tag{19}$$

2.4. Applying hierarchy theory to model multi-scale interactions

Scales and scaling are important concepts in ecology, but also one of the biggest challenges in the dynamic modeling of ecosystems (Bugmann et al., 2000; Urban, 2005). In iLand, we apply a hierarchical multi-scale approach (HMS, see Mäkelä, 2003) to consistently couple individual-based vegetation dynamics (Section 2.2) and ecophysiological processes (Section 2.3). Hierarchical multi-scale modeling entails addressing processes at their respective inherent scale, and results in multiple temporal and spatial scales being employed in a model (Bugmann et al., 1997; Mäkelä, 2003). In general, dynamics emerging at lower hierarchical levels feed into processes at higher levels, while feedbacks from higher hierarchical levels exert constraints on processes at lower levels.

iLand simulates resource competition at the level of individual trees, while overall resource availability with regard to radiation, water and nutrients is modeled explicitly at the stand level (i.e., for regular cells of 100 × 100 m resolution with homogeneous environmental conditions). The individuals provide the means to utilize potential resources at the stand level from the bottom-up, e.g., the leaf area necessary to absorb radiation. The (constraining) feedback loop requires that in total only the resources available at the higher hierarchical level can be used for growth at the individual-tree level. To unify EFT and LUE, and consistently couple these two hierarchical levels, we apply the concept of weighted leaf area (WLA, Brunner and Nigh, 2000) as a link between individual-based light resource availability (LRI_j) and stand-level absorbed radiation (p_{PAR}) (i.e., the relative radiation absorption calculated independently at the two hierarchical levels). Considering species-specific light utilization potential (i.e., accounting for different strategies in light utilization of shade tolerant and shade intolerant species) and an individual's leaf area share within a stand we derive $uAPAR_j$, i.e., the contribution of every individual to stand level $uAPAR$ (cf. Eq. (10), see also Fig. 1 and Appendix D in the Online Supplement for more details).

3. Evaluation experiments

To evaluate the ability of iLand to simulate forest ecosystem dynamics as an emergent property of complex process interactions we conducted a suite of experiments (E1–E4), in particular addressing the following questions:

Is the model able to reproduce observed productivity and mortality patterns over an extensive ecological gradient (E1)?

Can the model be applied in different forest ecosystem types, thus representing a generalized model of temperate forest dynamics (E2)?

Is the model able to simulate structurally and compositionally complex old-growth forest ecosystems (E3)?

Is the model computationally scalable and thus able to address large spatial scales with fine grain (E4)?

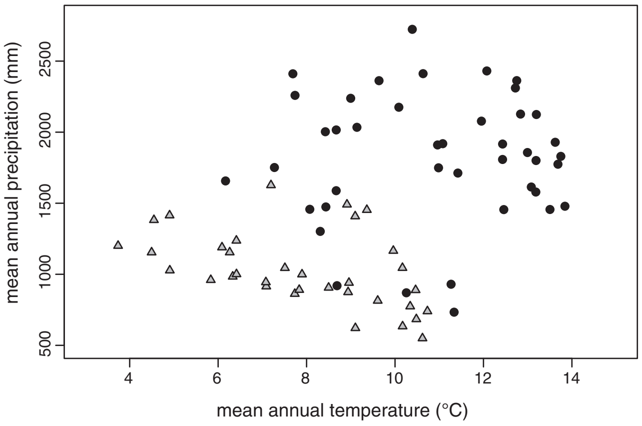

Fig. 3. The climatic envelope covered by the inventory plots used in testing functional complexity and generality of iLand. Circles: Forest Inventory and Analysis plots, Oregon, USA (E1). Triangles: Austrian Forest Inventory plots, elevation transect, Austria (E2).

To evaluate E1 we utilized data of Forest Inventory and Analysis (FIA) phase 3 plots (USAD, 2009) across central western Oregon, USA. A sampling window (between the longitudes −124.25W and −121.25W, the latitudes 43.75N and 45.25N) was defined to capture the major environmental gradients of the Oregon Transect (Peterson and Waring, 1994) from the Pacific Coast through the Coast and Cascade ranges into arid central Oregon (Fig. 3). Daily weather data (1980–2003) for the approximate coordinates of the FIA plots were used (Thornton et al., 1997; http://www.daymet.org), and years were randomly sampled with replacement to obtain a 100 year time series as driver for the simulations. Physical soil parameters and C and N pools were available from FIA data. The effect of nutrient limitation (f_N) was calculated following Swenson et al. (2005), applying the response functions of Pastor and Post (1985) to derive corresponding plant-available N. The first target variable tested under E1 was the site index at age 100 (SI_{100}), i.e., the dominant height reached by a species (sp) at age 100 years. Since focusing on model behavior over environmental gradients in E1 we decided to use the widely available SI_{100} as a proxy for stand productivity rather than restricting our analysis to the limited number of sites where actual GPP and NPP measurements are available (see also Swenson et al., 2005). Model simulations were conducted for the site index species of every FIA plot on generic one hectare simulation units ($n = 42$ with sp = 6). We initialized the model with 30 year old homogeneous stands of uniformly distributed individuals (i.e., with individual tree positions determined randomly to result in an overall uniform distribution of stand basal area in space), and simulated regular stand treatments emulating the stand densities reported in yield tables for the respective SI_{100} (Hanson et al., 2002). In this first set of simulations under E1 we thus focused solely on evaluating tree growth. The second analysis variable addressed in E1 was mortality, for which the same simulation experiment was replicated without management over a 100 year simulation period. Here, model results were tested against the general empirical self-thinning coefficients of Reineke (1933) and Yoda et al. (1963).

To test the generality of iLand (E2) we replicated E1 for a region with strongly contrasting environmental conditions (Fig. 3) and species. We evaluated productivity and mortality of even-aged stands over an elevation gradient in the eastern Alps in Austria, with sites ranging from the colline elevation belt to the subalpine vegetation belt ($n = 34$, sp = 4; for a detailed description of climate and soil data see Seidl et al. (2009)). Using the identical model formulation and structure as for E1 we compared simulated dominant height at age 100 to observations of the Austrian Forest Inventory (BFW, 1997).

While E1 and E2 mainly addressed the models' ability to simulate ecosystem functioning E3 was designed to evaluate structural aspects. To that end we chose old-growth forest ecosystems in the central western Cascades of Oregon, renowned for their complex structural dynamics and widely undisturbed by anthropogenic influences (Franklin and Dyrness, 1973; Spies and Franklin, 1991). Vegetation data (22–24 year time series with four

Table 1
Characteristics of the old-growth stands selected to test the model with regard to structural complexity. The vegetation state at the beginning of the study period is reported as initialized in the simulations. T = mean annual daytime temperature, P = mean annual precipitation, *dbh* = diameter at breast height, h = tree height.

ID	Obs. period	Plant association[a,b]	Elevation	T (°C)	P (mm)	Species[b,c]	Stems (ha^{-1})	Mean *dbh* (range) (cm)	Mean h (range) (m)
RS20	77–99	Psme/Hodi	700	12.2	2491	Psme	470	29.8 (5.0–170.3)	18.9 (2.3–49.6)
						Acma	6	27.8 (20.0–41.0)	21.3 (17.6–23.1)
						Tshe	2	8.3 (7.1–9.5)	10.2 (10.0–10.4)
RS02	78–99	Tshe/Rhma-Bene	520	11.5	2225	Tshe	257	28.2 (5.5–98.0)	23.2 (4.0–62.3)
						Psme	63	109.6 (65.1–152.9)	56.9 (39.3–75.8)
						Thpl	13	20.4 (5.1–46.5)	15.9 (3.7–34.2)
RS31	78–01	Tshe-Abam/Rhma-Bene	900	11.1	2341	Tshe	287	28.6 (5.0–91.2)	20.1 (3.3–58.0)
						Psme	57	101.9 (18.6–188.7)	50.7 (12.9–74.6)
						Thpl	10	59.8 (5.6–105.4)	38.0 (4.6–56.8)
						Abam	5	22.2 (5.0–49.2)	17.6 (4.2–38.1)
RS22	77–99	Abam/Vame-Xete	1290	9.0	2675	Abam	393	14.4 (5.0–81.7)	8.6 (2.1–46.1)
						Tshe	84	21.3 (5.4–115.7)	12.6 (2.3–53.2)
						Abpr	82	78.1 (16.2–143.6)	42.3 (6.7–58.0)
						Tsme	62	30.9 (5.0–84.2)	19.3 (2.5–45.3)
						Psme	30	88.0 (49.6–118.3)	47.5 (33.9–52.8)
RS21	77–99	Abam/Tiun	1190	10.1	2609	Abam	342	12.7 (5.0–61.6)	7.7 (2.2–53.5)
						Tshe	224	23.5 (5.0–142.9)	13.7 (1.9–55.0)
						Psme	44	143.4 (45.6–194.7)	58.4 (32.8–77.1)
						Abpr	3	25.4 (22.4–28.4)	17.0 (13.7–18.8)

[a] Following Dyrness and Acker (1999).

[b] Abam = *Abies amabilis* Dougl. ex Forbes, Abpr = *Abies procera* Rehd., Acma = *Acer macrophyllum* Pursh, Psme = *Pseudotsuga menziesii* (Mirb) Franco, Thpl = *Thuja plicata* Donn ex D. Don, Tshe = *Tsuga heterophylla* (Raf.) Sarg., Tsme = *Tsuga mertensiana* (Bong.) Carr. Bene = *Berberis nervosa* (Pursh) Nutt., Hodi = *Holodiscus discolor* (Pursh) Maxim., Rhma = *Rhododendron macrophyllum* D. Don ex G. Don, Tiun = *Tiarella unifoliata* (Hook.) Kurtz, Vame = *Vaccinium membranaceum* Dougl. ex Torr., Xete = *Xerophyllum tenax* (Pursh) Nutt.

[c] Species and vegetation data as initialized; some minor species were omitted in the simulation.

re-measurements after the initial inventory) including individual tree coordinates were available for one hectare reference stands (RS) at the H.J. Andrews experimental forest, situated near Blue River, Oregon. Spatially interpolated climate data were taken from Daly (2005) and soil information was extracted from the H.J. Andrews soil database (Dyrness, 2001), applying the same methodology as for E1 to derive f_N. We selected five RS representing different plant associations and elevation belts of the H.J. Andrews watershed for our evaluation (Table 1). Simulations were initialized with the initial vegetation inventory and were run over the time period covered by the observations (Harmon and Munger, 2005). Two sets of simulations were conducted to evaluate E3: First, we ran the model *sans* dynamically simulated mortality (i.e., deterministically removing trees that were recorded as mortality and adding trees that regenerated) to test its ability with regard to individual tree growth in the strongly heterogeneous multi-storey canopies of old-growth stands. Second, we dynamically simulated tree growth and mortality to evaluate simulations against observed mortality rates. Due to the stochastic nature of the mortality model 100 replicates of the latter simulation series were run.

Finally, the ability to address large spatial areas with a detailed individual-based approach was evaluated by E4. Here we focused on computational scalability as a prerequisite to address ecological processes and their interactions across large scales (Yang et al., 2011). While a number of IBM approaches addressing detailed functional and structural aspects of ecosystem dynamics exist, they are limited with regard to applications at watershed or landscape scales due to limits in both conceptual and computational scalability (but see e.g., Chertov et al., 2006; Sato et al., 2007). To evaluate computational scaling performance we simulated landscapes of identical characteristics (i.e., artificial landscapes of homogeneous soil and climate conditions, 500 stems per hectare on average, trees of a single species with quasi-randomly assigned tree positions) and different sizes, ranging from 10^0 ha to 10^4 ha. The performance of the iLand competition computations (*sans* pre-processing of *LIP*s, i.e., as in a default simulation run with the model) was compared to the light competition indices of three well-established IBMs, the GLI of SORTIE (Pacala et al., 1996), the KKL of SILVA (Pretzsch et al., 2002) and the ALI of PICUS (Lexer and Hönninger, 2001). The light competition algorithm of the models was isolated to the degree possible for this performance experiment in order to provide comparability. To demonstrate computational scalability we compared the models' performance (i.e., computing time per annual simulation cycle for the landscape) over landscape size. While the absolute level of this performance measure is likely to be of little significance due to differences in implementation and rapid increases in computing power (we here used a Intel © DualCore, 2.66 GHz, 3GB RAM, Windows © XP 32bit), the relative scaling with landscape size (i.e., relative to the computing time for a 1 ha stand) was deemed to be a relevant indicator with regard to spatial scalability.

The same set of species- and biome-specific parameters was applied in all evaluation experiments (see Appendix E in the Online Supplement). iLands sensitivity to these parameters was analyzed in a local sensitivity analysis with regard to functional as well as structural response variables (Appendix F in the Online Supplement). Significance levels for all statistical tests were set to $\alpha = 0.05$, and all statistical analyses were conducted using the R project for statistical computing (R Development Core Team, 2009).

4. Results

4.1. Simulating productivity and mortality over ecological gradients (E1)

Over an extended environmental gradient from coastal conditions to the rainshadow of the Cascade mountains in Oregon iLand explained approximately two thirds of the variation in site index ($R^2 = 0.634$). In a linear regression between simulation results and observed values intercept (5.47 m) and slope (0.860) did not differ significantly from their expected values of 0 and 1, respectively (Fig. 4a). Simulated dominant heights at age 100 years were not significantly biased (mean bias = −1.22 m), with a root mean square error (RMSE) of 4.62 m.

Simulated mortality was compared to the theoretical models of self-thinning mortality by Reineke (1933) and Yoda et al. (1963). Over all 42 sites the slope (a_R) in the relationship between quadratic mean diameter (d_g) and stem number (N), $\log(N) = a_1 + a_R \cdot \log(d_g)$, was −1.62, and not significantly different from the value of −1.605 reported by Reineke (1933). Also with regard to Yodas law, expressed in terms of mean tree volume (v), $\log(v) = a_1 + a_Y \cdot \log(N)$, the simulated coefficient of −1.52 did not differ significantly from the a_Y of −1.5 reported by Yoda et al. (1963).

4.2. Evaluating ecological generality (E2)

Process-based approaches are expected to be robust over a wide range of environmental conditions, and are thus imperative for applications under changing climate conditions. To evaluate iLand with regard to its robustness under different environmental conditions, i.e., to test its ecological generality, we replicated

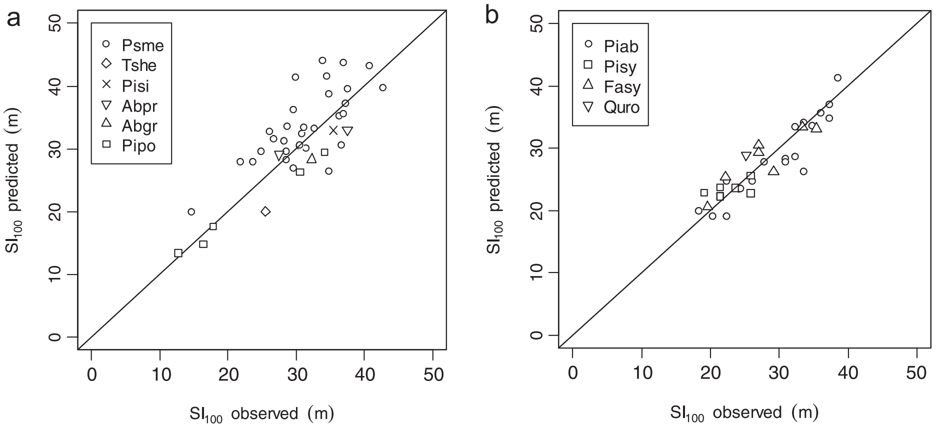

Fig. 4. Simulated and observed site index (SI_{100}, dominant height at age 100) over ecological gradients in Oregon (a) and Austria (b). Psme = *Pseudotsuga menziesii* (Mirb) Franco, Tshe = *Tsuga heterophylla* (Raf.) Sarg., Pisi = *Picea sitchensis* (Bong.) Carr., Abpr = *Abies procera* Rehd., Abgr = *Abies grandis* (Dougl. ex D. Don) Lindl., Pipo = *Pinus ponderosa* Dougl. ex. Laws., Piab = *Picea abies* (L.) Karst., Pisy = *Pinus sylvestris* L., Fasy = *Fagus sylvatica* L., Quro = *Quercus robur* L.; Note that the definitions of SI_{100} differ between the regions in panels (a) and (b).

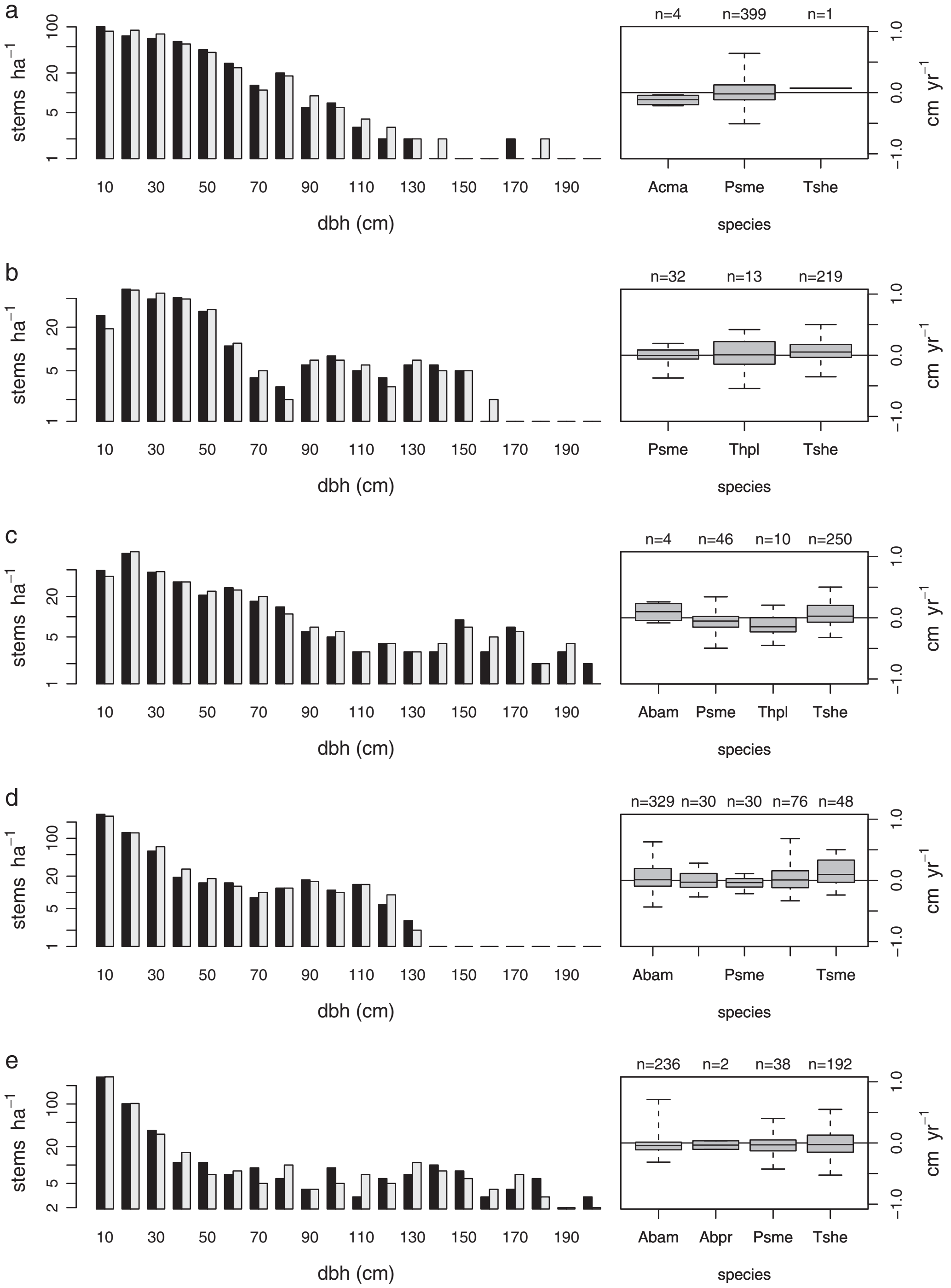

Fig. 5. Observed (dark grey bars) and simulated (light grey bars) diameter distributions at the end of the study period (after 22–24 simulation years) in five 1 ha old-growth stands at the H.J. Andrews experimental forest: (a) RS20, (b) RS02, (c) RS31, (d) RS22, (e) RS21. Note the logarithmic scale on the *y*-axis of the histograms. Boxplots show the diameter increment residuals at the level of individual trees (*n* = number of individuals) grouped by species. Boxes denote interquartile range and median, whiskers extend to the minimum and maximum datapoints. See Table 1 for detailed stand description and species codes.

the experiment of E1 for different ecosystem types and species in Austria (Fig. 4b). We found similar satisfactorily model performance over the elevation transect in the Eastern Alps, with the model explaining 83.1% of the observed variance in site index. While the intercept of the linear relationship between model and observation (3.75 m) was not significantly different from 0 the slope (0.859) indicated a moderate but significant underestimation of high productivities. Both mean bias (−0.23 m) and RMSE (2.47 m) were lower than for the Oregon simulations in E1. In this regard it has to be noted, however, that the sites for E2 were sampled stratified by elevation zones (see description in Seidl et al., 2009), i.e., site selection differed from E1. As for the sites in Oregon, the self-thinning coefficients for Reinekes rule and Yodas law did not differ significantly from the expected values over the 34 sites evaluated under E2 (simulated a_R and a_Y were −1.645 and −1.605, respectively).

4.3. Simulation of structurally complex old-growth stands (E3)

To thoroughly evaluate the ability of iLand to simulate competition in structurally complex systems we selected old-growth stands of three to five canopy species and a vertical canopy

Table 2
Mean annual mortality rate (% basal area) ± standard deviation over the four inventory periods. CI = observed confidence interval.

	Observed (5%–95% CI)	Predicted envelope mean	Predicted best run[a]
RS20	0.44 ± 0.15 (0.20–0.68)	0.90 ± 0.19	0.61 ± 0.20
RS02	1.81 ± 1.84 (<0.01–4.75)	1.49 ± 0.45	1.44 ± 0.98
RS31	0.42 ± 0.29 (<0.01–0.89)	1.18 ± 0.74	0.71 ± 0.75
RS22	1.78 ± 0.70 (0.66–2.89)	1.54 ± 0.26	2.13 ± 0.93
RS21	0.52 ± 0.30 (0.04–1.01)	1.47 ± 0.40	0.89 ± 0.48

[a] The replicate with the least sum of squared deviations between the observed and predicted basal area trajectories over the whole study period is reported (cf. Fig. 6).

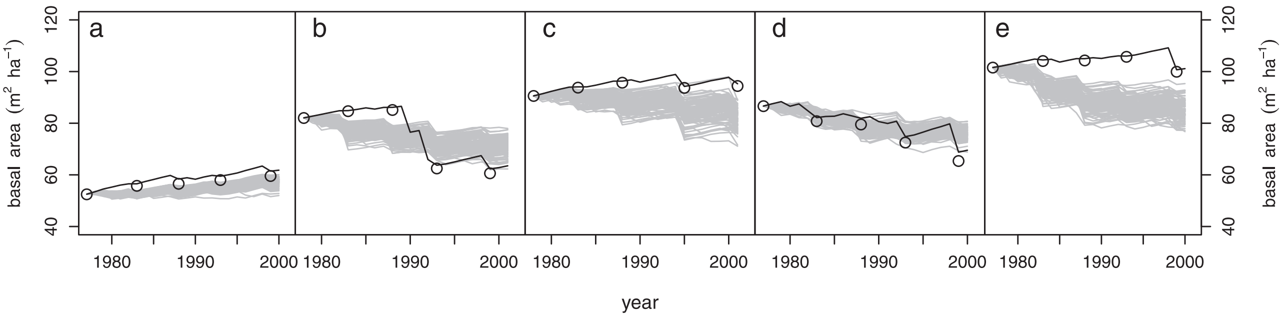

Fig. 6. Observed (circles) and simulated (lines) basal area trajectories for five old-growth stands at the H.J. Andrews experimental forest: (a) RS20, (b) RS02, (c) RS31, (d) RS22, (e) RS21. Black line: simulation sans dynamically simulated mortality (i.e., trees recorded as mortality were killed deterministically in the simulation). Grey lines: envelope of 100 replicates with dynamically simulated tree mortality.

gradient between 50 and 75 m (Table 1). After the 22–24 year simulation period, the simulated diameter distribution differed significantly from the observation for only one of the five reference stands (RS21, $P = 0.014$, Fig. 5). Model predictions for tree height distributions differed significantly from observations only for RS22 ($P = 0.005$). At the individual-tree level, a linear regression of simulated versus observed basal area increments resulted in R^2 values between 0.375 and 0.521. The mean individual tree bias in basal area increment ranged from +0.64 cm^2 yr^{-1} to +2.91 cm^2 yr^{-1} at the five study sites, and no particular trend was detected in analyzing residuals over species or tree diameter (Fig. 5).

Observed mortality rates differed substantially between the five reference stands (Table 2), and also varied between the observation periods. RS02 and RS22 had considerably higher mortality rates than the other three stands, a distinction that was reproduced also by the simulations with iLand (Fig. 6). For the other three reference stands, the mean simulated mortality rate over all 100 replicates exceeded the observed confidence interval. However, the highest (4.18%) and lowest (0.08%) simulated annual mortality rates over all stands corresponded well to the observed range (3.93% and 0.01%, respectively).

4.4. *Evaluating the scalability of individual-based simulations (E4)*

Scalability has been an important factor limiting the adoption of individual-based approaches to a larger set of ecological questions. We evaluated a generic measure of computational scalability over landscape sizes from 10^0 to 10^4 hectares to test the ability of iLand to address large spatial scales. Three established IBM approaches were also included to provide reference for readers not intimately familiar with the challenges in scaling individual-based models. Fig. 7 shows that the approaches relying explicitly on a neighborhood search for the computation of individual-based competition (i.e., the KKL index of SILVA and the GLI of SORTIE) scale strongly nonlinearly, i.e., computational demands increase disproportionately with increasing landscape size. While the rendering of canopy space in 3D ‘voxels’ in PICUS is more efficient for small areas it quickly approaches its limits in terms of memory usage. In comparison, the pattern-based approach of iLand was found to scale approximately linear, i.e., simulating a landscape of 10^4 hectares requires roughly the 10^4 fold computation time of simulating one hectare. With standard office computing resources an annual simulation cycle of light computation for 10^4 hectares, i.e., 5×10^6 trees, requires approximately 15 s in iLand, underlining the ability of the model to address large spatial scales and a large number of simulation years (as required e.g., in scenario analyses).

5. Discussion

In their analysis of the state-of-the-art of modeling plant populations under changing environmental conditions Jeltsch et al. (2008) found the need to simultaneously address fundamental processes of plant physiology while scaling over several levels of organization to be a key challenge for current modeling. In addition, Fourcaud et al. (2008) highlighted the increasing importance

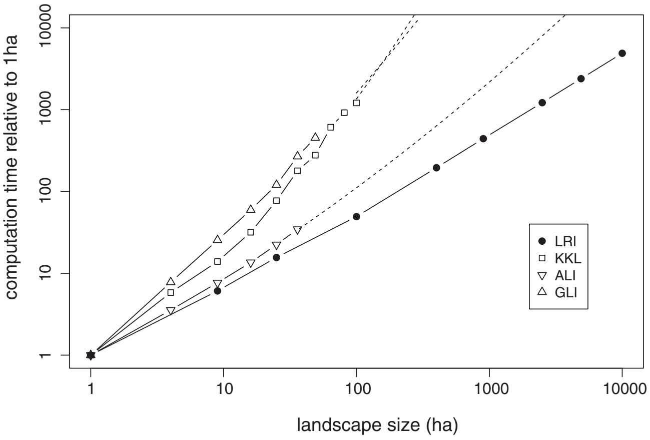

Fig. 7. Computational scaling of individual-based models over landscape size. Model performance was scaled relative to the performance of the respective model for 1 ha to make the different model implementations comparable. GLI = gap light index as used by Pacala et al. (1996), KKL = competition index as described by Pretzsch et al. (2002), ALI = available light index as used by Seidl et al. (2005), LRI = this study. Dashed lines indicate extrapolations beyond landscape sizes feasible with the particular implementations (based on nonlinear fits).

of vegetation structure and plant architecture in modeling plant growth. Here we have presented a modeling approach addressing those challenges, unifying structural and functional approaches of modeling forest dynamics while retaining scalability.

5.1. Integrated modeling of forest ecosystem structure and functioning

At its core, iLand employs an IBM approach to simulate individual trees as adaptive agents of a complex system. Here we thus discuss iLand in the context of the main aspects of individual-based modeling as summarized by Berger et al. (2008):

Exploitation: Competition is modeled as the struggle for limited resources in iLand, and individual trees compete explicitly for their exploitation.

Heterogeneity: Temporal variability of climatic drivers is simulated on a daily time step and resources are heterogeneously distributed over the simulated landscape, i.e., the location of an individual defines potential resource availability. iLand is thus well suited to explicitly address the intricacies of climate change impacts in strongly heterogeneous mountain landscapes (Daly et al., 2009). At the stand scale (i.e., currently 100 × 100 m), however, the physical environment (i.e., climate, soil) is considered homogeneous. We thus explicitly recognize hierarchies in ecosystems in addressing heterogeneity (see also Robinson and Ek, 2000).

Modification: Plants exploit resources and decrease light levels in their domain of light interference in iLand, thus modifying the light environment of others. The light regime is an emergent property of the simulation, which is dynamically influenced by mortality, management, and disturbances.

Configuration: Spatial configuration matters in our approach, i.e., competition for resources is inherently local in iLand and the distance between competitors as well as their spatial arrangement (e.g., orientation, clustering) influence their competitive interactions (see Miina and Pukkala (2002) for an empirical example applying EFT).

Symmetry: Light competition in iLand is asymmetric, i.e., larger individuals have a disproportionate advantage over smaller individuals, while competition for below-ground resources (i.e., water, N) is assumed to be size-symmetric (see Bernston and Wayne, 2000; Stoll and Weiner, 2000). Competition for soil resources, currently addressed as a spatially non-explicit process at stand level, could be extended by applying an EFT approach similar to the one developed for light competition also for soil resources in the future (i.e., an additional spatially explicit interference field for soil water and N, e.g., Casper et al., 2003; O'Brien et al., 2007).

Adaptation: Individuals adapt dynamically to their environment in iLand. A major individual adaptation mechanism is the dynamically simulated partitioning of biomass growth to height and diameter increment, acknowledging the competitive environment of an individual (see also Seidl et al., 2010). Trees thus dynamically adapt their stem increment strategy to the respective growing conditions. However, plasticity in crown length, form and position in response to a trees environment is neglected in our pattern-based rendering of EFT (see discussion below). Yet, adaptive crown feedbacks are implemented via the process-based simulation of leaf area dynamics, influencing crown transmissivity and competitive status of a tree as well as its influence on others (see Appendix A (Online Supplement) for details, and Didion et al. (2009) for a recent modeling study applying similar dynamic leaf area feedbacks on competition). Adaptive mechanisms such as changes in shade tolerance (e.g. in different life stages of a tree) and adaptive allocation (e.g., due to increasing atmospheric CO_2 concentrations) are, however, currently neglected in iLand.

Ecological field theory proved a powerful approach for an integration of individual-tree competition with physiological processes: Process-based resource use efficiency approaches provide dynamic estimates of resource availability at the stand level as well as a framework for their utilization based on tree physiology, while EFT quantifies the share of the resource every individual obtains and its spatial distribution resulting from local exploitation by individuals. The *WLA* concept, applied here to achieve consistency between stand level resource availability and individual tree success in resource competition, was recently applied successfully in a related context also by Weiskittel et al. (2010). The encouraging results with regard to individual tree mortality, mechanistically modeled based on C starvation (i.e., as an end-of-pipe emergent property of production and allocation, see Fig. 2), strongly support the approach to model interactions between resource availability, resource competition, and resource utilization in iLand. They underline the utility of EFT in providing process-based estimates of individual tree mortality (see also Li et al., 2000), an ecosystem process that is often imposed (e.g., Landsberg and Waring, 1997) or modeled with only limited process resolution in many ecosystem models (see the analysis by Wunder et al., 2006).

5.2. Scaling individual tree dynamics to landscape scales

To achieve scalability of the explicitly modeled individual tree interactions we harnessed two key characteristics of ecosystems, modularity and repetitiveness (Green et al., 2006). Modularity, i.e., the fact that ecosystem characteristics (such as the canopy light regime) can be decomposed into distinct units (such as the shading of individual tree crowns), allows us to reduce the complex 3D light computations to a finite number of individuals of various sizes and crown shapes (rather than computing the infinite possible combinations and configurations of trees occurring across a forest landscape). Repetitiveness entails that these tree shapes and sizes repeat themselves over and over in a forest landscape, and that the respective pre-processed light interference patterns apply to all trees of the same size and shape. Utilizing these two characteristics in a pattern-based approach of light interference resolved conceptual scaling issues with previous IBMs and enabled robust (i.e., linear) computational scaling, allowing for a continuous simulation of individual tree interactions across forest landscapes with iLand.

Purves et al. (2007) and Ogle and Pacala (2009), also addressing the question of scalability of individual-tree competition in a process-based framework, recently demonstrated the utility of assuming perfect plasticity of tree crowns within the stand canopy. While iLand explicitly considers spatial configuration (yet assuming rigid tree crowns), their (analytically solvable) approach implies that plasticity in tree crowns allows within-stand positions of individual trees to be neglected. Both approaches thus relax a degree of freedom (albeit a different one) in modeling local tree interactions to achieve scalability and tractability.

A second important assumption to achieving scalability – particularly with regard to integrating the complex interactions between structure and functioning in forest ecosystems – was adopted in the form of a hierarchical multi-scale model design. Acknowledging a number of discrete hierarchical levels (i.e., individual tree, stand, landscape) and their interactions provides a means to combining a high level of process detail with an extensive scope. Compared to "brute force" scaling via simply summing an increasingly large number of individually simulated trees (and their errors), accounting for constraints of higher hierarchical levels on lower level processes makes individual-based simulations of landscape-scale forest ecosystem dynamics more robust. This HMS approach also has great potential for the integration of ecosystem processes such as natural disturbances, where susceptibilities are frequently related to tree or stand level attributes, but impacts may affect forest structure and composition at the landscape scale (see the analysis by Seidl et al., 2011a). Future work will focus on using this framework to integrate the spatially explicit simulation of disturbance and regeneration dynamics, as well as on modeling belowground processes such as litter and soil organic matter dynamics.

6. Conclusions

We have presented a novel approach to simulating forest ecosystem dynamics as an emergent property of environmental drivers, fundamental physiological processes, and dynamic interactions between adaptive agents. Taking up the "complexity challenge" sensu Green et al. (2005) in our modeling we found support for the integrated simulation of functional, structural and spatial complexity in a suite of evaluation experiments scrutinizing iLand with regard to a number of key ecosystem attributes. Since climatic changes are going to affect a variety of processes across a wide range of scales simultaneously, such an integrated, multi-scale perspective is particularly relevant for addressing the impacts of these changes on forest ecosystem dynamics. Furthermore, since ecosystem resilience results from the interplay of local and global, fast and slow processes (Holling and Gunderson, 2002) the presented multi-scale modeling approach can be a valuable tool for analyzing the resilience of forest ecosystems to a variety of disturbances. iLands' capacity to efficiently simulate alternative future trajectories will support emerging management concepts rooted in complexity theory in their efforts to increase resilience and sustainability of ecosystem stewardship (Chapin et al., 2009; Wolfslehner and Seidl, 2010). Our fine-grained approach will be particularly valuable to study spatial processes in heterogeneous environments like mountain areas (Schumacher and Bugmann, 2006; Seidl et al., 2011b). With the capacity to address competition and physiology in a process-based manner while retaining scalability to the landscape scale the presented approach has the potential to serve as a central building block for next generation landscape models.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2012.02.015.

References

Astrup, R., Coates, K.D., Hall, E., 2008. Finding the appropriate level of complexity for a simulation model. An example with a forest growth model. For. Ecol. Manage. 256, 1659–1665.

Berger, U., Hildenbrandt, H., 2000. A new approach to spatially explicit modelling of forest dynamics: spacing ageing and neighbourhood competition of mangrove trees. Ecol. Model. 132, 287–302.

Berger, U., Piou, C., Schiffers, K., Grimm, V., 2008. Competition among plants: concepts, individual-based modeling approaches, and a proposal for a future research strategy. Persp. Plant Ecol. Evol. System. 9, 121–135.

Bernston, G.M., Wayne, P.M., 2000. Characterizing the size dependence of resource acquisition within crowded plant populations. Ecology 81, 1072–1085.

Berthelot, M., Friedlingstein, P., Ciais, P., Dufresne, J.L., Monfray, P., 2005. How uncertainties in future climate change predictions translate into future terrestrial carbon fluxes. Glob. Change Biol. 11, 959–970.

BFW, 1997. Ergebnisse der Österreichischen Waldinventur 1992 bis 1996. Mit Vergleichsdaten 1986 bis 1990. Forstliche Bundesversuchsanstalt–Waldforschungszentrum Wien. CD-ROM.

Bigler, C., Bugmann, H., 2003. Growth-dependent tree mortality models based on tree rings. Can. J. For. Res. 33, 210–221.

Bond, B.J., Czarnomski, N.M., Cooper, C., Day, M.E., Greenwood, M.S., 2007. Developmental decline in height growth in Douglas-fir. Tree Phys. 27, 441–453.

Bossel, H., 1986. Dynamics of forest dieback: systems analysis and simulation. Ecol. Model. 34, 259–288.

Bossel, H., 1996. TREEDYN3 forest simulation model. Ecol. Model. 90, 187–227.

Botkin, D.B., 1993. Forest Dynamics. An Ecological Model. Oxford, Oxford University Press.

Bousquet, F., Le Page, C., 2004. Multi-agent simulations and ecosystem management: a review. Ecol. Model. 176, 313–332.

Brunner, A., Nigh, G., 2000. Light absorption and bole volume growth of individual Douglas-fir trees. Tree Phys. 20, 323–332.

Bugmann, H., 2001. A review of forest gap models. Clim. Change 51, 259–305.

Bugmann, H., Grote, R., Lasch, P., Lindner, M., Suckow, F., 1997. A new forest gap model to study the effects of environmental change on forest structure and functioning. In: Mohren, G.M.J., Kramer, K., Sabaté, S., (Eds.), Global Change Impacts on Tree Physiology and Forest Ecosystems. Kluwer Academic Publishers, pp. 255–261.

Bugmann, H., Lindner, M., Lasch, P., Flechsig, M., Ebert, B., Cramer, W., 2000. Scaling issues in forest succession modeling. Clim. Change 44, 265–289.

Busing, R.T., Mailly, D., 2004. Advances in spatial, individual-based modeling of forest dynamics. J. Veg. Sci. 15, 831–842.

Cadenasso, M.L., Pickett, S.T.A., Grove, J.M., 2006. Dimensions of ecosystem complexity, Heterogeneity, connectivity, and history. Ecol. Complex 3, 1–12.

Canham, C.D., 1988. Growth and canopy architecture of shade-tolerant trees: response to canopy gaps. Ecology 69, 786–795.

Casper, B.B., Schenk, H.J., Jackson, R.B., 2003. Defining a plant's belowground zone of influence. Ecology 84, 2313–2321.

Chapin, F.S., 2009. Managing ecosystems sustainability: the key role of resilience. In: Chapin, F.S., Kofinas, G.P., Folke, C. (Eds.), Principles of Ecosystem Stewardship. Resilience-based Natural Resource Management in a Changing World. Springer, New York, pp. 29–53.

Chapin, F.S., Kofinas, G.P., Folke, C., Carpenter, S.R., Olsson, P., Abel, N., Biggs, R., Naylor, R.L., Pinkerton, E., Smith, D.M.S., Steffen, W., Walker, B., Young, O.R., 2009. Resilience-based stewardship: strategies for navigating sustainable pathways in a changing world. In: Chapin, F.S., Kofinas, G.P., Folke, C. (Eds.), Principles of Ecosystem Stewardship. Resilience-based Natural Resource Management in a Changing World. Springer, New York, pp. 319–337.

Chertov, O., Komarov, A., Loukianov, A., Mikhailov, A., Nadporozhskaya, M., Zubkova, E., 2006. The use of forest ecosystem model EFIMOD for research and practical implementation at forest stand local and regional levels. Ecol. Model. 194, 227–232.

Coops, N.C., Waring, R.H., Landsberg, J.J., 2001. Estimation of potential forest productivity across the Oregon transect using satellite data and monthly weather records. Int. J. Remote Sens. 22, 3797–3812.

Cosby, B.J., Hornberger, G.M., Clapp, R.B., Ginn, T.R., 1984. A statistical exploration of the relationships of soil moisture characteristics to the physical properties of soils. Water Resources Res. 20, 682–690.

Daly, C., 2005. Average monthly and annual temperature spatial grids (1980-1990) (Rosentrater thesis), Andrews Experimental Forest. Long-Term Ecological Research. Forest Science Data Bank, Corvallis, OR. [Database]. Available: http://andrewsforest.oregonstate.edu/data/abstract.cfm?dbcode=MS028.

Daly, C., Conklin, D.R., Unsworth, M.H., 2009. Local atmospheric decoupling in complex topography alters climate change impacts. Int. J. Clim. 30, 1857–1864.

Didion, M., Kupferschmid, A.D., Zingg, A., Fahse, L., Bugmann, H., 2009. Gaining local accuracy while not losing generality–extending the range of gap model applications. Can. J. For. Res. 39, 1092–1107.

Donato, D.C., Campbell, J.L., Franklin, J.F., 2011. Multiple successional pathways and precocity in forest development: can some forests be born complex? J. Veg. Sci., doi:10.1111/j.1654-1103.2011.01362.x.

Duursma, R.A., Marshall, J.D., Robinson, A.P., Pangle, R.E., 2007. Description and test of a simple process-based model of forest growth for mixed-species stands. Ecol. Model. 203, 297–311.

Dyrness, C., 2001. Soil descriptions and data for soil profiles in the Andrews Experimental Forest, selected reference stands, Research Natural Areas, and National Parks. Long-Term Ecological Research. Forest Science Data Bank, Corvallis, OR. [Database]. Available: http://andrewsforest.oregonstate.edu/data/abstract.cfm?dbcode=SP001.

Dyrness, C.T., Acker, S.A., 1999. Reference Stands in or near the H.J. Andrews Experimental Forest. Permanent Plots of the Pacific Northwest. Report Number 2. http://www.fsl.orst.edu/lter/pubs/webdocs/permplot.cfm.

Fourcaud, T., Zhang, X., Stokes, A., Lambers, H., Körner, C., 2008. Plant growth modelling and applications. The increasing importance of plant architecture in growth models. Ann. Bot. 101, 1053–1063.

Franklin, J.F., Dyrness, C.T., 1973. Natural Vegetation of Oregon and Washington. USDA Forest Service General Technical Report PNW-8, Portland, Oregon. 417 pp.

Friedlingstein, P., Fung, I., Holland, E., John, J., Brasseur, G., Erickson, D., Schimel, D., 1995. On the contribution of CO2 fertilization to the missing biospheric sink. Glob. Biogeochem. Cycles 9, 541–556.

Garman, S.L., 2004. Design and evaluation of a forest landscape change model for western Oregon. Ecol. Model. 175, 319–337.

Green, D.G., Klomp, N., Rimmington, G., Sadedin, S., 2006. Complexity in Landscape Ecology. Springer, the Netherlands, 215 pp.

Green, D.G., Sadedin, S., 2005. Interactions matter—complexity in landscapes and ecosystems. Ecol. Complex 2, 117–130.

Green, J.L., Hastings, A., Arzerger, P., Ayala, F.J., Cottingham, K.L., Cuddington, K., Davis, F., Dunne, J.A., Fortin, M.J., Gerber, L., Neubert, M., 2005. Complexity in ecology and conservation: mathematical, statistical, and computational challenges. BioScience 55, 501–510.

Grime, J.P., 2001. Plant Strategies, Vegetation Processes, and Ecosystem Properties. 2nd ed., Wiley, Chichester. 417 pp.

Grimm V., Railsback, S.F., 2005. Individual-Based Modelling and Ecology. Princeton University Press, Princeton, 428 pp.

Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W.M., Railsback, S.F., Thulke, H.H., Weiner, J., Wiegand, T., DeAngelis, D.L., 2005. Pattern-oriented modeling of agent-based complex systems: lessons from ecology. Science 310, 987–991.

Güneralp, B., Gertner, G., 2007. Feedback loop dominance analysis of two tree mortality models: relationship between structure and behavior. Tree Phys. 27, 269–280.

Hanson, E.J., Azuma, D.L., Hiserote, B.A., 2002. Site Index Equations and Mean Annual Increment Equations for Pacific Northwest Research Station Forest Inventory and Analysis Inventories, 1985-2001. USDA Forest Service Research Note PNW-RN-533. 24 pp.

Hanson, P.J., Todd, D.E., Amthor, J.S., 2001. A six-year study of sapling and large-tree growth and mortality responses to natural and induced variability in precipitation and throughfall. Tree Phys. 21, 345–358.

Harmon, M., Munger, T., 2005. Tree Growth and Mortality Measurements in Long-term Permanent Vegetation Plots in the Pacific Northwest (LTER Reference Stands). Long-Term Ecological Research. Forest Science Data Bank, Corvallis, OR. [Database]. Available: http://andrewsforest.oregonstate.edu/data/abstract.cfm?dbcode=TV010.

Hawkes, C., 2000. Woody plant mortality algorithms: description problems and progress. Ecol. Model. 126, 225–248.

He, H.S., Mladenoff, D.J., Boeder, J., 1999. An object-oriented forest landscape model and its representation of tree species. Ecol. Model. 119, 1–19.

Heinimann, H.R., 2009. A concept in adaptive ecosystem management—an engineering perspective. For. Ecol. Manage. 259, 848–856.

Henry, H.A.L., Aarssen, L.W., 1999. The interpretation of stem diameter-height allometry in trees: biomechanical constraints, neighbor effects, or biased regressions? Ecol. Lett. 2, 89–97.

Holling, C.S., Gunderson, L.H., 2002. Resilience and adaptive cycles. In: Gunderson, L.H., Holling, C.S. (Eds.), Panarchy: Understanding Transformations in Human and Natural Systems. Island Press, Washington DC, pp. 25–62.

Jeltsch, F., Moloney, K.A., Schurr, F.M., Köchy, M., Schwager, M., 2008. The state of plant population modelling in light of environmental change. Persp. Plant Ecol. Evol. System. 9, 171–189.

Jolly, W.M., Nemani, R., Running, S.W., 2005. A generalized bioclimatic index to predict foliar phenology in response to climate. Glob. Change Biol. 11, 619–632.

Keane, R.E., Austin, M., Field, C., Huth, A., Lexer, M.J., Peters, D., Solomon, A., Wyckoff, P., 2001. Tree mortality in gap models: application to climate change. Clim. Change 50, 509–540.

Kelliher, F.M., Leuning, R., Raupach, M.R., Schulze, E.D., 1995. Maximum conductances for evaporation from global vegetation types. Agric. For. Met. 73, 1–16.

Kicklighter, D.W., Bruno, M., Dönges, S., Esser, G., Heimann, M., Helfrich, J., Ift, F., Joos, F., Kaduk, J., Kohlmaier, G.H., McGuire, A.D., Melillo, J.M., Meyer, R., Moore, B., Nadler, A., Prentice, I.C., Sauf, W., Schloss, A.L., Sitch, S., Wittenberg, U., Würth, G., 1999. A first-order analysis of the potential role of CO_2 fertilization to affect global carbon budget: a comparison of four terrestrial biosphere models. Tellus 51B, 343–366.

Kimmins, J.P., Blanco, J.A., Seely, B., Welham, C., Scoullar, K., 2008. Complexity in modelling forest ecosystems: how much is enough? For. Ecol. Manage. 256, 1646–1658.

Kuuluvainen, T., 2009. Forest management and biodiversity conservation based on natural ecosystem dynamics in Northern Europe: the complexity challenge. Ambio 38, 309–315.

Landsberg, J.J., Gower, S.T., 1997. Applications of Physiological Ecology to Forest Management. Academic Press, San Diego, 354 pp.

Landsberg, J.J., Waring, R.H., 1997. A generalised model of forest productivity using simplified concepts of radiation-use efficiency carbon balance and partitioning. For. Ecol. Manage. 95, 209–228.

Landsberg, J.J., Waring, R.H., Coops, N.C., 2003. Performance of the forest productivity model 3-PG applied to a wide range of forest types. For. Ecol. Manage. 172, 199–214.

Lexer, M.J., Hönninger, K., 2001. A modified 3D-patch model for spatially explicit simulation of vegetation composition in heterogeneous landscapes. For. Ecol. Manage. 144, 43–65.

Li, B.L., 2000. Why is the holistic approach becoming so important in landscape ecology? Landsc. Urban Plann. 50, 27–41.

Li, B.L., Wu, H., Zou, G., 2000. Self-thinning rule: a causal interpretation from ecological field theory. Ecol. Model. 132, 167–173.

Lindner, M., Maroschek, M., Netherer, S., Kremer, A., Barbati, A., Garcia-Gonzalo, J., Seidl, R., Delzon, S., Corona, P., Kolström, M., Lexer, M.J., Marchetti, M., 2010. Climate change impacts adaptive capacity, and vulnerability of European forest ecosystems. For. Ecol. Manage. 259, 698–709.

Lischke, H., Zimmermann, N.E., Bolliger, J., Rickebusch, S., Löffler, T.J., 2006. TreeMig. A forest-landscape model for simulating spatio-temporal patterns from stand to landscape scale. Ecol. Model. 199, 409–420.

Loehle, C., 1990. A guide to increased creativity in research–inspiration or perspiration? Bioscience 40, 123–129.

Loehle, C., 2004. Challenges of ecological complexity. Ecol. Complex 1, 3–6.

Loehle, C., LeBlanc, D., 1996. Model-based assessments of climate change effects on forests: a critical review. Ecol. Model. 90, 1–31.

Mäkelä, A., 2003. Process-based modelling of tree and stand growth: towards a hierarchical treatment of multiscale processes. Can. J. For. Res. 33, 398–409.

Mäkelä, A., Hari, P., Berninger, F., Hänninen, H., Nikinmaa, E., 2004. Acclimation of photosynthetic capacity in Scots pine to the annual cycle of temperature. Tree Phys. 24, 369–376.

Mäkelä, A., Pulkkinen, M., Kolari, P., Lagergren, F., Berbigier, P., Lindroth, A., Loustau, D., Nikinmaa, E., Vesala, T., Hari, P., 2008. Developing an empirical model of stand GPP with the LUE approach: analysis of eddy covariance data at five contrasting conifer sites in Europe. Glob. Change Biol. 14, 92–108.

Mäkelä, A., Valentine, H.T., 2001. The ratio of NPP to GPP: evidence of change over the course of stand development. Tree Phys. 21, 1015–1030.

Manion, P.D., 1981. Tree Disease Concepts. 1st Edn. Prentice-Hall, Englewood Cliffs, NJ, 402 pp.

Medlyn, B., Barrett, D., Landsberg, J.J., Sands, P., Clement, R., 2003. Conversion of canopy intercepted radiation to photosynthate: review of modeling approaches for regional scales. Funct. Plant Biol. 30, 153–169.

Medlyn, B.E., Dewar, R.C., 1999. Comment on the article by R.H. Waring, J.J. Landsberg and M. Williams relating net primary production to gross primary production. Tree Phys. 19, 137–138.

Medvigy, D., Wofsy, S.C., Munger, J.W., Moorcroft, P.R., 2010. Responses of terrestrial ecosystems and carbon budgets to current and future environmental variability. PNAS 107, 8275–8280.

Miina, J., Pukkala, T., 2002. Application of ecological field theory in distance-dependent growth modelling. For. Ecol. Manage. 161, 101–107.

Moorcroft, P.R., Hurtt, G.C., Pacala, S.W., 2001. A method for scaling vegetation dynamics: the ecosystem demography model (ED). Ecol. Monographs 71, 557–586.

Munne-Bosch, S., Alegre, L., 2002. Plant aging increases oxidative stress in chloroplasts. Planta 214, 608–615.

Niinemets, Ü., 2002. Stomatal conductance alone does not explain the decline in foliar photosynthetic rates with increasing tree age and size in Picea abies and Pinus sylvestris. Tree Phys. 22, 515–535.

Niklas, K.J., 1995. Size-dependent allometry of tree height diameter and trunk taper. Ann. Bot. 75, 217–227.

Norby, R.J., DeLucia, E.H., Gielen, B., Calfapietra, C., Giardina, C.P., King, J.S., Ledford, J., McCarthy, H.R., Moore, D.J.P., Ceulemans, R., De Angelis, P., Finzi, A.C., Karnosky, D.F., Kubiske, M.E., Lukac, M., Pregitzer, K.S., Scarascia-Mugnozza, G.E., Schlesinger, W.H., Oren, R., 2005. Forest response to elevated CO2 is conserved across a broad range of productivity. PNAS 102, 18052–18056.

O'Brien, E.E., Brown, J.S., Moll, J.D., 2007. Roots in space: a spatially explicit model for below-ground competition in plants. Proc. Royal Soc. B 274, 929–934.

Ogle, K., Pacala, S.W., 2009. A modeling framework for inferring tree growth and allocation from physiological morphological and allometric traits. Tree Phys. 29, 587–605.

Oren, R., Sperry, J.S., Katul, G.G., Pataki, D.E., Ewers, B.E., Phillips, N., Schäfer, K.V.R., 1999. Survey and synthesis of intra- and interspecific variation in stomatal sensitivity to vapour pressure deficit. Plant Cell Environ. 22, 1515–1526.

Pacala, S.W., Canham, C.D., Saponara, J., Silander, J.A., Kobe, R.K., Ribbens, E., 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. Ecol. Monographs 66, 1–43.

Pastor, J., Post, W.M., 1985. Development of a linked forest productivity-soil process model. United States Department of Energy ORNL/TM-9519.

Peng, C., Liu, J., Dang, Q., Apps, M.J., Jiang, H., 2002. TRIPLEX: a generic hybrid model for predicting forest growth and carbon and nitrogen dynamics. Ecol. Model. 153, 109–130.

Peterson, D.L., Waring, R.H., 1994. Overview of the Oregon transect ecosystem research project. Ecol. Appl. 4, 211–225.

Pretzsch, H., Biber, P., Dursky, J., 2002. The single tree-based stand simulator SILVA: construction application and evaluation. For. Ecol. Manage. 162, 3–21.

Puettmann, K.J., Coates, K.D., Messier, C., 2009. A Critique of Silviculture. Managing for Complexity. Island Press, Washington DC. 206 p.

Purves, D.W., Lichstein, J.W., Pacala, S.W., 2007. Crown plasticity and competition for canopy space: a new spatially implicit model parameterized for 250 North American tree species. PLoS ONE 2, e870.

R Development Core Team, 2009. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0.

Reineke, L.H., 1933. Perfecting a stand-density index for even-aged forests. J. Agric. Res. 46, 627–638.

Robinson, A.P., Ek, A.R., 2000. The consequences of hierarchy for modeling in forest ecosystems. Can. J. For. Res. 30, 1837–1846.

Running, S.W., Coughlan, J.C., 1988. A general model of forest ecosystem processes for regional applications. I. Hydrological balance, canopy gas exchange and primary production processes. Ecol. Model. 42, 125–154.

Ryan, M.G., Phillips, N., Bond, B.J., 2006. The hydraulic limitation hypothesis revisited. Plant Cell Environ. 29, 367–381.

Sato, H., Itoh, A., Kohyama, T., 2007. SEIB–DGVM. A new dynamic global vegetation model using a spatially explicit individual-based approach. Ecol. Model. 200, 279–307.

Scheller, R.M., Domingo, J.B., Sturtevant, B.R., Williams, J.S., Rudy, A., Gustafson, E.J., Mladenoff, D.J., 2007. Design, development, and application of LANDIS-II. A spatial landscape simulation model with flexible temporal and spatial resolution. Ecol. Model. 201, 409–419.

Scheller, R.M., Mladenoff, D.J., 2007. An ecological classification of forest landscape simulation models: tools and strategies for understanding broad-scale forested ecosystems. Landscape Ecol. 22, 491–505.

Scheller, R.M., Sturtevant, B.R., Gustafson, E.J., Ward, B.C., Mladenoff, D.J., 2010. Increasing the reliability of ecological models using modern software engineering techniques. Front. Ecol. Environ. 8, 253–260.

Schumacher, S., Bugmann, H., 2006. The relative importance of climatic effects, wildfires and management for future forest landscape dynamics in the Swiss Alps. Glob. Change Biol. 12, 1435–1450.

Schwalm, C.R., Ek, A., 2004. A process-based model of forest ecosystems driven by meteorology. Ecol. Model. 179, 317–348.

Seidl, R., Lexer, M.J., Jäger, D., Hönninger, K., 2005. Evaluating the accuracy and generality of a hybrid forest patch model. Tree Phys. 25, 939–951.

Seidl, R., Rammer, W., Lexer, M.J., 2009. Schätzung von Bodenmerkmalen und Modellparametern für die Waldökosystemsimulation auf Basis einer Großrauminventur. Allg. Forst-Jagdztg 180, 35–44.

Seidl, R., Fernandes, P.M., Fonseca, T.F., Gillet, F., Jönsson, A.M., Merganicova, K., Netherer, S., Arpaci, A., Bontemps, J.D., Bugmann, H., Gonzalez-Olabarria, J.R., Lasch, P., Meredieu, C., Moreira, F., Schelhaas, M.J., Mohren, F., 2011a. Modelling natural disturbances in forest ecosystems: a review. Ecol. Model. 222, 903–924.

Seidl, R., Rammer, W., Bellos, P., Hochbichler, E., Lexer, M.J., 2010. Testing generalized allometries in allocation modeling within an individual-based simulation framework. Trees 24, 139–150.

Seidl, R., Rammer, W., Lexer, M.J., 2011b. Climate change vulnerability of sustainable forest management in the Eastern Alps. Clim. Change 106, 225–254.

Sierra, C.A., Loescher, H.W., Harmon, M.E., Richardson, A.D., Hollinger, D.Y., Perakis, S.S., 2009. Interannual variation of carbon fluxes from three contrasting evergreen forests: the role of forest dynamics and climate. Ecology 90, 2711–2723.

Spies, T.A., Franklin, J.F., 1991. The structure of natural young, mature, and old-growth Douglas-fir forests in Oregon and Washington. In: Ruggiero, L.F., Aubry, K.B., Carey, A.B., Huff, M.H. (Eds.), Wildlife and Vegetation of Unmanaged Douglas-Fir Forests. USFS PNW-GTR-285, Portland, pp. 91–109.

Spies, T.A., Giesen, T.W., Swanson, F.J., Franklin, J.F., Lach, D., Johnson, K.N., 2010. Climate change adaptation strategies for federal forests of the Pacific Northwest. USA: ecological, policy, and socio-economic perspectives. Landscape Ecol. 25, 1185–1199.

Stoll, P., Weiner, J., 2000. Neighbourhood view of interactions among individual plants. In: Dieckmann, U., Law, R., Metz, J.A.J. (Eds.), The Geometry of Ecological Interactions. Cambridge University Press, Cambridge, pp. 11–27.

Swenson, J.J., Waring, R.H., Fan, W., Coops, N., 2005. Predicting site index with a physiologically based growth model across Oregon, USA. Can. J. For. Res. 35, 1697–1707.

Thornton, P.E., Running, S.W., White, M.A., 1997. Generating surfaces of daily meteorology variables over large regions of complex terrain. J. Hydrol. 190, 214–251.

Urban, D.L., 2005. Modeling ecological processes across scales. Ecology 86, 1996–2006.

USAD, 2009. The Forest Inventory and Analysis Database: Database Description and Users Manual Version 4.0. Phase 3 Indicators. Forest Inventory and Analysis Program. U.S. Department of Agriculture, Forest Service. 206 pp.

Walker, J., Sharpe, P.J.H., Penridge, L.K., Wu, H., 1989. Ecological field theory: the concept and field tests. Vegetatio 83, 81–95.

Waring, R.H., 1987. Characteristics of trees predisposed to die. BioScience 37, 569–574.

Waring, R.H., Landsberg, J.J., Williams, M., 1998. Net primary production of forests: a constant fraction of gross primary production? Tree Phys. 18, 129–134.

Weiskittel, A.R., Maguire, D.A., Monserud, R.A., Johnson, G.P., 2010. A hybrid model for intensively managed Douglas-fir plantations in the Pacific Northwest USA. Europ. J. For. Res. 129, 325–338.

Wolfslehner, B., Seidl, R., 2010. Harnessing ecosystem models and multi-criteria decision analysis for the support of forest management. Environ. Manage. 46, 850–861.

Wu, H., Sharp, P.J., Walker, J., Penridge, L.K., 1985. Ecological field theory: a spatial analysis of resource interference among plants. Ecol. Model. 29, 215–243.

Wu, J., David, J.L., 2002. A spatially explicit hierarchical approach to modeling complex ecological systems: theory and applications. Ecol. Model. 153, 7–26.

Wu, J., Marceau, D., 2002. Modeling complex ecological systems: an introduction. Ecol. Model. 153, 1–6.

Wullschleger, S.D., Hanson, P.J., 2003. Sensitivity of sapling and mature-tree water use to altered precipitation regimes. In: Hanson, P.J., Wullschleger, S.D. (Eds.), North American Temperate Deciduous Forest Responses to Changing Precipitation Regimes. Springer, New York, pp. 87–98.

Wunder, J., Bigler, C., Reineking, B., Fahse, L., Bugmann, H., 2006. Optimisation of tree mortality models based on growth patterns. Ecol. Model. 197, 196–206.

Yang, J., He, H.S., Shifley, S.R., Thompson, F.R., Zhang, Y., 2011. An innovative computer design for modeling forest landscape change in very large spatial extents with fine resolutions. Ecol. Model. 222, 2623–2630.

Yoda, K., Kira, T., Ogawa, H., Hozumi, K., 1963. Self-thinning in overcrowded pure stands under cultivated and natural conditions (Intraspecific competition among higher plants XI). J. Instit. Polytechn. Osaka City University, Series D 14, 107–129.