RESEARCH ARTICLE

Do small-grain processes matter for landscape scale questions? Sensitivity of a forest landscape model to the formulation of tree growth rate

Ché Elkin · Björn Reineking · Christof Bigler · Harald Bugmann

Abstract Process-based forest landscape models are valuable tools for testing basic ecological theory and for projecting how forest landscapes may respond to climate change and other environmental shifts. However, the ability of these models to accurately predict environmentally-induced shifts in species distributions as well as changes in forest composition and structure is often contingent on the phenomenological representation of individual-level processes accurately scaling-up to landscape-level community dynamics. We use a spatially explicit landscape forest model (LandClim) to examine how three alternative formulations of individual tree growth (logistic, Gompertz, and von Bertalanffy) influence model results. Interactions between growth models and landscape characteristics (landscape heterogeneity and disturbance intensity) were tested to determine in what type of landscape simulation results were most sensitive to growth model structure. We found that simulation results were robust to growth function formulation when the results were assessed at a large spatial extent (landscape) and when coarse response variables, such as total forest biomass, were examined. However, results diverged when more detailed response variables, such as species composition within elevation bands, were considered. These differences were particularly prevalent in regions that included environmental transition zones where forest composition is strongly driven by growth-dependent competition. We found that neither landscape heterogeneity nor the intensity of landscape disturbances accentuated simulation sensitivity to growth model formulation. Our results indicate that at the landscape extent, simulation results are robust, but the reliability of model results at a finer resolution depends critically on accurate tree growth functions.

Keywords Tree growth · Gap model · Forest disturbances · Model uncertainty

Introduction

Forest landscape models attempt to accurately represent forest dynamics in a spatially explicit manner by incorporating landscape level processes, such as disturbances and dispersal, while still retaining sufficiently detailed representations of smaller-grain processes such as tree growth and competition (e.g., Scheller and Mladenoff 2004, 2007; He 2008). Thus, these models must incorporate trade-offs regarding the

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type and amount of process detail included (Reynolds et al. 2001). In addition, forest landscape models must deal with the problem of accurately parameterizing smaller grain processes in a way that is robust to the natural variation that occurs within landscapes (Guisan and Thuiller 2005). The accuracy of landscape simulations therefore are expected to depend on the degree to which the model is suitable for the environment, but also on how robust the model framework is to uncertainty in model structure and parameterization of smaller-grain processes.

The importance of accurately representing and parameterizing small-grain processes, such as how individual trees grow and respond to environmental conditions, is likely to depend on the spatial extent at which model output is evaluated (Xu et al. 2004), and on the degree to which model dynamics are impacted by intrinsic model processes rather than extrinsic drivers such as landscape disturbances and landscape structure (Druckenbrod et al. 2005). For example, in environments where landscape disturbances are a primary driver of forest dynamics, model accuracy may be relatively insensitive to how late-stage succession dynamics are modelled. Conversely, accurately simulating forest development in landscapes where disturbances are infrequent and of low intensity may be highly sensitive to how intrinsic processes, such as tree growth, are modelled and parameterized. Thus, confidence in simulation results will depend on knowing in what type of landscapes, and under what environmental conditions the model predictions are most robust, but little is known on this issue.

Growth formulations commonly used in forest landscape models can be divided into three types: polynomial equations fit to empirical data (Peng 2000; Trasobares et al. 2004), sigmoidal phenomenological growth models premised on ecophysiology but containing few such processes explicitly (Zeide 1993; Bugmann 2001), and detailed physiological growth models which represent individual growth as the outcome of linked physiological processes (Smith et al. 2001). Phenomenological growth models, such as the logistic, Gompertz, Chapman-Richards and von Bertalanffy equations (Zeide 1993), have a biological, albeit theoretical, basis, and therefore are expected to be more suitable for simulating tree growth under novel conditions than polynomial equations (Fekedulegn et al. 1999). In addition, the number of parameters required by phenomenological growth models is comparatively low, a trait that is particularly beneficial when parameterizing a large number of species.

While phenomenological growth models are comparatively simple and robust, challenges remain with respect to: (1) selecting the form of the model that works best across a range of conditions, and (2) parameterizing the model such that accurate results are produced at the resolution of interest (MacFarlane et al. 2000; Colbert et al. 2004). A key constraint limiting both model selection and parameterization is the availability of empirical data (Alexandrov 2008). If data are not equally available across the lifespan of the tree species, parameter estimation and model selection will be biased (Fekedulegn et al. 1999; Falkowski et al. 2010), particularly if data from crucial stages such as early juvenile growth are missing (Rammig et al. 2007a). Similarly, in heterogeneous landscapes, such as mountain forests, site-specific conditions strongly influence tree growth (Li et al. 2003) as well as life-history strategy (e.g. a slow vs. fast growth strategy; cf. Wunder et al. 2008; Bigler and Veblen 2009), which can result in deviations from the standard trajectory of phenomenological models. For all these reasons, uncertainties in model structure and parameter values are inherent in any landscape-level forest model, but they have not received much attention to date.

Here we test the sensitivity of a landscape-level forest simulation to growth model uncertainty by comparing alternative model formulations across a range of parameter values. We compare three different growth models (logistic, Gompertz and von Bertalanffy; Zeide 1993) in landscapes that exhibit different levels of heterogeneity and which are subjected to different levels of disturbance. Our analysis comprises four aspects:

First, while forest landscape models are designed to incorporate landscape-level driving forces, the resolution at which model output is analysed often depends on the specific question. We therefore test how growth model differences influence simulation outputs at different spatial extents. Second, we test how growth models that are parameterized for particular tree life-history stages will influence simulation results. This corresponds to situations where empirical data are available for only a part of the trees' full life-history. Third, interactions between landscape characteristics and tree growth models have been suggested to influence the robustness of simulation results (Coates

2002; Getzin et al. 2008). We predict that the results from growth models parameterized to minimize differences in early tree growth would be most similar in heavily disturbed landscapes, while results from models parameterized to minimize differences in growth during the latter part of trees' lives would be more similar in relatively undisturbed landscapes. Fourth, we compare the individual growth trajectories predicted by the growth model variants to empirical data on Norway spruce (*Picea abies*) growth so as to evaluate the sensitivity of simulation results from different growth models to the ability to distinguish growth models using empirical tree growth data from heterogeneous landscapes.

Methods

We used the model LandClim (Schumacher et al. 2004; Schumacher et al. 2006), a spatially explicit, process-based model that incorporates competition-driven stand dynamics and landscape-level disturbances to simulate forest dynamics at a landscape resolution. In LandClim the tree and stand-level processes that determine competition are modified versions of the respective processes used in forest gap models (Liu and Ashton 1995; Bugmann 1996; Bugmann 2001; Scheller and Mladenoff 2007) that continue to be extensively used. This modelling framework allowed us to assess the importance of growth model formulation at both the landscape and smaller spatial resolutions, and to examine the influence of landscape heterogeneity and disturbances (i.e. fire, wind-throw).

We provide a brief overview of the stand-level formulations of the model; for further details see Schumacher et al. (2004). LandClim simulates forest growth in 25 m by 25 m cells using simplified versions of tree recruitment, growth and competition processes that are commonly included in gap models (Bugmann 2001). Forest growth is determined by climatic variables, soil properties and topography, land use, and large-scale disturbances. Individual cells are linked by the spatially explicit processes of seed dispersal and landscape disturbances. Succession processes within each cell are simulated on a yearly time step, while landscape-level processes are simulated on a decadal time step. Forest dynamics within each cell are simulated by following tree size cohorts, where cohorts are characterized by the mean biomass

of an individual tree (B_i) and the number of trees in the cohort.

Growth model formulation

Maximum individual tree growth is modelled as a sigmoidal function (Fig. 1) that is defined by a species-specific maximum growth rate (r_s) and a species-specific maximum biomass (K_s). The realized growth rate of trees ($r_i(t)$) is the maximum growth rate constrained by three growth-limiting factors: light availability, the sum of degree-days, and a drought index (Schumacher et al. 2004). Similarly, the realized maximum biomass of a tree ($K_i(t)$) is the maximum biomass constrained by the size-limiting factors of sum of degree days and drought index (for details see Schumacher et al. 2004).

Growth model types

We compare three phenomenological growth models: (1) logistic, (2) Gompertz, and (3) von Bertalanffy (cf. Zeide 1993).

Logistic

$$\frac{dB_i}{dt} = r_i(t)\left(1 - \frac{B_i(t)}{K_i(t)}\right)B_i(t) \qquad (1)$$
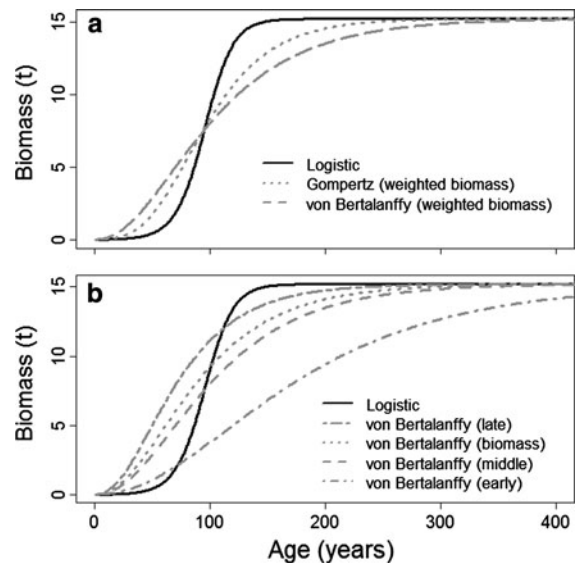
Fig. 1 a Growth model formulations; unconstrained growth trajectories are shown for *Picea abies*. **b** von Bertalanffy growth models parameterized to represent different periods of a tree's development

Gompertz

$$\frac{dB_i}{dt} = r_i(t) \cdot (\log(K_i) - \log[B_i(t)]) \cdot B_i(t) \qquad (2)$$

von Bertalanffy

$$\frac{dB_i}{dt} = 3 \cdot r_i(t) \cdot K_i(t)^{1/3} \cdot B_i(t)^{2/3} - B_i(t) \qquad (3)$$

The logistic growth function is used as the baseline here because it is the simplest growth model and has been used in all previous applications of LandClim (e.g., Schumacher et al. 2006). We tested the importance of the formulation of the growth function by contrasting the output of the Gompertz or von Bertalanffy model with the results obtained using the logistic function. To focus on the importance of the parameterization of the growth rate, we fixed the maximum biomass of a tree and fit the models using the growth rate parameter ($r_i(t)$). Independent fitting was performed for each of the 30 central European species included in the simulations. We parameterized the Gompertz and von Bertalanffy models to approximate the logistic model using five measures of similarity, selected so as to examine where along the growth curves the model was most sensitive to variation. We started by fitting the model using two measures of similarity that were designed to minimize the difference between the models across a tree's whole life span. The first measure minimized the squared difference in biomass predictions between the growth models for trees growing optimally. While this makes the formulations most similar across their whole range it does not account for the fact that mortality results in fewer large trees being present in a stand. We took this into account in the second metric by weighting the difference in biomass at a specific age by the tree's survival probability, such that differences at later stages (to which few trees survive) influence the model fit less than differences early in tree life (where many trees are typically present). The other three measures of similarity were aimed at making the growth formulations most similar to the logistic model during three periods of a tree's development; the juvenile stage, up until the tree has achieved 1/3 of its total maximum biomass, the middle part when the tree is growing fastest, i.e. between 1/3 and 2/3 of its maximum biomass, and the later part, i.e. from 2/3 of the tree's maximum biomass upwards. Models fit to tree development stage were not weighted by mortality.

Case study landscapes

We used two environments to compare the growth models: a realistic environment that is spatially heterogeneous, and an idealized environment designed to minimize the impact of landscape heterogeneity on forest dynamics. The real environment represented the Dischma valley near Davos in southeastern Switzerland (46°47′N and 9°53′E; elevation range 1,500–2,290 m a.s.l.). We chose to use the Dischma valley because it is characteristic of European Alpine valleys, its forest dynamics have previously been simulated using LandClim (Schumacher and Bugmann 2006), and it encapsulates natural variation in slope, aspect and soil depth. The idealized environment was a 4 km by 4 km area designed to approximate conditions in the European Alps, while at the same time minimizing landscape heterogeneity that can produce spatial variation in forest structure and dynamics (Li et al. 2003; Li and Yang 2004). Thus we assumed the area had an east facing valley side (constant aspect of 90°), a constant slope of 21° and constant soil conditions. In the idealized environment we tested a broader elevation range (700–2,290 m a.s.l.) so as to include the wider range of tree species that occur at lower elevations.

Disturbances

We compared the performance of the three growth models in the two environments under three disturbance regimes: no disturbance, intermediate disturbance and heavy disturbance. While avalanches are a common natural disturbance in the Dischma valley today, they occur in certain parts of the landscape only (avalanche tracks), thus leaving most parts of the forest area unaffected (cf. Schumacher and Bugmann 2006; Rammig et al. 2007b). By contrast, windthrow and fire can affect any part of the landscape, the former being important today, the latter likely becoming more important in a changing climate (Schumacher et al. 2006). Therefore, we focus on windthrow and fire. In the 'no disturbance' scenario, both wind and fire were excluded from the simulations. In the 'intermediate disturbance' scenario wind and fire were set to approximate their natural occurrence (Schumacher et al. 2006), while in the 'heavy disturbance' scenario, we increased the probabilities of fire initiation and spread such that there was approximately a fivefold increase in fire disturbances (Fig. 2).
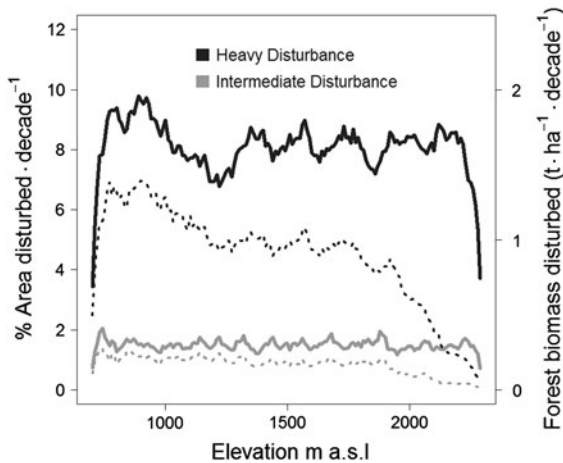
Fig. 2 Mean forest area disturbed (*solid line*) and biomass burnt (*dashed line*) in intermediate and heavy disturbance scenarios

In all simulations the same monthly inputs of mean temperature and precipitation were used and spatially extrapolated across the case study landscapes. These data were obtained from a climate station at the Davos case study region (Davos-Platz climate station, MeteoSwiss, elevation 1,560 m a.s.l).

Simulation experiments

All simulations were initialized with an empty landscape in which all tree species had the same probability (10%) of contributing seedlings to each cell on the landscape. The first 1,000 years of each simulation was a spin-up period during which the simulation reached a pseudo-equilibrium state; in most simulations this occurred after c. 300 years. After the 1,000 year spin up we ran the simulations for another 2,000 years. The mean forest state (mean biomass of each tree species and cohort) within 10 m elevation bands was calculated for the last 500 years of the simulation. Each landscape and treatment was independently simulated 25 times.

For each treatment we calculated the elevation-specific mean biomass for each species from each of the 25 replicates. To facilitate comparisons between the growth models we standardized our results by examining the difference between the output from the logistic model and the output from the two other growth models. This allowed the species, location and model-specific differences to be compressed into a single metric. We focus on three differences: difference in total landscape biomass (tons of aboveground biomass per ha averaged across the landscape), elevation-specific differences in total biomass (the sum of differences in biomass in 10 m elevation bands), and species- and elevation-specific differences in biomass. Comparisons were aggregated according to whether the simulations were based on the simplified or real topography, and by disturbance intensity, such that the differences reflect deviations due to model structure and model parameterization only.

Analysis

We assessed the relative impact of landscape heterogeneity, disturbance intensity and growth model formulations by evaluating the effect size (proportion of the total variance) associated with each factor (Tabachnick and Fidell 2007). First, we tested for these effects using an ANOVA that included all second order interactions. The Gompertz and von Bertalanffy models were compared using only parameters from the weighted biomass fitting. To allow for comparison between landscape types, this first analysis was restricted to data from the elevation band present in both landscapes (1,530–2,300 m a.s.l.). The logistic growth model run on the idealized landscape with no disturbance was used as the baseline model from which deviations were calculated. Following this initial analysis we separated the two simulation landscapes and analysed each using an ANOVA that included disturbance intensity, growth model formulation, and the five types of growth model parameterization (see above). All second order interactions between the main factors were included, and the analysis was performed across the full elevation range in each landscape type. For this analysis the baseline model was the logistic growth model with no disturbance from the corresponding landscape simulation.

Testing growth models against empirical growth data

Growth data were obtained from increment cores taken from *Picea abies* trees on southwest-facing slopes within the Dischma (17 trees) and the adjacent Flüela valley (24 trees) (Bigler and Veblen 2009). These trees were sampled between 1,720 and 2,000 m a.s.l. where *Picea abies* is the dominant species. From

each tree two increment cores were taken at breast height. Tree age and size was determined by measuring tree rings at a resolution of 0.01 mm (Bigler and Veblen 2009).

Growth of the 41 real trees was tested against the simulated growth of comparable trees in the Dischma valley. Tree growth data were extracted from each of the eleven different growth model simulations that were run for the Dischma valley. For each growth model the age and biomass of all *Picea abies* individuals that occurred between 1,720 and 2,000 m a.s.l. were extracted from each of the 25 simulation replicates. The biomass of simulate *Picea abies* was converted into diameter at breast height (DBH) using allometric relationships that are embedded in LandClim (Schumacher et al. 2004). We compared the fit of each of the eleven growth models using a permutation procedure that compared the size at age of the real trees with the size at age of the simulated trees. For each model, predicted tree size was drawn randomly (with replacement) from simulated trees that were within ±10 m of the real tree's elevation. The model that fit the empirical data best was recorded. This randomization procedure was repeated 100,000 times. Using this procedure, we calculated the percent of times that each growth model provided the best fit. We summarized the best model fit by taking the median fit for each model across the 41 trees.

Results

Disturbances

At the higher elevations the inclusion of disturbances slightly decreased total landscape biomass (0.13% reduction by intermediate disturbances and 0.5% reduction by heavy disturbances), and accounted for ca. 10% of the observed variation (Table 1, Fig. 3). Disturbance intensity had a large impact on elevation-specific forest biomass (ca. 50% of variation explained, Table 1), and a very large impact on species-specific biomass differences (79%). The large impact of disturbances on the latter was primarily driven by disturbances facilitating larch (*Larix decidua*) between 1,700 and 2,200 m a.s.l. (Fig. 3). At lower elevations, forest disturbances altered the relative abundance of species but did not promote the inclusion of species that would otherwise be absent (Fig. 3). As a result, when a broader elevation range was analysed the relative effect size of disturbance intensity was reduced (Table 2).

Landscape heterogeneity

Forest species composition did not substantially differ between the idealized and the heterogeneous, 'realistic' landscape. None of the three metrics we used (total biomass, elevation-specific difference, species- and elevation-specific difference) were strongly influenced by the inclusion of natural landscape heterogeneity (Table 1, Fig. 3). Landscape-level biomass was on average 0.53% lower in the heterogeneous landscape (range −0.25% to −0.76%). The difference in elevation-specific forest biomass was 0.23% greater in the heterogeneous landscape, and the species-specific elevation differences was 5.41% greater, but in both cases the amount of variation explained by landscape differences was less than 9%. There was also no strong interaction effect between landscape type and disturbance, or between landscape type and growth model, for any of the metrics (Table 1).

Because the effect size of landscape heterogeneity was small (Table 1), for the remainder of the analysis we focus on results from the idealized landscape as it included a broader elevation range.

Table 1 Effect size (% variance explained) of landscape heterogeneity, disturbance intensity and growth model formulation on forest model output when aggregated at three different resolutions

Response variable	Landscape heterogeneity (LH)	Disturbance intensity (DI)	Growth model (GM)	LH* DI	LH* GM	DI* GM	Residual
Total landscape biomass	1.9	10.4	76.4	0.2	0.0	9.3	1.8
Elevation-specific differences in biomass	0.2	49.5	39.3	0.4	1.3	7.1	2.3
Species- and elevation-specific differences in biomass	8.9	79.0	8.8	1.5	0.5	1.1	0.8

Fig. 3 Simulate forest composition using the logistic growth model in the heterogeneous (Dischma valley, **a** and **b**) and homogeneous (idealized, **c** and **d**) landscapes, under different disturbance scenarios
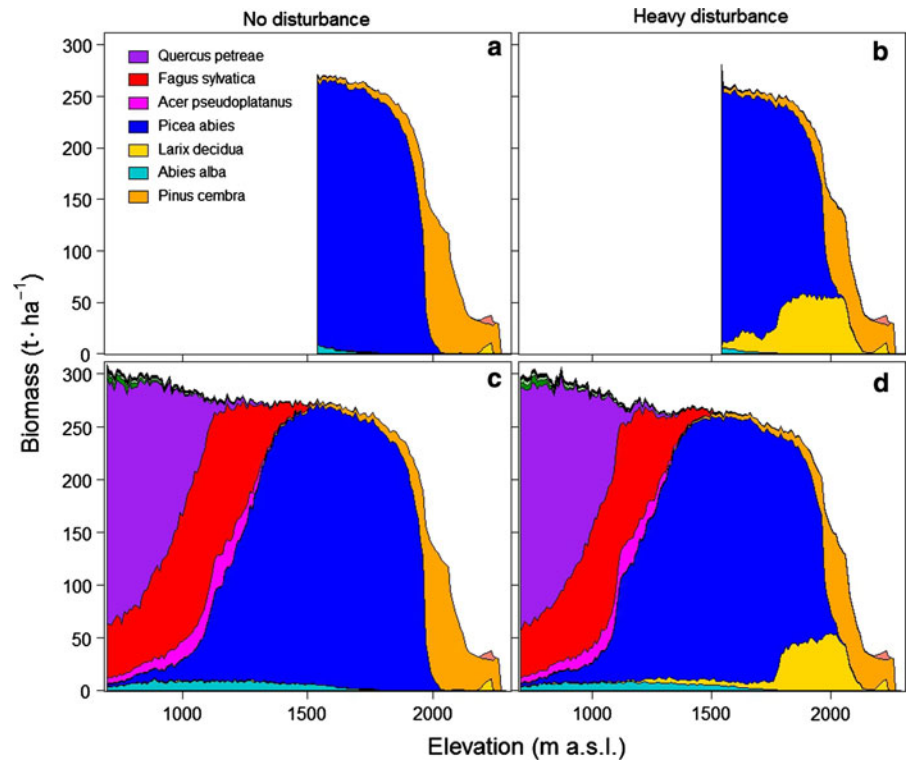
Table 2 Effect size (% variance explained) of disturbance intensity, growth model formulation, and model parameterization on forest model output when aggregated at three different resolutions

| Response variable	Disturbance intensity (DI)	Growth model (GM)	Growth model parameterization (MP)	DI* GM	DI* MP	GM* MP	Residual
Total landscape biomass	0.9	2.6	84.8	0.1	0.0	11.5	0.1
Elevation-specific differences in biomass	0.5	49.7	42.1	0.0	2.8	4.1	0.9
Species- and elevation-specific differences in biomass	1.8	39.0	42.4	0.4	2.7	12.6	1.1

Growth model formulation

At intermediate disturbance levels the logistic model simulated a landscape average of 229 t/ha of forest biomass in the idealized landscape (Fig. 4a). Under identical conditions the Gompertz growth model, fit using the weighted biomass method, simulated 237 t/ha (+3%, Fig. 4b), and the von Bertalanffy model 243 t/ha (+6%, Fig. 4c). The largest increase in biomass occurred at intermediate elevations (~1,000–500 m a.s.l.) where the forest was dominated by a mixture of deciduous species (*Fagus sylvatica*, *Quercus* sp.) and *Picea abies*, above which *Picea abies* became dominant.

Species- and elevation-specific differences in biomass varied considerably between growth models (Fig. 4), being most pronounced at the lowest (700–1,200 m) and highest elevations (1,900–2,050 m) (Fig. 4). These regions represent elevational transition zones that are characterized by shifts of dominant tree species.

At the landscape resolution the difference between growth model formulations accounted for little of the observed variance (Table 2, Fig. 5). The majority of the variance in total landscape biomass (85%) was due to differences in how the models were parameterized (Table 2). The large effect size was driven by the low

Fig. 4 Forest composition as simulated using the logistic (**a**), Gompertz (**b**), and von Bertalanffy (**c**) growth models under intermediate disturbance conditions. Deviation of the simulation output from Gompertz (**d**, difference between **b** and **a**) and von Bertalanffy (**e**, difference between **c** and **a**) models compared to the logistic model
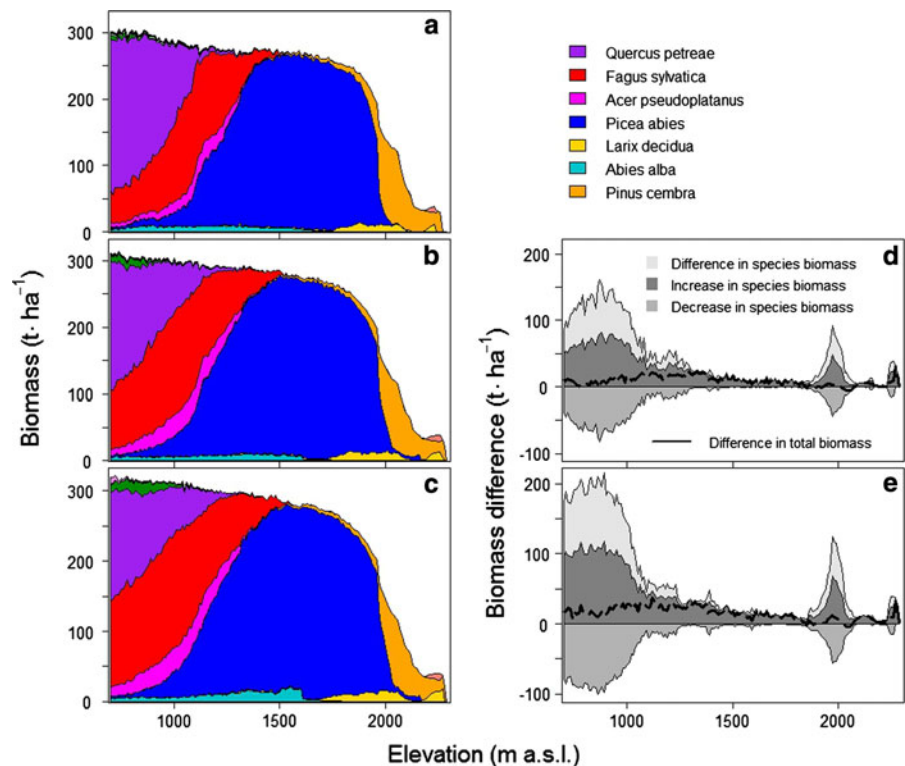
average total biomass that was simulated by the Gompertz and von Bertalanffy models when they were fit to the early part of the growth curve (Fig. 5).

In contrast to landscape biomass, the effect size associated with model formulation and parameterization was high for both the elevation-specific biomass difference, and elevation- and species-specific biomass difference (Table 2, Fig. 5). The effect size associated with model fit was primarily due to "late" fit models varying considerably with respect to elevation-specific differences, and "early" fit models differing with respect to elevation- and species-specific differences (Fig. 5).

Growth model parameterization and disturbance interactions

The effect size for the interaction between growth model parameterization and disturbance intensity was small for each of the three metrics (<2%, Table 2). The "early" fit model produced the biggest differences compared to the logistic model with regard to both the elevation-specific, and the elevation- and species-specific difference (Fig. 6a, d, g). Even with heavy disturbance the "middle" and "late" fit models

were closer to the logistic model than the "early" fit models.

The Gompertz and von Bertalanffy models fit to the middle and late logistic growth period simulated larger elevation-specific forest biomass due to the higher growth rates of young trees (Fig. 1, age <100 years). Conversely, models fit to the early sections simulated lower elevation-specific biomass (Fig. 6) due to the trees not approaching their maximum size until later in their lives (Fig. 1).

Species-specific differences were greatest at elevations where there was a transition between species. The models fit to the middle and late sections of the growth curve exhibited the largest discrepancies at low elevations (<1,300 m a.s.l.) where there were elevation-defined transitions between deciduous species, and at high elevations (∼2,000 m a.s.l.) where there was a transition of species within the pine genus (Fig. 6).

Testing growth models against empirical growth data

None of the eleven growth models tested provided a comparatively superior fit to the empirical data across

Fig. 5 Impact of growth model structure and parameterization on simulation output. Median (±range) total forest biomass of Gompertz and von Bertalanffy growth models (*dashed lines* show the range of forest biomass simulated using the logistic growth model). Median (±range) deviation in elevation-specific biomass, and species- and elevation-specific biomass of the Gompertz and von Bertalanffy growth models compared to the logistic model. Note that the range of values for some of the models is sufficiently narrow that the range is masked by the median line marker
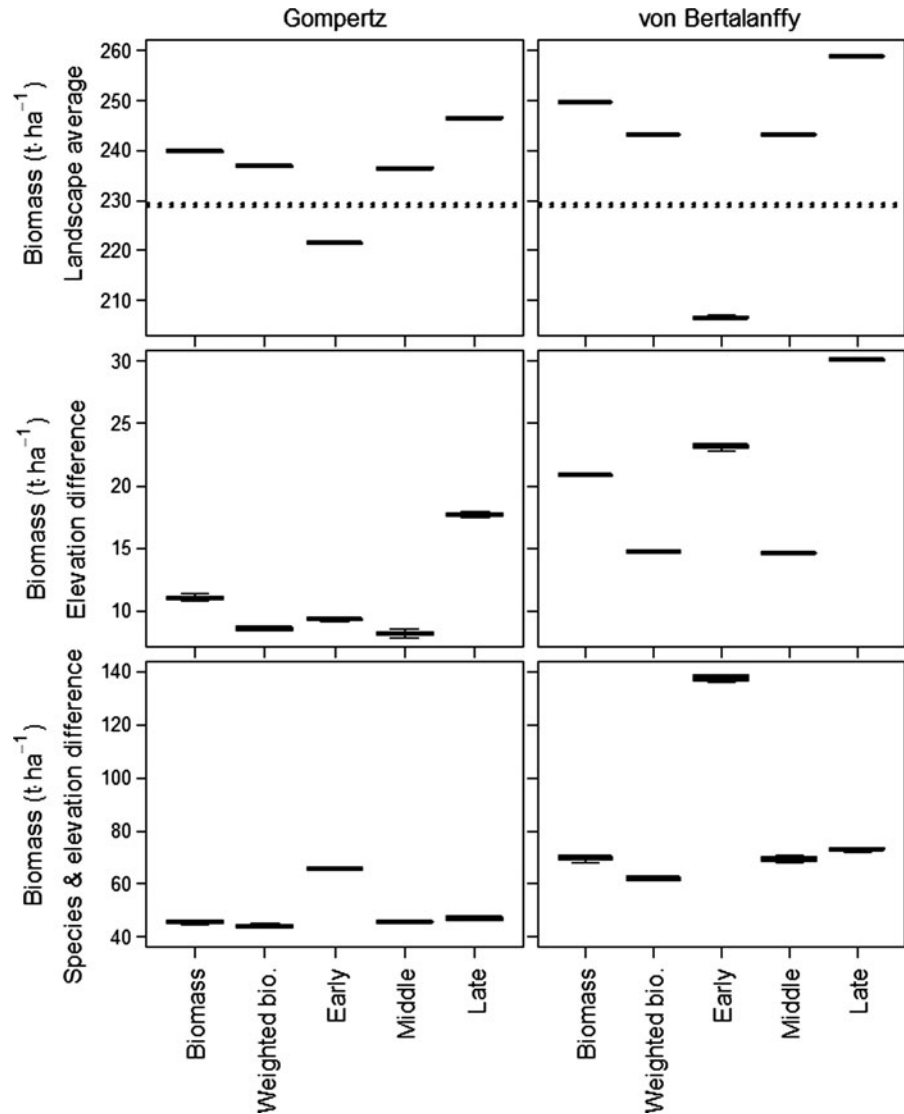

the full *Picea abies* growth trajectory (Fig. 7). Assessing the growth models between age zero and 250, the logistic model was the best model in 9.4% of the permutations. The range of von Bertalanffy models (biomass fit, weighted biomass fit, and early, middle and late fit) were best in 8.2, 8.3, 11.5, 11.3, 7.7 and 8.9% of the permutations respectively, while equivalent Gompertz models were best in 8.9, 9.1, 6.2, 11.4 and 7.8% of the permutations.

While there were only small differences between the suitability of the models when assessed across all tree ages, the models did differ considerably in where along the trees' growth trajectory they fit best. The logistic model was comparatively poor at

simulating the size of young (<150 years) and old trees (>250 years), but was one of the better models at simulating the size of intermediate aged trees (150–250 years; Fig. 7a). The Gompertz models, fit using the biomass and weighted biomass method (Fig. 7b), were poor at simulating young trees (<80 years), but were reasonably good at simulating tree size of individuals >80 years old. Conversely, the von Bertalanffy models, fit using the biomass and weighted biomass method (Fig. 7c), were good at simulating tree size up to 80 years but were less suitable for older trees.

Gompertz and von Bertalanffy models that were fit to correspond to the early logistic growth were poor at
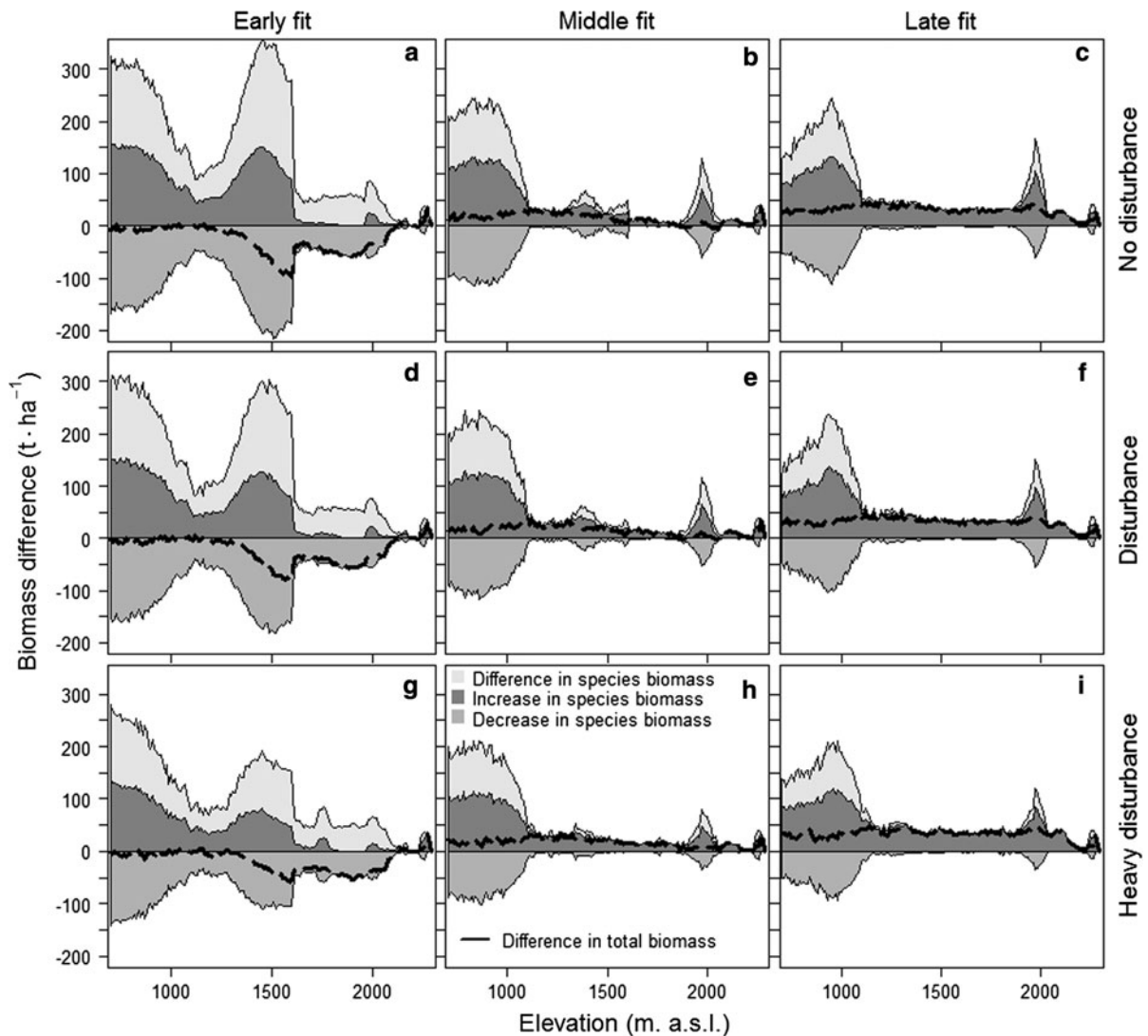
Fig. 6 Deviation of von Bertalanffy simulation output from the logistic model at different disturbance intensities and when the von Bertalanffy model is parameterized so as to approximate logistic growth during the early, middle and late stages of a tree's development

accurately simulating the size of young trees, but were very good at simulating the size of old trees (>270 years, Fig. 7d). The reason for the good fit with older trees is that in order to get the von Bertalanffy and Gompertz models to approximate logistic growth of young trees the age at which the trees achieve their maximum size under optimal growth conditions increased to >400 years (Fig. 1b). Gompertz and von Bertalanffy models that were fit to the intermediate logistic growth performed reasonably well across all ages.

Discussion

Spatial resolution of forest model sensitivity

Our results indicate that forest landscape models are robust when results are aggregated at the landscape level. Uncertainty in growth model structure, and to a lesser degree parameter uncertainty, had very little impact on estimated forest biomass at the landscape level. The spatial resolution at which landscape models are evaluated often depends on the specific
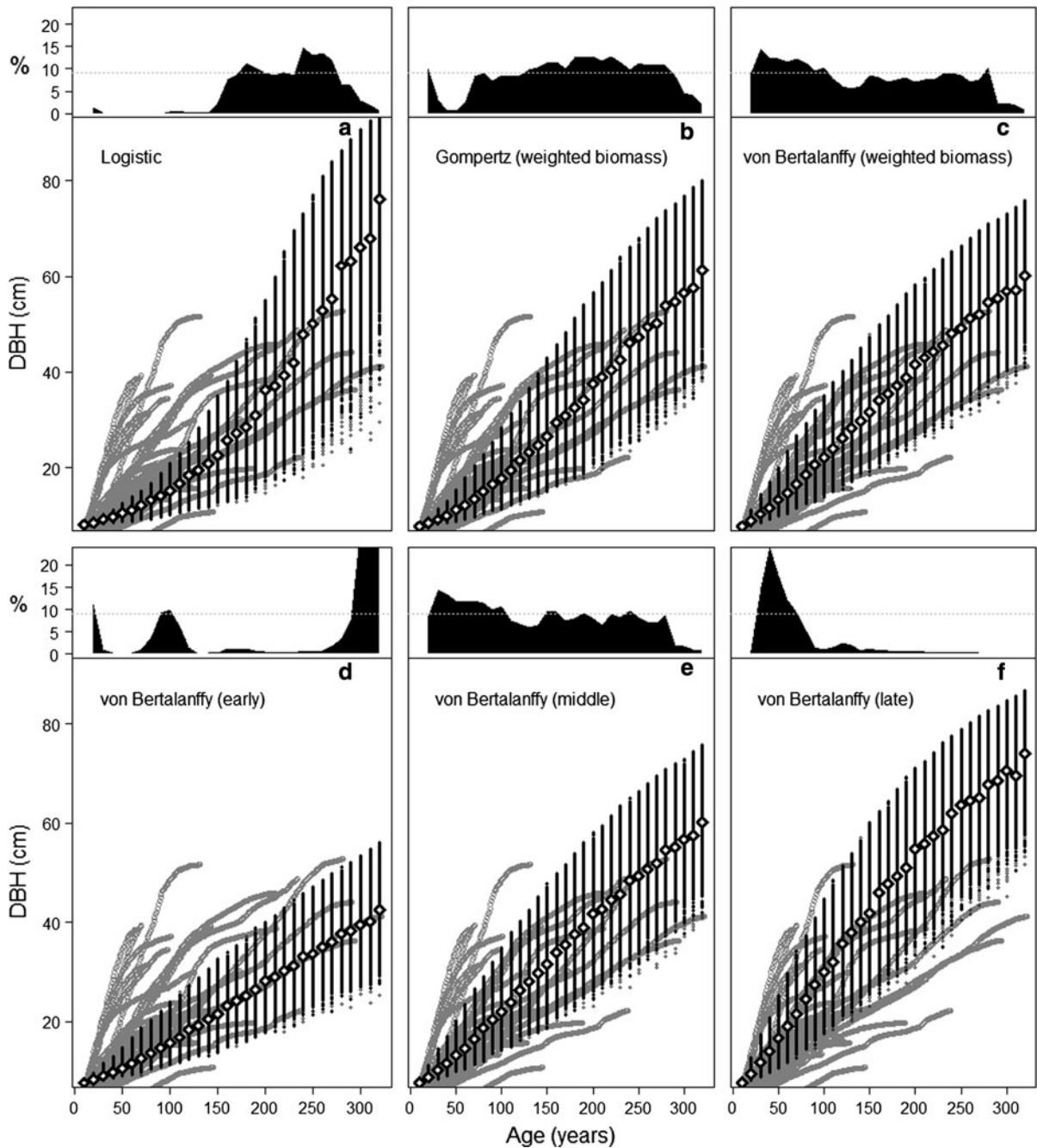
Fig. 7 Fit of simulation model growth projections to empirical *Picea abies* growth data. *Grey points* show the size at age for the 41 measured trees. *Black points* in the lower figures show the size at age from comparable simulations. Median simulated tree size for each age class is shown as a *black open diamond*. The upper figures in each plot show the percent of the permutation test in which the given growth model provided the best fit with the empirical data. The null expectation (if all models are equal) is that each would be best in 9.09% of the permutation (*dotted grey line* in upper figure)

question that they are being used to address. For example, carbon dynamics (Stoy et al. 2008; Fahey et al. 2010), the impact of forest cover on hydrology

(Wilby and Schimel 1999; Zierl et al. 2007), or biodiversity estimates that focus on species presence and relative abundance (Hartmann et al. 2010), are

commonly assessed at the landscape or regional level. In these cases, simulation results aggregated at the landscape level should be resilient to uncertainty regarding the simulation of fine grain processes such as tree growth, thus confirming earlier results regarding the sensitivity to initialization data (Xu et al. 2004, 2005).

Conversely, when the output of landscape models is evaluated at a finer resolution, the accuracy of the growth model becomes increasingly important. When assessing forest state on a species-specific basis we found that growth model variation had a strong impact on simulation results. Both the structure of the growth model, and to a greater extent how it was parameterized, influenced the simulated species composition when the results were aggregated by elevation. A principle benefit of using a landscape model is that the spatial distribution of forest properties can be explicitly analysed. This finer grained detail is often needed to assess forest ecosystem goods and services, such as protection from gravitational hazards and biodiversity (Fahrig 2003; Lindner et al. 2010), evaluate the impact of alternative forest management strategies (He et al. 2002; Radeloff et al. 2006), and assess the impact of forest disturbances (Schmidt et al. 2008). Our results suggest that when forest landscape models are used to assess such finer grained metrics, great care needs to be taken to make sure that the form and parameterization of the growth model are appropriate.

We found the largest impact of growth model differences occurred in areas where there was an elevation dependent transition between dominant species (Fig. 4). In these transition regions the abundance of a species depends critically on its relative competitive ability, which in turn depends on how environmental constraints such as light and moisture impact growth rate (Urban and Shugart 1992; Schumacher et al. 2004). In our simulations the response of each species to environmental growth reduction factors was held constant. The simulated shifts in species abundance were therefore solely driven by changes in the species' relative competitive ability that resulted from alterations to the growth equation.

We suggest that growth model formulation can have a large impact on the relative competitive ability of species in forest landscape models. This implies that model applications aiming to examine the influence of shifts in environmental conditions on species interactions and species distribution, must be

cognisant of the need for the growth models to be accurate (Fekedulegn et al. 1999; He et al. 2011). Similarly, accurately formulating and parameterizing other ecological process that influence the relative competitive ability of species, such as seed production and dispersal, is expected to be equally important.

Species transition zones in our simulations were driven by elevation gradients that entailed shifts in temperature and precipitation. While using forest landscape models to explore forest dynamics along spatial environmental gradients is common (Bugmann 2001; Scheller and Mladenoff 2007), forest models are also frequently used to evaluate shifts in environmental state that occur through time (He et al. 2008; Taylor et al. 2009). The impacts of climate change (Bugmann 2003; Lindner et al. 2010), changes in forest management plans (Boyland et al. 2005), shifts in the frequency of landscape disturbance (Klenner et al. 2000), human-induced landscape change (Bolte et al. 2009), and dispersal of pest or invasive species (Wermelinger 2004; Netherer and Schopf 2010) are all mechanisms that will alter the environmental conditions that competing tree species experience through time. When landscape models are used to examine the effects of these processes on forests, the focus is often on areas where competition between species is known a priori to be an important factor influencing forest dynamics, such as the limits of species distributions and ecotones (Pastor and Post 1988; He et al. 2005). Our work clearly indicates that in these regions the accuracy of landscape models will be highly sensitive to the formulation and parameterization of the growth model.

Landscape structure and disturbances

Landscape heterogeneity had little influence on our simulation results. One reason for this is that even in our finer resolution assessments we still spatially aggregated results such that the impact of landscape variation at the cell level was averaged out. Landscape characteristics, such as soil depth and aspect, interact with species' growth-rates to determine the realized competition between species. Therefore, landscape characteristics have the potential to systematically magnify problems with poorly formulated or parameterized growth models, similar to the environmental transition zones described above. However, the impact on simulation output is expected to only be important

when the results are evaluated at a resolution that is at, or below, the grain of landscape heterogeneity.

While disturbances have the potential to substantially alter landscape properties and influence forest dynamics (Schumacher and Bugmann 2006; Reyes and Kneeshaw 2008), we found that the sensitivity of model output to growth model formulation was not substantially increased or decreased by disturbances, at least not for the range of disturbance intensity tested here. This suggests that uncertainty associated with the growth model formulation will not be magnified when forest landscape models are used to evaluate scenarios where forest disturbance regimes are predicted to change in the future.

We predicted that with increased disturbance, simulation output would be most sensitive to accurately estimating the growth of young trees. Therefore, we expected that growth model formulations parameterized to reduce growth differences during the first third of the trees' development would result in the smallest differences in heavily disturbed landscapes. However, parameterizing the models to minimize early growth differences resulted in the greatest deviation (Fig. 6). This deviation was primarily driven by increases of the relative competitive ability of slow-growing species, such as silver fir (*Abies alba*). While past studies have noted the problems associated with deriving parameters for dominant tree species (Pacala et al. 1996; Fekedulegn et al. 1999; MacFarlane et al. 2000; Alexandrov 2008), our results are novel in that they highlight that growth model formulation and parameterization must be accurate not only for a single species, but ideally must have the same level of accuracy across all species included in the simulations. This is most likely to be a considerable problem when non-commercial species, for which there is less empirical growth information, are included in simulations.

Across all three levels of disturbance, simulations were most accurate, with output deviating least from the known base state, when the alternative growth models were parameterized to minimize the difference across the full life history of each species. Our results suggest that developing a growth model that accurately captures all stages of an individual's growth is important irrespective of whether forest dynamics are subject to weak disturbances only and thus assumed to be dominated by late successional processes, or heavily disturbed and assumed to be driven by the

growth rate of early successional species. Our results imply that once a suitable growth model is defined, the accuracy of the simulation results will be maintained irrespective of whether or not there are extrinsically driven shifts in forest disturbance regimes, such as may occur due to shifts in land use policy or change in forest management (McEwan et al. 2011).

Growth model variation and individual tree growth

We found that growth model formulation and parameterization had a large impact on simulation results at a sub-landscape resolution. Conversely, when we compared the growth of simulated and real trees we found that drastically different growth models differed little with respect to their ability to reproduce the growth trajectory of real trees. None of the growth model forms that we tested were substantially better at replicating individual tree growth over the full duration of a tree's life (Fig. 7).

While our analysis is an inverse of the normal growth model fitting procedure, it highlights the difficulties associated with determining the best growth model form and parameters (Fekedulegn et al. 1999; Colbert et al. 2004). Our results demonstrate that small changes to the model formulation or parameterization can substantially alter the results of forest landscape models. Thus, modifications to the growth models used in landscape simulations should be evaluated at both the resolution of tree growth and at larger spatial scales such as forest composition.

Conclusions

Our results demonstrate that, first, growth model uncertainty is most important when model results are assessed at a sub-landscape resolution, particularly when the simulation region includes environmental transition zones (both spatial and temporal) where each species' relative competitive ability critically depends on its realized growth rate. Conversely, when the outputs of forest landscape models are aggregated at the landscape level, the results are relatively resilient to uncertainty in small-grain processes.

Second, we show that growth model form and parameterization should accurately represent all stages of a tree's life history. When growth models were parameterized to focus on specific life-history

stages we found that simulation results were less accurate than those that trade off accurate parameterization of specific life stages in order to better describe the tree's whole lifespan.

Third, although we predicted that growth models biased towards accurately representing early tree grow would be more suitable in heavily disturbed landscape, we found that even under these conditions growth models fit equally across a trees lifespan were better.

Fourth, our results indicate that while the output of forest landscape models are sensitive to how small-grain processes are modelled and parameterized, the power to distinguish the best model structure and parameterization using empirical data may be comparatively low.

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