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Petter, Gunnar; Mairota, Paola; Albrich, Katharina; Bebi, Peter; Bruna, Josef; Bugmann, Harald; Haffenden, Austin; Scheller, Robert M.; Schmatz, Dirk R.; Seidl, Rupert; Speich, Matthias; Vacchiano, Giorgio; Lischke, Heike

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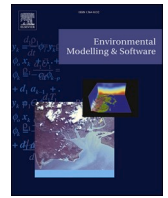
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How robust are future projections of forest landscape dynamics? Insights from a systematic comparison of four forest landscape models

Gunnar Petter^{a,*}, Paola Mairota^b, Katharina Albrich^{c,j}, Peter Bebi^d, Josef Brůna^e, Harald Bugmann^a, Austin Haffenden^f, Robert M. Scheller^g, Dirk R. Schmatz^h, Rupert Seidl^{c,j}, Matthias Speich^h, Giorgio Vacchianoⁱ, Heike Lischke^h

^a ETH Zürich, Department of Environmental Systems Science, Forest Ecology, Universitätstrasse 16, 8092, Zürich, Switzerland

^b Department of Agri-Environmental and Territorial Science, University of Bari "Aldo Moro", Via G. Amendola 165/A, 70126, Bari, Italy

^c Institute of Silviculture, Department of Forest- and Soil Sciences, University of Natural Resources and Life Sciences (BOKU) Vienna, Peter Jordan Straße 82, 1190, Wien, Austria

^d Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Community Ecology/Mountain Ecosystems, Flüelästrasse 11, CH-7260, Davos Dorf, Switzerland

^e Institute of Botany of the Czech Academy of Sciences, Zámek 1, 252 43, Průhonice, Czech Republic

^f Univ. Grenoble Alpes, Irstea, LESSEM, 2 Rue de La Papeterie - BP 76, 38402, St-Martin-d'Hères Cedex, France

^g Department of Forestry and Environmental Resources, North Carolina State University, Campus Box 7106, Raleigh, NC, 27695, USA

^h Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Land Change Science, Dynamic Macroecology, Zürcherstr. 111, CH-8903, Birmensdorf, Switzerland

ⁱ Università Degli Studi di Milano, DISAA, Via Celoria 2, 20133, Milan, Italy

^j Technical University of Munich, Ecosystem Dynamics and Forest Management Group, Hans-Carl-von-Carlowitz-Platz 2, 85354, Freising, Germany

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ABSTRACT

Projections of landscape dynamics are uncertain, partly due to uncertainties in model formulations. However, quantitative comparative analyses of forest landscape models are lacking. We conducted a systematic comparison of all forest landscape models currently applied in temperate European forests (LandClim, TreeMig, LANDIS-II, iLand). We examined the uncertainty of model projections under several future climate, disturbance, and dispersal scenarios, and quantified uncertainties by variance partitioning. While projections under past climate conditions were in good agreement with observations, uncertainty under future climate conditions was high, with between-model biomass differences of up to 200 t ha⁻¹. Disturbances strongly influenced landscape dynamics and contributed substantially to uncertainty in model projections (~25–40% of observed variance). Overall, model differences were the main source of uncertainty, explaining at least 50% of observed variance. We advocate a more rigorous and systematic model evaluation and calibration, and a broader use of ensemble projections to quantify uncertainties in future landscape dynamics.

1. Introduction

Forest landscape models (FLMs) are used to simulate the dynamics of forest ecosystems at the landscape level (~10²–10⁶ ha in extent) over decades to centuries (He et al., 2008; Shifley et al., 2017). Climatic and edaphic conditions within landscapes can vary widely in space and time, and a hallmark of FLMs is that they explicitly represent this variation. FLMs typically represent climatic and edaphic variation by dividing the

landscape into smaller grid cells, in which regeneration, growth, and mortality of either height-structured populations, cohorts or individual trees are modelled over time, as a function of both local abiotic conditions and biotic interactions (e.g., Lischke et al., 2006; Seidl et al., 2012). In addition to local demographic processes, FLMs explicitly simulate spatial interactions among grid cells, such as seed dispersal or dynamically spreading disturbances like forest fires or insect attacks (e.g., Temperli et al., 2015). The combined simulation of relatively detailed

* Corresponding author. Kompetenzzentrum Boden, Berner Fachhochschule, HAFL, Länggasse 85, 3052, Zollikofen, Switzerland.

E-mail addresses: gunnar.petter@bfh.ch (G. Petter), paola.mairota@uniba.it (P. Mairota), katharina.albrich@boku.ac.at (K. Albrich), peter.bebi@wsl.ch (P. Bebi), josef.bruna@gmail.com (J. Brůna), harald.bugmann@env.ethz.ch (H. Bugmann), aushaff@zoho.eu (A. Haffenden), rschell@ncsu.edu (R.M. Scheller), dirk.schmatz@wsl.ch (D.R. Schmatz), rupert.seidl@boku.ac.at (R. Seidl), matthias.speich@wsl.ch (M. Speich), gvacchiano@gmail.com (G. Vacchiano), heike.lischke@wsl.ch (H. Lischke).

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demographic processes and spatially explicit interactions is a unique characteristic of FLMs that distinguishes them from other model types such as forest stand models, succession models, or global vegetation models.

Over the past decades, several FLMs were developed for the simulation of temperate forest landscape dynamics. These models have been successfully applied in a number of studies, for instance projecting the impacts of climate change on landscape dynamics (Elkin et al., 2013; Thom et al., 2017a), evaluating the effects of disturbance interactions on forest structure (Temperli et al., 2013a), assessing the effects of migrational lags along latitudinal and elevation gradients (Epstein et al., 2007; Scherrer et al., 2020), and analyzing the consequences of adaptive forest management at the landscape level (Mairota et al., 2014; Rammer and Seidl, 2015). However, considerable uncertainties in the projection of forest landscape dynamics remain. The scarcity of input data with high spatial resolution is one source of uncertainty. As FLMs are spatially explicit, they require input data representing the heterogeneity in environmental conditions. Some environmental conditions such as soil properties or the microclimate can vary considerably over short distances, particularly in topographically complex landscapes, and the available data often do not capture this variation. In addition, environmental drivers of forest dynamics also vary over time, but time-series data covering the extended periods that are of interest in forest landscape dynamics are often not available. Furthermore, empirical time series of spatial data of forest composition and structure covering an entire landscape are rare. It is hence common that FLMs are evaluated based on data at a single point in time (He et al., 2011). In some model applications, vegetation data are also used during initialization, e.g. to reflect past management or disturbance history, and particularly shorter-term simulation (<150 years) can be sensitive to initialization uncertainty (Temperli et al., 2013b). Finally, further uncertainty stems from differences in model formulations. Although FLMs are based on similar general principles, their model structures vary substantially, for instance regarding their spatial and temporal resolution, whether individuals or cohorts are simulated, at which level of detail trees are represented, how mortality, growth, dispersal and regeneration are simulated, whether specific processes such as CO₂ fertilization effects are considered, or which and how disturbances are simulated (e.g., Lischke et al., 2006; Scheller et al., 2007; Seidl et al., 2012). Together, these uncertainties raise questions about the robustness of the projections made with FLMs (here, we use the term robustness to indicate the similarity of the projections of different models, i.e. the larger the differences, the lower the robustness).

Multi-model comparisons can help to understand and quantify uncertainties underlying a particular model type (Shifley et al., 2017). In some scientific fields such as climate modeling, it is common to apply several models under unified conditions in ensemble simulations, representing the range of possible futures and helping to quantify average trends and confidence intervals (IPCC, 2014). Ensemble simulations can also be used to partition the observed variance among different factors (Diniz-Filho et al., 2009; Yip et al., 2011). For example, the uncertainty due to differences between models (parameters and/or structure) can be compared to uncertainty from different scenarios simulated (e.g., climate scenarios). While such analyses have recently been carried out for other types of vegetation models (e.g., global vegetation models: Nishina et al., 2015; species distribution models: Thuiller et al., 2019), they are lacking for FLMs.

Here we present the first systematic comparison of all FLMs that are currently applied in the temperate forests of Europe, i.e. LandClim (Schumacher et al., 2004), TreeMig (Lischke et al., 2006), LANDIS-II (Scheller et al., 2007), and iLand (Seidl et al., 2012). The aim of this comparison is twofold: First, we examine the robustness of model projections under several future climate, disturbance, and dispersal scenarios. Second, we assess and discuss the contribution of different scenarios and model structures to overall uncertainty using variance partitioning.

2. Methods

2.1. Study landscape

The Dischma valley near Davos in Switzerland is a subalpine valley located between 1560 and 3146 m a.s.l. (Appendix A: Fig. A.1) and characterized by steep topographic gradients. Mean annual temperature in Davos (1560 m a.s.l.) was 3.5 °C during the period 1981–2010, with an average annual precipitation sum of ~1020 mm (MeteoSwiss; Fig. A2). Soils are mainly loamy sands and sandy loams (Fig. A3). Norway spruce (*Picea abies* (L.) Karst.), European larch (*Larix decidua* Mill.) and Swiss stone pine (*Pinus cembra* L.) are the most abundant tree species in the landscape. The elevation of the upper treeline is partly influenced by cattle grazing and is currently located at ~2100–2200 m a.s.l. Avalanches are common and cause considerable damage to forests, particularly on the northeast-facing slopes of the valley (Fig. A4). We chose the Dischma valley as study landscape based on the availability of robust drivers (climate, substrate and disturbances by avalanches) and evaluation data (forest composition and structure). Additionally, three of the four models presented here have already been applied in this or similar mountain landscapes, which expedited the model set-up and testing process.

2.2. Models and parameterizations

The main characteristics of the four FLMs used are summarized in Table 1. Detailed descriptions of all models are provided in Appendix B, following the “Overview, Design concepts, and Details” (ODD) protocol (Grimm et al., 2010, 2006). Appendix B also contains a detailed comparison of model characteristics (Table B1), the list of species parameterized in each model (Table B2), as well as the species parameters and state variables used in the models (Table B3–B10).

2.3. Model input data

We assembled a common input data set for all models to ensure consistency and minimize differences due to contrasting driver data. This input data set contained the following environmental attributes: elevation (m a.s.l.), slope (°), aspect (°), daily maximum, minimum, and mean temperature (°C), daily precipitation sums (mm), daily radiation (W m⁻¹), effective soil depth (cm), soil texture class (-), total soil water holding capacity (WHC, cm), avalanche occurrence (ha⁻¹ year⁻¹), and annual CO₂ concentration (ppm). Note that not all models require all data (see *Attributes of grid cells* in Table 1 for model-specific input data).

All attributes were spatially explicit at a resolution of 100 × 100 m, except for CO₂ concentration, which was spatially invariant. The full dataset covered both cells that are currently forested and areas that can potentially be colonized by trees in the future (e.g., above the current treeline). All areas currently under management (settlements, pastures) were considered to remain under the same management regime and were excluded from the simulations. The total simulated area comprised 923 cells of 1 ha size (Fig. A1). For all models that internally use a resolution finer than 1 ha, the environmental attributes of each 1-ha cell were assigned to all cells contained in it. This was always possible as the internal cell sizes that are being used for modeling the different ecological processes were 2 × 2 m, 10 × 10 m, 20 × 20 m, 25 × 25 m, and 100 × 100 m (cf. Table 1).

Historic CO₂ concentrations from 1765 to 2010, as well as future concentrations from 2011 to 2100 for four Representative Concentration Pathway (RCP) scenarios (RCP2.6, RCP4.5, RCP6.0, RCP8.5) were taken from Meinshausen et al. (2011).

Topographic and soil data were time-invariant. Topographic data were provided by Swisstopo (2018). WHC data (i.e., the difference between soil water content at field capacity and permanent wilting point) were taken from Remund and Augustin (2015), with soil texture data derived from Wildi and Ewald (1986). Using the volumetric WHC

Table 1
Summary of main model characteristics. Details are provided in Table B1 in Appendix B.

	LANDIS-II	LandClim	iLand	TreeMig
Version used	V6.2, PnET Succession extension v2.0, Land Use extension 1.1	V1.6	V1.0	V1.10
Main references	Scheller et al. (2007), De Bruijn et al. (2014)	Schumacher et al. (2004), Schumacher and Bugmann (2006)	Seidl et al. (2012), Seidl et al. (2014)	Lischke et al. (2006)
Regions where the model has been applied	USA, Canada, Mexico, Siberia, Kyrgyzstan, Ecuador, Chile, Sweden, UK, Czech Republic, Italy, Ukraine, China, Japan	Central Europe, Southern Europe, Rocky Mountains, Pacific Northwest of the US	Central Europe, Western North America	Central Europe, Siberia
Size of grid cell	Here 100 × 100 m (Size can be adjusted by model user, typically 10 × 10 to 1000 × 1000 m)	Here 25 × 25 m (Size can be adjusted by model user, typically 20 × 20 to 25 × 25 m)	100 × 100 m for environmental drivers 20 × 20 m for seed dispersal 10 × 10 m for calculation of dominant canopy height 2 × 2 m for calculation of light availability and regeneration cohorts	Here 100 × 100 m (Size can be adjusted by model user, typically 100 × 100 m to 1000 × 1000 m)
Main time step	Here decade	Decade	Year	Year
Tree entities	Age cohort by species	Age cohort by species	Individual tree	Trees of species in height classes and grid cells
Main state variables of tree entities	Species identity, age, biomass	Stem numbers per cohort, biomass, age, species identity	ID, x-y coordinates, species identity, age, height, dbh, foliage biomass, woody biomass, fine and coarse root biomass, carbohydrate reserves, stress index	Number per cell and species of trees in each height class and of seeds in the seed bank
Attributes of grid cells (including the environmental drivers)	Location, elevation, aspect, soil texture, soil depth, precipitation runoff fraction, leakage fraction, monthly max and min T, monthly precipitation sum, monthly CO ₂ concentration, monthly PAR, biomass	Location, elevation, slope, aspect, monthly mean temperature, monthly precipitation, maximum soil WHC, browsing intensity, establishment probability	Location, stockable area, effective soil depth, sand-silt-clay content, plant-available nitrogen, minimum and maximum temperature, precipitation sum, vapor pressure deficit, radiation (climate variables at daily resolution)	Location, elevation, slope, aspect, monthly mean temperature, monthly precipitation sum, maximum soil WHC, stockability (0/1)
Processes simulated on decadal time step	Regeneration, allocation, mortality, avalanches (via Land Use change extension)	Regeneration, avalanches	None	None
Processes simulated on annual time step	None	Growth, mortality	Avalanches, regeneration, carbon cycling, mortality, competition	Growth, mortality, regeneration, competition, avalanches, bioclimate, environmental responses
Processes simulated on monthly time step	Growth, competition, soil water balance	None	Growth	None
Processes simulated on daily time step	None	None	Environmental responses	None
Number of species parameters	28 = 10 LANDIS-II + 18 PnET Succession v2.0	17	60	22
Species parameters tuned for this study?	Yes	No	No	Slightly
CO ₂ fertilization effect simulated?	Yes	No	Yes	No
Nitrogen considered?	No	No	Yes	No
Sprouting simulated?	Yes	No (Can be simulated in general)	No (Can be simulated in general)	No
Aggregation of grid cells to climatically homogeneous ecoregions?	Yes	No	No	No

estimates for different soil textures from Blume et al. (2010), effective soil depth was estimated from WHC and texture data (Fig. A3).

Climate and avalanche data varied in space and time. Historic climate data grids for the years 1930–2010 were generated by spatially interpolating measurements of surrounding weather stations (MeteoS-wiss) using the DAYMET algorithm (Thornton et al., 1997). Projected climate data grids for the years 2011–2100 were produced by down-scaling climate projections of the general circulation model HadGEM2-ES (<https://esg.pik-potsdam.de/projects/isimip2a>) for all four RCPs (RCP2.6, RCP4.5, RCP6.0 and RCP8.5; van Vuuren et al. (2011); Figs A5 and A6). We used the delta change method with a reference period of 1961–1990 and applied the anomalies of the projected data to the historic data. Increases in annual mean temperatures until 2100 ranged from <1.5 °C (RCP2.6) to > 6 °C (RCP8.5), whereas annual precipitation in all climate scenarios slightly decreased by ~ 10% (Fig A5). The differences between scenarios were more pronounced in summer, with summer temperatures in the RCP8.5 scenario increasing by up to 10 °C by 2100 and summer precipitation being

noticeably lower than in the other scenarios (Fig A6). The spatial and temporal distribution of avalanches was estimated based on the avalanche database of the Swiss Avalanche Institute SLF, which recorded avalanches with a resolution of 1 m from 1960 to 2016 for the target landscape (Fig. A4). For this study, every 1-ha cell of which at least 25% was hit by an avalanche in one year was considered disturbed. Avalanche data were identical for all models, i.e. the same cells were disturbed in the same years.

2.4. Simulation design

2.4.1. Past-to-present simulations

In past-to-present simulations, forest dynamics in the study landscape were simulated from AD 1100–2010 (10 replicates per model). Climate data were used as model input from 1930 to 2010; data for the period from 1100 to 1929 were generated by randomly sampling from the period 1930 to 1950 for each replicate run. CO₂ data were used from 1765 to 2010, with the concentration fixed to the pre-industrial level of

278 ppm for years prior to 1765. We assumed that the simulated forests were not influenced by management but were disturbed by avalanches. The available spatio-temporal avalanche data for 1960 to 2010 were implemented as observed. For the pre-1960 period, we generated a randomized avalanche data set based on the location and frequency of observed avalanches, hence mimicking the avalanche disturbance regime of the recent past. We assumed that in cells disturbed by avalanches, all trees were killed in the corresponding year. We chose this approach to ensure the same implementation of avalanches in all models; however, this might have led to an overestimation of avalanche-induced mortality in the simulations. In the initial period from 1100 to 1400, a regular supply of seeds of all species (Table B2) to all cells was simulated, to allow potential establishment of all suitable species. From 1401 on, only seed dispersal by established mature trees was allowed, in combination with a regular seed supply to a small area at the valley entrance to allow potential immigration of species that are not present in the landscape. LandClim, TreeMig, and iLand were initialized from “bare ground”, meaning that the landscape was initially empty and was successively colonized by trees via the model-specific dispersal and regeneration processes. In LANDIS-II, each cell in the landscape was instead initialized with one-year old tree cohorts of every species, because the model version used in this study cannot be initialized from bare ground.

2.4.2. Future projections

To assess and compare the climate sensitivity of the FLMs, we simulated future forest dynamics under four climate scenarios (RCP2.6, RCP4.5, RCP6.0 and RCP8.5) from 2001 to 2100 (10 replicates per model). All FLMs were initialized with the forest state the models simulated for the end of the year 2000 in the past-to-present runs. We used the observed CO₂ and climate data from 2001 to 2010 and the climate scenario data from 2011 onwards as drivers (Figs A5 and A6). We assumed no changes in avalanche disturbance patterns in the future, and generated an avalanche disturbance sequence from 2001 to 2100 by randomly drawing from the observation data from 1960 to 2016 (see below). For the entire simulation period, seeds dispersed exclusively from established mature trees, and an additional regular seed supply of all species to a restricted area at the valley entrance was simulated.

2.4.3. Disturbance and dispersal scenarios

To compare the response of FLMs to different assumptions regarding dispersal and disturbance, four disturbance scenarios and three dispersal scenarios were simulated. For these runs, we first carried out past-to-present simulations from 1100 to 2000, which were identical to those described above with the exception that no disturbances by avalanches were simulated (to start from undisturbed conditions in all models). Initialized with the forest state at the end of the year 2000, each FLM simulated future forest dynamics from 2001 to 2100 under all combinations of climate scenarios (RCP2.6, RCP4.5, RCP6.0, RCP8.5) and disturbance scenarios (Dist0: no, Dist1: low, Dist2: medium, Dist3: high) in a full factorial design. The disturbance scenarios were randomly generated based on avalanche observation data from 1960 to 2016. The medium disturbance scenario mimics the observed avalanche patterns, while in the low and high disturbance scenario the frequency of avalanche occurrence was altered to 10% and 200% relative to the observations, respectively. Furthermore, to elucidate the role of dispersal, simulations from 2001 to 2100 were run under all combinations of four climate scenarios and three dispersal scenarios (Disp1: *global dispersal*, Disp2: *local dispersal*, Disp3: *local dispersal with additional restricted seed supply*). In the *global dispersal* scenario, corresponding to no dispersal limitations, seeds of all species (Table B2) were supplied to all simulated cells regardless of the location of mature trees in the landscape. In the *local dispersal* scenario, only seed dispersal by established mature trees was simulated, thus effectively excluding the establishment of tree species that were not present on the landscape in the beginning of the simulations. In the *local dispersal with additional seed supply* scenario, this

restriction was relaxed by additionally allowing external seed supply to a small area at the valley bottom. This scenario allowed for the immigration of new species that are likely to occur under climate change, but it considers that tree migration is a slow process, particularly in the presence of topographic barriers such as mountain ranges.

2.5. Analyses

2.5.1. Model comparison

To evaluate FLMs against observations, we used total biomass and dominant species maps based on remote sensing data as well as plot biomass data derived from the Swiss National Forest Inventory (Tanase et al., 2019). Furthermore, estimates of species composition along the elevation gradient based on forest inventory maps of the Canton of Graubünden (AWN, 2014) as well as local expert knowledge (P. Bebi) were consulted to evaluate model performance.

For all forested cells, the total biomass of each species was recorded first in 50-year time steps (1100–1900) and subsequently in 10-year time steps (1900–2100). These results allowed the comparisons among models or between models and observations to be based on (1) the total biomass per cell, (2) the biomass per species per cell, (3) the temporal biomass dynamics of each species averaged over the entire landscape, and (4) the species-specific biomass per unit area along the elevation gradient (100 m elevation steps). All analyses were based on simulation results averaged over 10 replicate runs.

2.5.2. Variance partitioning

For all future simulations, we quantified how much of the variance across all FLM runs was explained by different sources of uncertainty (i. e., model differences, climate scenarios, disturbance or dispersal scenarios, and stochasticity as represented by replicated runs). For this purpose, we first estimated simulated total biomass and biomass-based gamma diversity across the landscape, expressed by the Shannon Index (Shannon and Weaver, 1976), at decadal time steps for 2000 to 2100 for each model run (future projections: 4 models × 4 climate scenarios × 10 replicates = 160 runs; disturbance scenarios: 4 models × 4 climate scenarios × 4 disturbance scenarios × 10 replicates = 640 runs; dispersal scenarios: 4 models × 4 climate scenarios × 3 dispersal scenarios × 10 replicates = 480 runs). Subsequently, we estimated average change rates for biomass and Shannon Diversity for the first half (2010–2050) and the second half of the century (2060–2100). Based on these values, we estimated the variance components as the proportions of the sum of squares that could be attributed to the different sources of uncertainty using the Package VCA (Variance Component Analysis; version 1.3.4) within the R language and environment for statistical computing (R Core Team, 2018).

In addition, we tested if the variation between models generally changed over time and with intensifying climate forcing. For this purpose, we used the results of the future projections and calculated the coefficient of variation (CV) of the total biomass and the biomass of the four most important species in each decadal time step, based on the results of all replicates of all models, for each climate scenario separately. We fitted linear regressions using CV over time as response variable and estimated slopes and p-values. This allowed us to assess whether CV generally changed with time, and whether the trend (slope) differed between climate scenarios.

3. Results

3.1. Past-to-present simulations

The most abundant species observed in the Dischma valley (Norway spruce, European larch, Swiss stone pine) were present in simulations by all FLMs, with the exception of European larch being absent in LANDIS-II (Fig. 1). All models simulated a general shift from a dominance of spruce to a dominance of larch or Swiss stone pine with increasing

elevation. However, while there was general agreement in the simulated species composition among the models, notable differences emerged with regard to both the abundance and spatial distribution of species (Fig. 1). Furthermore, some of the simulated landscapes featured tree species not currently observed in the Dischma valley. In LandClim, for instance, the lowest elevation areas were co-dominated by European silver fir (*Abies alba* Mill.), while TreeMig and LANDIS-II simulated a number of other species particularly in the frequently disturbed avalanche tracks.

The observed total aboveground biomass along the elevation gradient decreased slightly from 210 t/ha to 170 t/ha between 1600 and 2100 m, and then dropped to zero at 2300 m. All models were generally able to reproduce decreasing biomass levels with increasing elevation, and the location of the treeline was simulated relatively accurately in three out of the four models. The patterns simulated by iLand and LandClim were fairly congruent, with an average biomass of ~200 t/ha at lower elevations and linearly decreasing biomass above 1800 m, with the simulated treeline located between 2200 m and 2400 m in both models (Fig. 1). LANDIS-II behaved similarly up to an elevation of ~2300 m, but no clear treeline emerged from the simulations. TreeMig generally predicted a lower biomass of ~120 t/ha at elevations below 2100 m, and a linear decrease up to the treeline simulated at ~2300 m.

3.2. Future projections

Projections of future changes in total biomass and species composition differed strongly between the models (Fig. 2). Three models (iLand, LandClim, LANDIS-II) projected a strong increase in total biomass with increasing temperatures, whereas in TreeMig biomass increased slightly under the RCP2.6-RCP6.0 scenarios and decreased under the RCP8.5 scenario. Projected biomass changes for Norway spruce (*Picea abies*) showed a similar pattern (Fig. 2). While all models projected a decline in Swiss stone pine (*Pinus cembra*) under climate change, the trend for European larch (*Larix decidua*) varied among models and ranged from a slight decrease in LandClim to a substantial increase in iLand. With increasing temperatures, the biomass of the drought-tolerant Scots pine (*Pinus sylvestris* L.) increased in iLand and TreeMig, whereas other species increased in abundance in LandClim and LANDIS-II. Overall, uncertainty in future biomass projections increased with increasing severity of climate change, with scenario RCP8.5 showing the strongest disagreement between model projections.

Both increases in biomass in existing forests and the colonization of areas above the current treeline contributed to the simulated increase in total biomass at the landscape level (Fig. 3). iLand and LandClim simulated comparable changes in treeline location, with a slow upward shift within the first 50 years of the simulation, and an accelerated shift

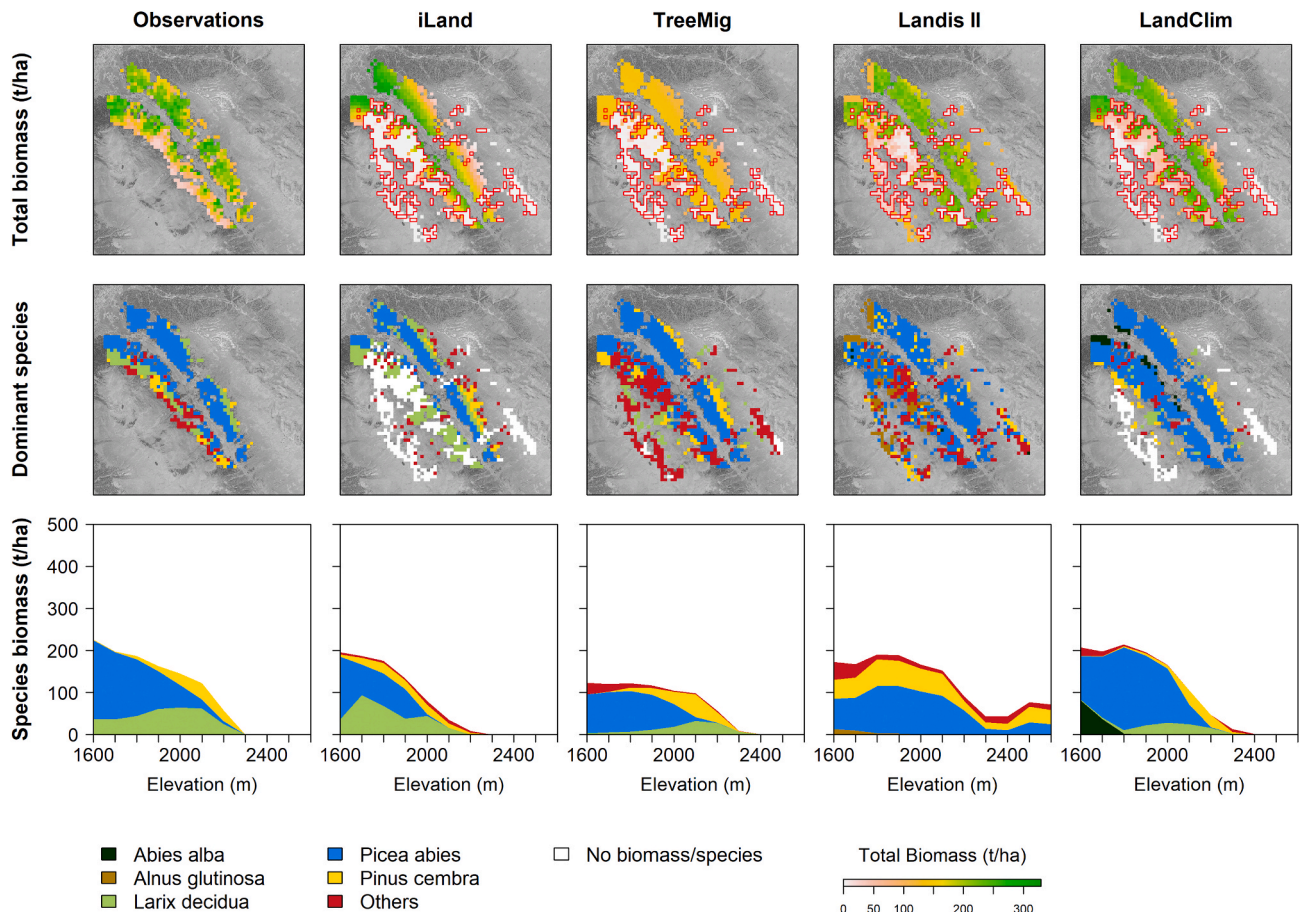


Fig. 1. Simulated forest states of four landscape models in the year 2010 (i.e., after 910 simulation years) compared to observations. Total biomass and dominant species maps are shown at a resolution of 100×100 m. The observational data include only currently forested cells, while the simulations include all areas that can potentially be colonized by trees. In the upper panels, the areas affected by avalanches are outlined in red. In the lower panels, the total biomass of each species within a given 100 m elevation belt was calculated and divided by the total area of all cells within this elevation belt. For the sake of comparability, the same scale was chosen for the y-axis as in Fig. 3. Only species exceeding 20 t/ha in a single grid cell are explicitly shown, all other species are summarized as *Others*. Please note that the lower biomass between 2200 and 2400 m a.s.l. compared to higher elevations in LANDIS-II simulations is the result of high avalanche activity in this elevation belt. In iLand, saplings are simulated separately and are recruited into the individual-based model structure once exceeding the height threshold of 4 m; this is the reason why frequently disturbed avalanche tracks appear empty. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

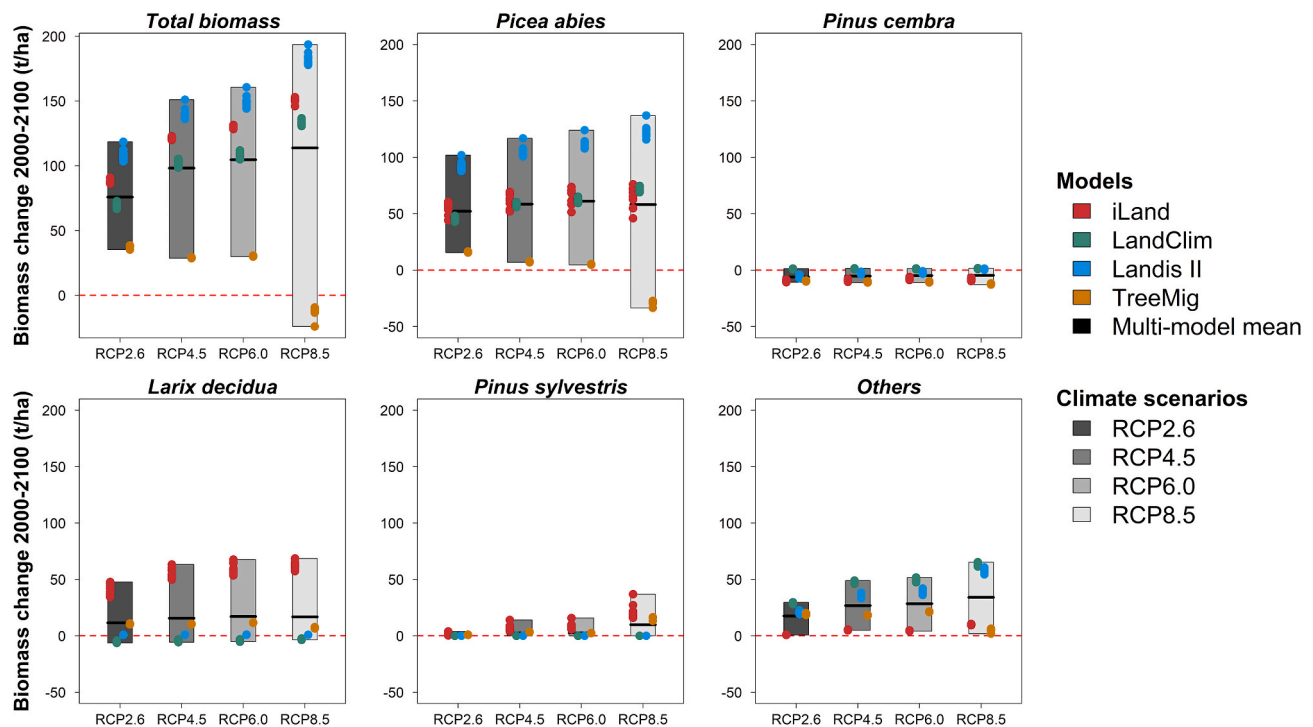


Fig. 2. Projected changes in total and species-specific biomass from 2000 to 2100 under four RCP scenarios. Biomass changes were estimated as the difference between the biomass in year 2100 and in year 2000, divided by the total area of the landscape. The results for all ten replicate runs per model are represented by dots. The grey bars show the range of biomass changes across all models for each RCP scenario, while mean changes are indicated by black lines. All species apart from the species analyzed explicitly, i.e., Norway spruce (*Picea abies*), Swiss stone pine (*Pinus cembra*), European larch (*Larix decidua*) and Scots pine (*Pinus sylvestris*), are pooled under the category *Others*.

in the following 50 years, particularly under severe climate change (RCP8.5; Fig. 3). In contrast, TreeMig simulated a faster upward shift of the upper treeline already in the first decades of the 21st century even under moderate warming. In this model, a remarkable decrease in Norway spruce biomass at lower elevations was simulated under the RCP8.5 scenario, induced by frequent hot-dry summers particularly at the end of the simulation period (Fig. A6).

The CV of the simulated total biomass increased significantly ($p < 0.05$) with time, regardless of the climate scenario (Fig. 4, Table C1). With the exception of Norway spruce under RCP2.6, significant positive trends of CV with simulation time were observed for all major species (Table C1). The slopes of linear regressions were consistently higher under RCP8.5 than under RCP2.6, indicating an increase in predictive uncertainty with an intensification of climate change.

3.3. Disturbance and dispersal scenarios

Avalanche disturbances strongly influenced future biomass dynamics (Fig. 5 and C1) and species composition (Fig. C2) in all models. Compared to no-disturbance simulations, average total biomass decreased by 8–20 t/ha in the low-disturbance scenario, 36–84 t/ha in the medium-disturbance scenario and 44–90 t/ha in the high-disturbance scenario (Fig. 5), corresponding to a relative biomass loss of 5–7%, 20–30% and 18–32%, respectively (Fig. C1). In iLand, TreeMig, and LandClim, the amount of biomass lost increased with increasing disturbance frequency, while in LANDIS-II biomass loss was highest in the medium-disturbance scenario. Within the disturbance scenarios, climate influenced disturbance-mediated biomass dynamics, but the effects varied among models. Particularly in the medium and high-disturbance scenarios, biomass loss was intensified with increasing temperature in iLand and LandClim, whereas in TreeMig and LANDIS-II, higher temperature reduced the disturbance-mediated loss of biomass.

Differences among models were pronounced at the species level

(Fig. C2). Whereas the biomass of the main species decreased consistently in all models as a result of disturbance, the biomass of previously rare species increased in comparison to the no-disturbance scenario particularly in LANDIS-II and LandClim.

Different dispersal scenarios had a minor impact on total biomass. Compared to unrestricted dispersal, dispersal limitation resulted in a biomass reduction between 0 and 10 t/ha (corresponding to a relative loss between 0% and 3%; Fig. 6 and C3). Climate change did not significantly influence these results. At the species level, the effects of dispersal limitation were more pronounced (Fig. C4). In LANDIS-II, Norway spruce experienced a strong decrease in biomass, while Swiss stone pine and other previously rare species increased when considering dispersal limitation. Positive effects of dispersal limitation on biomass of individual species were also observed in iLand (Swiss stone pine, Scots pine), TreeMig (Norway spruce) and LandClim (other species), but they were much less pronounced than in LANDIS-II.

3.4. Variance partitioning

Differences between models contributed more strongly to changes in total biomass and species diversity in future projections than differences between climate scenarios (Fig. 7). The uncertainty introduced by different climate scenarios increased in the second half of the century, yet climate scenario differences never explained more than ~15% of the total variance in the simulations. Climate scenario uncertainty also contributed only marginally to the overall variance in all disturbance and dispersal scenarios (Fig. 7). In the disturbance scenarios, disturbance frequency was the most important factor, explaining >40% of the total variance in the second half of the century. In contrast, different assumptions regarding dispersal contributed little to the overall variance in the results. In all simulations, the uncertainty due to replicate runs was negligible.

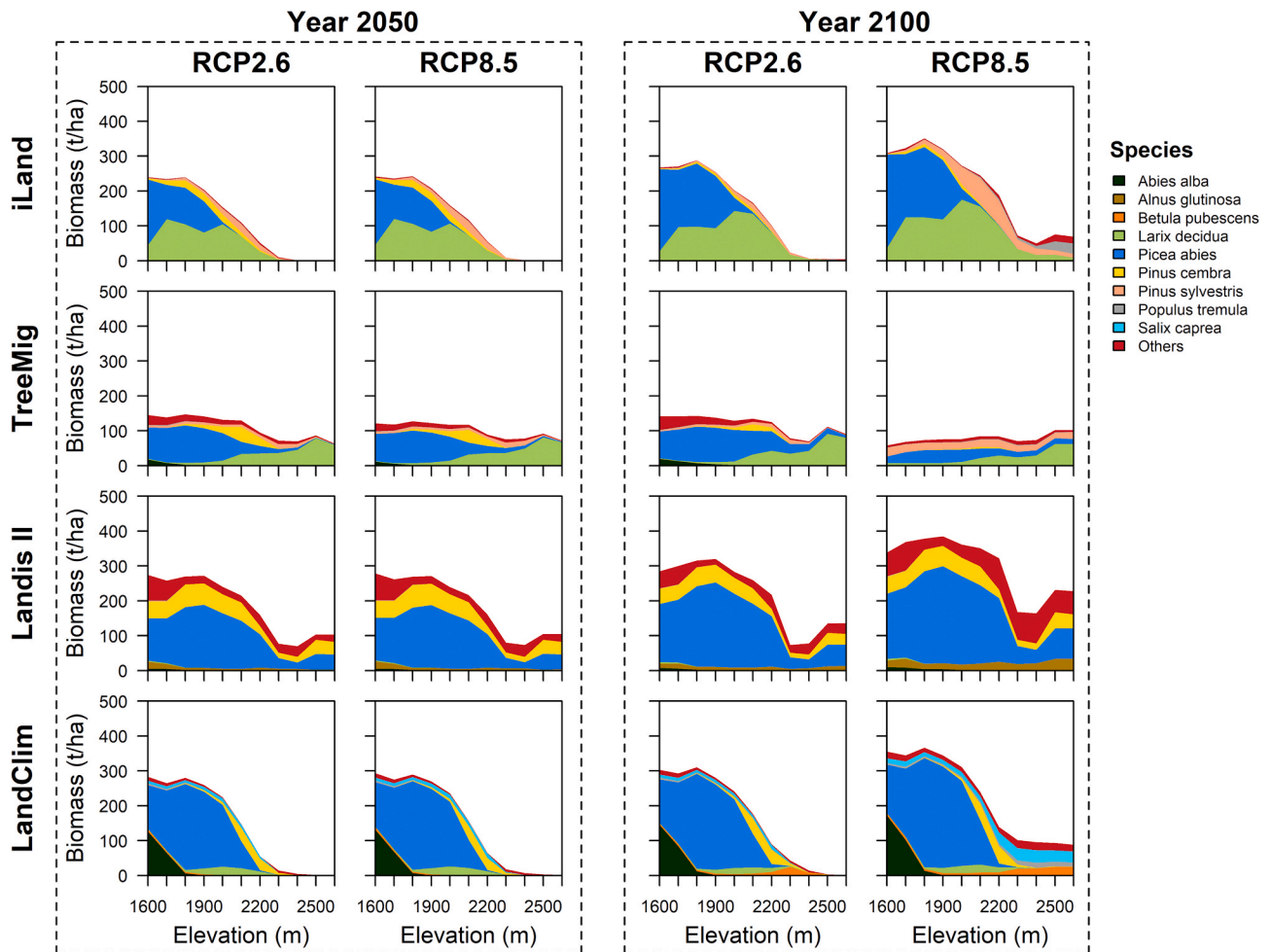


Fig. 3. Projected biomass along the elevation gradient in the years 2050 and 2100 under RCP2.6 and RCP8.5 for four forest landscape models. The total biomass of each species within a given 100 m elevation belt was estimated and divided by the total area of all cells within this elevation belt. Comparatively low biomass values between 2200 and 2400 m a.s.l. in some simulations are the result of high avalanche activity in this elevation belt. Only species exceeding 20 t/ha in a single grid cell are explicitly shown, all other species are summarized as *Others*.

4. Discussion

In this first systematic FLM comparison, we found fair agreement between four state-of-the-art forest landscape models when simulating vegetation dynamics under past-to-present climatic conditions. Simulated current forests were generally in agreement with current observations. However, under future climate conditions, the agreement among projections was low and differences among the models were substantial. Furthermore, different assumptions about disturbance and dispersal had a strong influence on simulated landscape dynamics, with disturbance effects being stronger than climate and dispersal effects. These results indicate that the uncertainty in simulated future landscape trajectories remains high not only because of climate scenario uncertainty but also because of model uncertainty.

4.1. Past-to-present simulations

Past-to-present simulations – i.e., where forest dynamics are simulated over a long time period until quasi-equilibrium and compared with observations – are a common approach in forest landscape modeling (He et al., 2011). Such simulations are frequently applied for fine-tuning of model parameters and for model evaluation (e.g., Temperli et al., 2015). Here, three of the four models (iLand, TreeMig, LandClim) reproduced the observed species composition and location of the treeline fairly well. This is not surprising, as these models have been used and evaluated in

the current (LandClim) or similar (TreeMig, iLand) mountain landscapes, indicating that their structures are appropriate to reproduce forest dynamics under these environmental conditions. Furthermore, fine-tuning for some species parameters was applied for TreeMig to increase consistency between data and simulations.

The discrepancy between simulations and observations was larger for LANDIS-II (Fig. 1). This does not *per se* indicate an inappropriate model structure for long-term simulations until quasi-equilibrium, although the models of the LANDIS family were rather developed with a focus on non-equilibrium successional dynamics and realistic short-term projections over decades to a few centuries (Mladenoff, 2004). The discrepancy is likely to be the combined result of: (I) The specifications imposed on the model to ensure the same initial conditions as the other models (i.e., initialization with even-aged one-year cohorts instead of age-structured cohorts and stand types). This may have enhanced the simulated age-dependent mortality effect when a single species (i.e., Norway spruce) gains dominance over the stands and the landscape (Fig. C5). (II) The choice of maintaining the typical ecoregion approach, defined by classified elevation, aspect and slope, with the area above the current treeline binned into a single ecoregion. This resulted in a less gradual treeline change in the simulations compared to the other models, in which each cell had its own environmental and climatic conditions (Fig. 1). (III) The choice, due to resource constraints, of not performing a formal model calibration (cf. Scheller and Mladenoff, 2004) for the European Alps. In contrast to the other models, only earlier

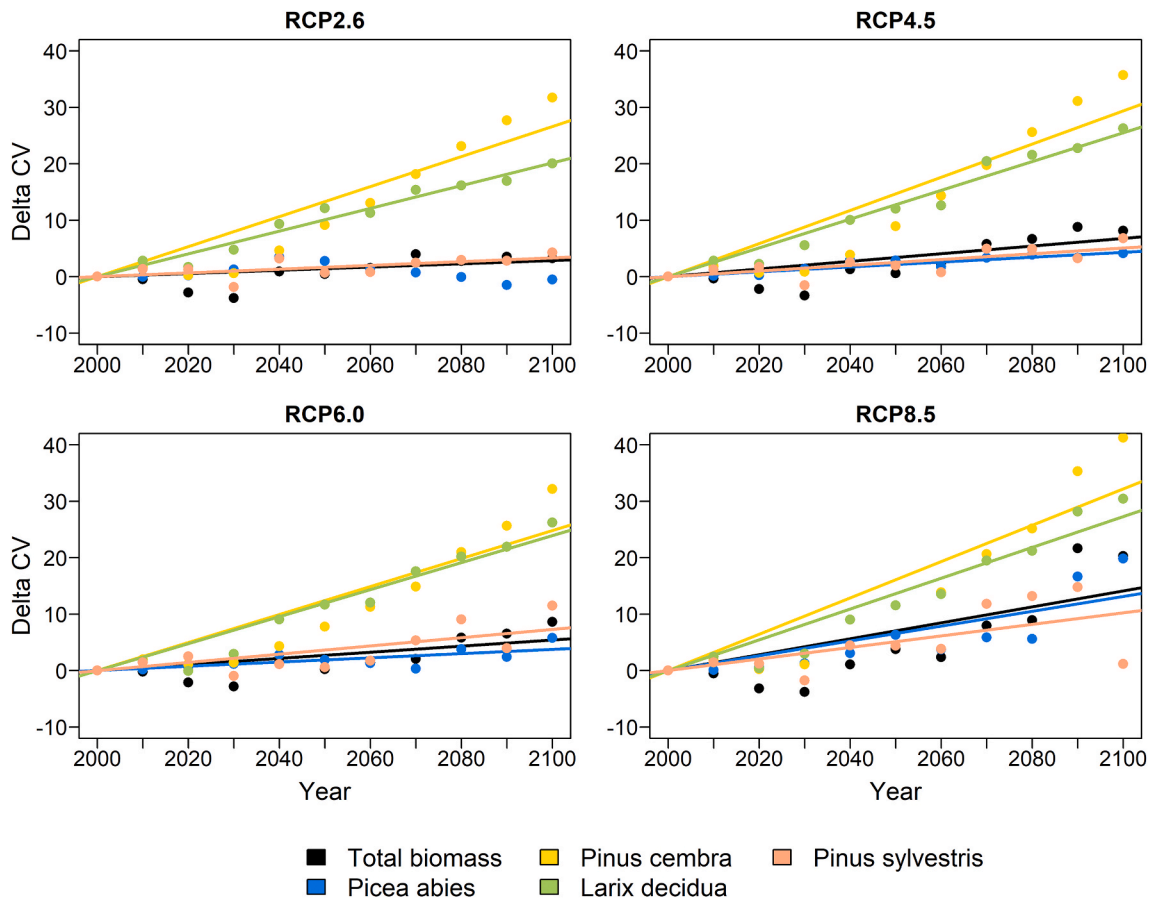


Fig. 4. Coefficient of variation (CV) of total and species biomass over time under four climate scenarios (RCP2.6, RCP4.5, RCP6.0, RCP8.5). CVs were estimated for each decade based on the simulation results of ten replicate runs of four forest landscape models (LANDIS-II, LandClim, iLand, TreeMig). Delta CVs (i.e., the CV in the respective decade minus the CV in year 2000) are shown. Linear models ($\Delta CV \sim Year$) were calculated and significant relationships ($p < 0.05$) are shown as solid lines (see Table C1 for details).

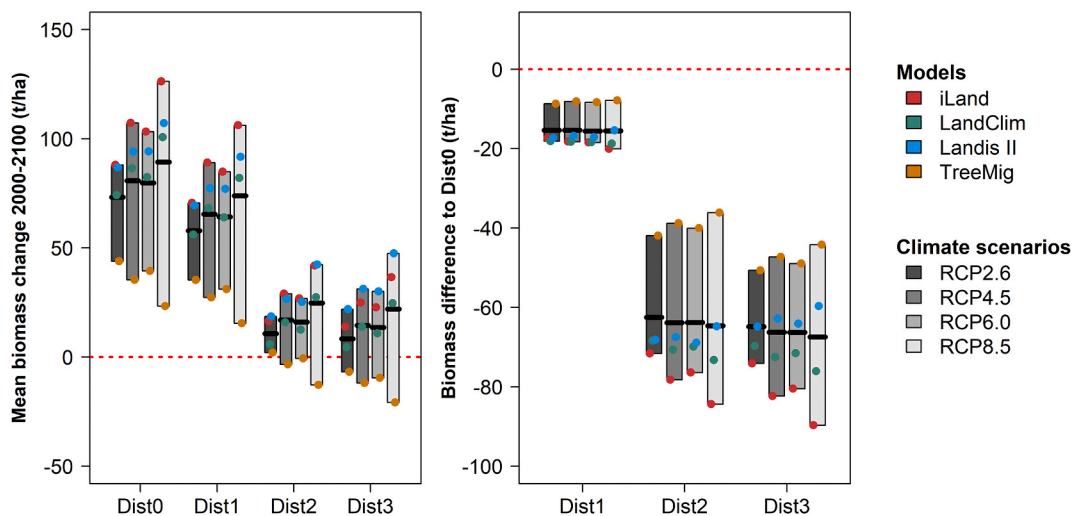


Fig. 5. Projected mean biomass changes of four landscape models under combinations of four disturbance (Dist0-Dist3) and four climate scenarios (RCP2.6-RCP8.5). Due to the stochasticity in avalanche disturbances, biomass changes were estimated by relating the mean biomass changes over the 21st century to the biomass in the year 2000 (i.e., $(1/10 * \sum Biomass \text{ decade } 2010 \dots 2100) - Biomass \text{ } 2000$). The results, averaged over all ten replicate runs, are represented by dots in the left panel, while the right panel shows the mean biomass differences in relation to the no-disturbances scenarios (Dist0). The grey bars show the range of biomass changes/differences across all models for each RCP scenario, mean changes/differences are indicated by black lines.

versions of the core LANDIS-II model in combination with different extensions have so far been applied and calibrated for different biogeographical regions in Europe (e.g., Atlantic, Cantarello et al., 2017;

Continental, Kruehlov et al., 2018; Mediterranean, Mairota et al., 2013). With regard to the detailed patterns emerging from the simulations, e.g. when comparing individual grid cells, the detailed species

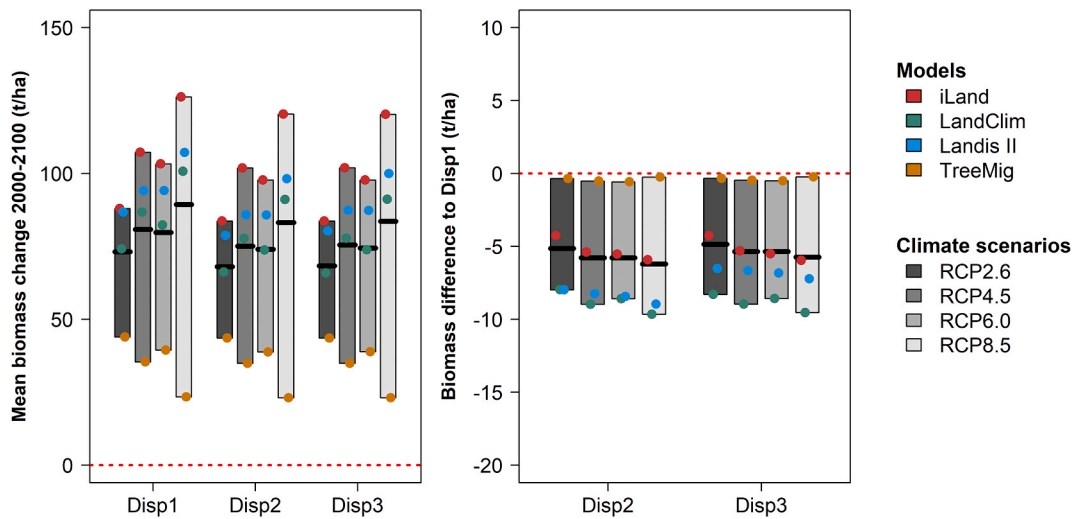


Fig. 6. Projected mean biomass changes of four landscape models under combinations of three dispersal (Disp1-Disp3) and four climate scenarios (RCP2.6-RCP8.5). Biomass changes were estimated by relating the mean biomass changes over the 21st century to the biomass in the year 2000 (i.e., $(1/10 * \sum \text{Biomass decade } 2010 \dots 2100) - \text{Biomass } 2000$). The results, averaged over all ten replicate runs, are represented by dots in the left panel, while the right panel shows the mean biomass differences in relation to the global dispersal scenarios (Disp1). The grey bars show the range of biomass changes/differences across all models for each RCP scenario, mean changes/differences are indicated by black lines.

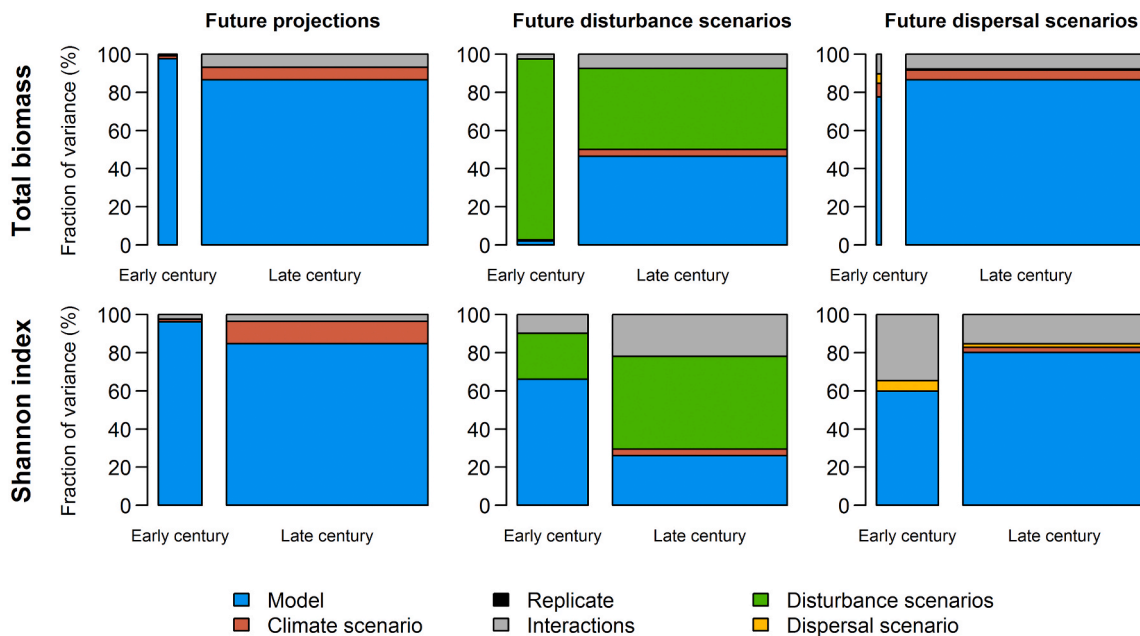


Fig. 7. Mosaic plots indicating the fraction of variance explained by different sources of uncertainty (i.e., model differences, climate scenarios, disturbance and dispersal scenarios, stochasticity by replicates runs) in future projections, disturbance and dispersal scenarios. Interactions include the sum of variations of interaction terms representing unexplained variance. Analyses are based on average change rates for the first half (i.e., 2010–2050, “early century”) and the second half of the 21st century (i.e., 2060–2100, “late century”), with the width of the bars representing the relative proportion of total variance.

composition along the elevation gradient, or the species composition in the avalanche tracks, considerable deviations between the simulations of *all* FLMs and observations were discernible (Fig. 1). Performing a formal model calibration with *all* models could have reduced these deviations, but whether such a fitting of process-based models to landscape-level data increases the robustness of future projections is questionable. In this context, it is important to keep in mind that both the observational data and the model input data are uncertain. Uncertain or unknown processes that were not considered in the simulations, e.g. land use and historical management practices (Elkin et al., 2013), may have strongly influenced the observed species pool or structure of the forests. Furthermore, single or averaged stochastic realizations of

model simulations (i.e., forest landscapes) are compared to observations that are also only one single realization of stochastic processes in the real landscape. Performing a formal model calibration and achieving a better correspondence with observations would hence not guarantee that a model faithfully simulates forest dynamics, as the risk of making the right predictions for the wrong reasons remains. Consequently, past-to-present simulations with FLMs must often be regarded as test of plausibility rather than a validation in a strict sense, which remains a major challenge for landscape modeling studies.

4.2. Future projections

We observed substantial uncertainty in future model projections over the next 100 years. It was high for all analyzed indicators, i.e. biomass trajectories, species composition, and species distribution along the elevation gradient of the study landscape. Uncertainty increased over time and with more extreme climatic conditions (Figs. 2 and 4). Such an increase in uncertainty over time is expected for process-based vegetation models, as their complex structures with many different processes and parameters generally facilitate the propagation of errors over time (Nishina et al., 2015). In addition, it should be noted that, although we generally refer to FLMs as process-based or mechanistic models, they necessarily combine mechanistic and phenomenological components, like almost any ecological model (Gustafson, 2013). This implies that the more extreme climatic conditions become, the more likely the models will operate outside the ecological state space for which they were parameterized, often leading to larger uncertainty in ensemble model simulations (e.g., Ito et al., 2016).

We found the amount of variance in simulation results that was explained by model differences to be high, indicating that the selection of any given model had a larger impact on future projections than differences between climate scenarios. This is in line with studies based on different global vegetation models and species distribution models that showed that model differences were the main source of uncertainty for projected future changes in vegetation (Nishina et al., 2015; Thuiller et al., 2019).

The simulated positive biomass development at the landscape level, when averaged over all models (Fig. 2), agrees with expert- and observation-based trends in mountain areas (Lindner et al., 2014, 2010). High-elevation forests like those in the Dischma valley are currently mostly temperature-limited, and warming is expected to increase their productivity and biomass accumulation (Elkin et al., 2013). In addition, an upward shift of the treeline is expected because of climate change (Bolli et al., 2007; Jochner et al., 2018). Both processes were captured in our simulations; however, their importance differed between FLMs. While the positive biomass development in TreeMig (RCP2.6-RCP6.0) was mainly driven by the fast upward movement of treeline, biomass increase in already established forests contributed most to the positive trends in the other models (Figs. 1 and 3).

The differences in forest dynamics resulted mainly from different implementations of the main demographic processes, i.e. dispersal, establishment, growth, and mortality in the four FLMs. Among others, this relates to the choice of environmental factors that are considered as external forcing, and how the models are parameterized and calibrated. With respect to dispersal and seedling establishment, for instance, the models use different parameterizations determining the effective and maximum dispersal distance as well as the age when a tree starts producing propagules, and different approaches determining the number of new recruits. Also, we used a finer grid for dispersal for iLand and LandClim (20 and 25 m, respectively) than TreeMig and LANDIS-II (100 m), which may further limit the speed at which the area above treeline can be colonized in these models. This is because of the implicit assumption that trees are uniformly distributed within grid cells and species with short dispersal distances can always disperse to an adjacent cell. Therefore, the dispersal rate when using a coarser grid can be higher compared to using a finer grid. In addition, TreeMig is the only model in our ensemble that simulates a seed bank explicitly, which, besides different parametrization of the dispersal functions, contributes to the fast treeline shift in this model, as seeds are assumed to be available above the treeline and can germinate once conditions become favorable. In the other models, the dispersal of some species into previously unsuitable habitat above treeline may be slower than the rate at which new suitable habitat becomes available.

Growth is also implemented quite differently in the models: Two models incorporate tree growth directly as a function of environmental conditions (TreeMig, LandClim), whereas the other two incorporate the

carbon budget more mechanistically (iLand, LANDIS-II). Moreover, iLand and LANDIS-II also included the CO₂ fertilization effect, i.e. the stimulation of photosynthesis by increased atmospheric CO₂ concentrations. It is thus not surprising that these were the models with the highest overall increase in biomass.

Mortality is probably the least understood process (Bigler and Bugmann, 2004), and it remains a major uncertainty in vegetation modeling (Bugmann et al., 2019). Due to the lack of mechanistic understanding, it remains challenging to develop and parameterize robust mortality algorithms (Hülsmann et al., 2018; Sala et al., 2010). The mortality algorithms of all models used in this study are based on the principle that severe limitations in resource supply or other suboptimal growing conditions will increase mortality rates, but this principle is implemented in different ways. In iLand and LANDIS-II, where the carbon balance is simulated explicitly, including pools of non-structural carbohydrate reserves, mortality increases strongly when these reserves are low or depleted. The reserve pools serve as a buffer preventing mortality from drastically increasing when conditions are unfavorable only over a limited period of time. Likewise, in LandClim mortality rates increase when growth is lower than a defined threshold for at least three consecutive years. In contrast, mortality in TreeMig can increase already after one year of unfavorable conditions; frequent but non-consecutive extreme years, such as the projected hot and dry summers under RCP8.5 towards the end of the 21st century, are hence sufficient to induce severe landscape-wide mortality in this model. This shows that the choice of mortality algorithms can have a large impact on forest projections, with the effects of different algorithms becoming particularly evident when comparing models under extreme conditions. Large-scale mortality events due to drought are likely to have increased globally in recent decades (Allen et al., 2010), but they remained restricted mainly to dry valleys at lower elevations in the Alps (Bigler et al., 2006; Etzold et al., 2019). Nevertheless, when considering the commonly shallow soils and cold-adapted provenances in high mountain landscapes, and the tendency to underestimate the risk of drought-induced forest die-offs (Allen et al., 2015), significantly increased mortality rates under extreme climate conditions cannot be ruled out.

It is not trivial to identify the main causes of differences in model behavior because the mechanisms within each model interact in complex ways. This would require systematic tests in which mechanisms or model properties are modified one by one (e.g., changed spatial resolution, implementation of alternative algorithms for growth/establishment/mortality, switching specific processes such as CO₂ fertilization on or off; cf. Huber et al., 2020) to quantify effects on simulation results. Such an analysis was, however, beyond the scope of this study. Nonetheless, we can derive cues about the main causes from our data and experiences with the models. The most obvious difference was the diverging biomass development with increasing temperature when comparing TreeMig and the other models (Fig. 2). For the latter, total biomass was clearly temperature limited and increasing temperatures resulted in biomass increases in grid cells below and above the current treeline (Figs. 1 and 3). In TreeMig, biomass was generally lower than in the other models due to a different dbh/stem-volume allometry that was introduced to better match the allometric functions applied in the Swiss national forest inventory. Below the treeline, the biomass simulated in TreeMig remained largely unchanged, probably because increased interspecific competition cancelled out the positive temperature effects, and the higher sensitivity of the mortality algorithm to high temperatures even led to a biomass decrease in the RCP8.5 scenario (see above). A temperature effect was clearly seen in the area above the treeline, which was colonized faster than in the other models due to the seedbank dynamics (see above) and the generally fast biomass accumulation during early succession (Fig. C5).

The distinctly different model behavior during early succession also caused the different species composition above the current treeline and in avalanche tracks. Both the model behavior during early succession

and under extreme environmental conditions are particularly important for future projections under environmental change, but were not explicitly considered in the evaluation of our models against observations. During the FLM development process, the plausibility of simulation results under such conditions might be tested in one or few landscapes, but this does not guarantee a consistently plausible behavior in general. Consequently, evaluation efforts need to be intensified when applying models in new landscapes or under novel environmental conditions.

4.3. Disturbance and dispersal scenarios

The study landscape is regularly disturbed by avalanches, and our simulations showed that disturbances were of particular importance for future forest dynamics (Fig. 7). The avalanche disturbance regime of the study landscape is unlikely to be representative of landscapes at lower elevations; however, disturbances in general are expected to increase strongly due to climate change in most European landscapes (Seidl et al., 2017). A meaningful integration of disturbance processes in FLMs is thus of paramount importance.

Our comparative study focused on how models respond to prescribed disturbances, finding substantial differences among models. On the one hand, because each model simulated a unique species distribution, spatially fixed disturbances affected the total biomass and the species composition differently. On the other hand, model behaviors with respect to the rate of colonization of disturbed areas and the emerging early forest succession were also important for the dynamics in avalanche tracks (Fig. C5). These model-specific behaviors may explain why the relative biomass loss was smallest in LANDIS-II and previously rare species even increased in biomass with increasing disturbance intensity, while total biomass loss was highest in iLand. Taken together, the interpretation of changes in forest structure and composition under different disturbance regimes would differ substantially across models. To improve the simulation of disturbances in FLMs, modelers should focus not only on the effects of disturbances on forests, but also on the response of forests to disturbances and possible feedback effects between forests and disturbances (e.g., Zurbriggen et al., 2014).

Within each disturbance scenario, the model-specific responses to climate forcing (Fig. 5) were comparable to the responses in the future projection scenarios (Fig. 2), i.e. the biomass in three models increased from RCP2.6 to RCP8.5 while it decreased in TreeMig. This is because the *a priori* defined avalanche disturbances were independent of the effect of climate change. In reality, increasing climate forcing is likely to affect the frequency and distribution of both snow precipitation and avalanches, but the climate sensitivity of avalanches remains uncertain. In some studies no significant impact of climate on avalanche regimes in the Alps was observed (Eckert et al., 2010; Schneebeli et al., 1997), in another study a general decrease in avalanche activity of up to 30% in the next century was projected (Castebrunet et al., 2014). The consideration of such a relationship between climate and avalanche activity and the feedback between forest and avalanche release (Zurbriggen et al., 2014) could have strongly changed the simulated patterns in our study. In addition, we did not consider additional disturbances like windthrow or insect and pathogen outbreaks, whose effects on forest ecosystems are likely to increase with climate change (Seidl et al., 2011b, 2017).

Dispersal is a further crucial process for forest landscape dynamics under climate change. At the continental scale along latitudinal climate gradients, dispersal determines whether species will be able to keep track with a changing climate (Epstein et al., 2007; Meier et al., 2012; Thuiller et al., 2019). In mountain landscapes with their steep gradients, dispersal especially affects treeline dynamics, the colonization after disturbances, and the speed of species turnover. When applying FLMs, implicit assumptions have to be made about the external seed input to the landscape, as landscapes are usually not closed systems and receive an (unknown) amount of seeds from the outside. The effect of different

dispersal assumptions was rather low for the total biomass development in our current simulations, but more pronounced at the species level where the relative share of species was influenced by dispersal limitation, particularly in LANDIS-II. This shows that assumptions about dispersal limitations can alter the species composition, even if the effect may seem small in our scenarios. Furthermore, it must be kept in mind that we have only analyzed landscape dynamics over the next 100 years, which represent a short time for tree migration; over longer time spans, dispersal limitation effects could amplify and change the species composition (Scherrer et al., 2020; Albrich et al., 2020). This indicates that the decision about how dispersal should be simulated should be considered carefully in landscape modeling studies.

4.4. Implications and outlook

We have shown that differences in model structure are the main source of uncertainty in future forest landscape simulations, at least in our case study. This finding highlights several important issues in the context of projecting the future of forest landscapes.

First, the fact that FLM simulations agree under current environmental conditions does not guarantee that their projections remain consistent under climate change. One way towards robust projections for non-analog futures may be to integrate more mechanism based on appropriately scaled “first principles” of ecology into FLMs (cf. Gustafson, 2013). In fact, the available FLMs, like almost all other ecosystem models, are not purely mechanistic models but rather hybrid models that contain mechanistic but also phenomenological components. Purely mechanistic models are hard to parameterize and not tractable, purely phenomenological models are not robust under novel conditions – we need to find the right balance between these extremes. Other model types such as global vegetation or gap models tend to be based more on processes than FLMs, which might thus also benefit from a shift towards a better and more widespread incorporation of processes (Gustafson, 2013). Simultaneously, a more rigorous and systematic model evaluation, parameterization, and calibration is needed, for instance by applying pattern-oriented modeling (Grimm et al., 2005, cf. Huber et al., 2020) based on the increasing availability of large forest data streams (e.g., remote sensing).

Second, model uncertainty increases with simulation time and severity of environmental change. This is a particular concern in landscape modeling, as FLMs are rarely used to make short-term projections under a continuation of past conditions but are frequently employed to study ecosystem trajectories over centuries to millennia under changing environmental conditions (Henne et al., 2015; Thom et al., 2017b).

Third, being able to simulate future disturbance regimes more accurately is of paramount importance. Disturbance scenarios contributed at least as much variance to our results as differences between the models, which underlines the importance of improving disturbance projections in FLMs, and of considering disturbance processes also in other model types (Fisher et al., 2018; Seidl et al., 2011a).

Fourth, although all FLMs are based on similar principles, they have been developed for different purposes (e.g. short-term dynamics vs. equilibrium simulations), use different spatial and temporal scales, represent trees at different levels of detail, implement the main processes (dispersal, growth, mortality) in different ways, and are calibrated for different species and regions. Consequently, when using a FLM, the model characteristics should be carefully matched to the study question in order to minimize uncertainty. The comparative model description provided in Appendix B provides a good basis for such an endeavor.

Lastly, by conducting the first FLM comparison study, we showed that ensemble projections with FLMs are possible, and advocate for a wider use of multiple models in future studies. The observed differences among models are at least partly due to differing assumptions about processes that are not fully understood, leading to competing, equally plausible model formulations. Hence, ensemble simulations with

ecosystem models reflect a “range of potential futures”. Moreover, ensemble projections allow for the quantification of model uncertainty, but they also help us to scrutinize the potential causes for the simulated differences (e.g., mortality formulation, drought effects, reproduction, or regeneration feedback) and stimulate important discussions among the modeling community.

5. Software availability

LandClim is developed by the Forest Ecology Group at ETH Zürich, Switzerland. It is available online at <https://ites-fe.ethz.ch/openaccess/> and can freely be used under the terms of the “GNU General Public License v3”. LANDIS-II is developed by the LANDIS-II Foundation, a registered non-profit in the USA; it is open-source (Apache License 2.0) and available online at <http://www.landis-ii.org>. iLand is developed and maintained at the Ecosystem Dynamics and Forest Management Group, Technical University of Munich. Source code, executable, and model documentation are available at <http://iLand.boku.ac.at>. The model is open source under the GNU General Public License. TreeMig is developed by the Dynamic Macroecology Group, WSL, Switzerland. It is available upon request from heike.lischke@wsl.ch and can freely be used under the terms of the “GNU General Public License v3”.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.envsoft.2020.104844>.

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