

Modeling postglacial vegetation dynamics of temperate forests on the Olympic Peninsula (WA, USA) with special regard to snowpack

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Abstract Past and future forest composition and distribution in temperate mountain ranges is strongly influenced by temperature and snowpack. We used LANDCLIM, a spatially explicit, dynamic vegetation model, to simulate forest dynamics for the last 16,000 years and compared the simulation results to pollen and macrofossil records at five sites on the Olympic Peninsula (Washington, USA). To address the hydrological effects of climate-driven variations in snowpack on simulated forest dynamics, we added a simple snow accumulation-and-melt module to the vegetation model and compared simulations with and without the module. LANDCLIM produced realistic present-day species composition with respect to elevation and precipitation gradients. Over the last 16,000 years, simulations driven by transient climate data from an atmosphere-ocean general circulation model (AOGCM) and by a chironomid-based temperature reconstruction captured Late-glacial to Late Holocene transitions in forest communities. Overall, the reconstruction-driven vegetation simulations matched observed vegetation changes better than the AOGCM-driven simulations. This study also indicates that forest composition is very sensitive to snowpack-mediated changes in soil moisture. Simulations without the snow module showed a strong effect of snowpack on key bioclimatic variables and species composition at higher elevations. A projected upward shift of the snow line and a

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decrease in snowpack might lead to drastic changes in mountain forests composition and even a shift to dry meadows due to insufficient moisture availability in shallow alpine soils.

1 Introduction

Climate is the most important determinant of plant species abundance and distribution across sub-continental and Late Quaternary spatial and temporal scales (Woodward 1987). In North America, local-to-continental-scale changes in plant communities over the past 14,000 years, as recorded by detailed pollen records, are strongly associated with regional climate change (Prentice et al. 1991; Shuman et al. 2004). In the Pacific Northwest (PNW) for example, the low-elevation vegetation transitioned from tundra and open parkland in the Late-glacial to woodland and dry forest in the early Holocene and then to temperate conifer rainforest in the middle Holocene (Cwynar 1987; Whitlock 1992). However, interpreting the particular climatic drivers of vegetation change is very complex. A promising avenue to pinpoint the specific climatic controllers of tree distributions exists in the comparison of explicitly simulated vegetation dynamics with observed vegetation change and modern forest biogeography (Miller et al. 2008). Accurately predicting future effects of climate change relies on our ability to correctly model the dynamics of the past (McMahon et al. 2011).

In the hypermaritime PNW, temperature as well as persisting spring snowpack play a very important role in creating a striking elevational zonation of the dominant tree species and the alpine treeline (Fonda and Bliss 1969; Ettinger et al. 2011). During winter, a strong Aleutian low-pressure system delivers moist air from the Pacific, causing intense precipitation, which falls as snow at high elevations. Summers in the PNW are consistently dry, due to a subtropical high-pressure system over the eastern Pacific. The melting snowpack in late spring and summer therefore constitutes an important source of moisture during the growing season (Mote et al. 2005; Gavin and Brubaker 2015). No study has yet attempted to model the dynamic postglacial vegetation changes in this region, and how changing snowpack may affect species distributions in past and future climate. The results from such a model would have important implications considering the ongoing climate change with reduced snowpack, and warmer temperatures predicted (Salathé et al. 2010).

We simulated forest growth at six study areas on the Olympic Peninsula, Washington, using LANDCLIM, a spatially explicit, dynamic, forest landscape model that integrates bioclimatic variables, topography and soil properties to drive stand-scale gap dynamics interacting with landscape-scale disturbances (Schumacher et al. 2004). A process-based model such as this is ideally suited for understanding the coupled effects of climate, disturbance, and competition among species. We compared model results, driven by both a transient climate simulation from an atmosphere-ocean general circulation model (AOGCM) (Liu et al. 2009), as well as chironomid-inferred temperatures (Chase et al. 2008) to the vegetation history captured in five radiocarbon-dated pollen and macrofossil records. We addressed four questions each focusing on modeling vegetation at particular spatial and temporal scales: 1) Does LANDCLIM reproduce modern tree-species distribution along elevation gradients on the Olympic Peninsula, 2) What is the hydrological effect of snowpack on montane to subalpine tree species distribution, 3) can the model replicate vegetation dynamics of the past ca. 14,000 years observed in the pollen and macrofossil records, and 4) can we use the model-data comparison to test the accuracy of the climate data used for the simulations?

2 Methods

2.1 Study area

The Olympic Peninsula is a topographically complex and heavily forested region. Coastal plains of the southern and western peninsula rise to the Olympic Mountains (highest point 2430 m a.s.l.) that have been shaped by a series of Pleistocene glaciations. Mountainous terrain and predominantly southwesterly onshore flow create a very steep precipitation gradient across the peninsula (Fig. 1). Western slopes at high elevation can receive over 5000 mm of annual precipitation while locations in the rainshadow region to the northeast receive less than 500 mm. The majority of precipitation occurs in the winter months, but snow is rare below 800 m elevation. The strong topographic and climatic gradients produce a variety of different vegetation zones on the peninsula (Fig. 1). Whereas this forest zonation is well established (Fonda and Bliss 1969), individuals of any species may be found on certain microsites outside of their zone of dominance. The environmental and ecological factors controlling tree species distributions are further explored by Nakawatase and Peterson (2006) and Henderson et al. (2011).

Five postglacial lake-sediment records on the Olympic Peninsula have been previously analyzed for pollen, macrofossils and charcoal (McLachlan and Brubaker 1995; Gavin et al. 2001; Gavin et al. 2013; Gavin and Brubaker 2015). These sites span the range of forest types and reflect the spatial heterogeneity of the topography and climate on the peninsula (Fig. 1; Table S1). We simulated forest dynamics in six circular study areas with a 5 km radius (i.e. 78.5 km²) and a grid size of 30 m (Table S1). We refer to each site with respect to its elevation (low, middle or high) and occurrence in the windward (west) or rainshadow (east) portion of the peninsula. We also simulated forest dynamics at a site with no corresponding sediment record, to complete the elevation transect in the eastern peninsula.

2.2 Vegetation model description

We used LANDCLIM to simulate post-glacial forests dynamics in the six study areas. LANDCLIM simulates establishment, growth and mortality of tree cohorts as well as competitive

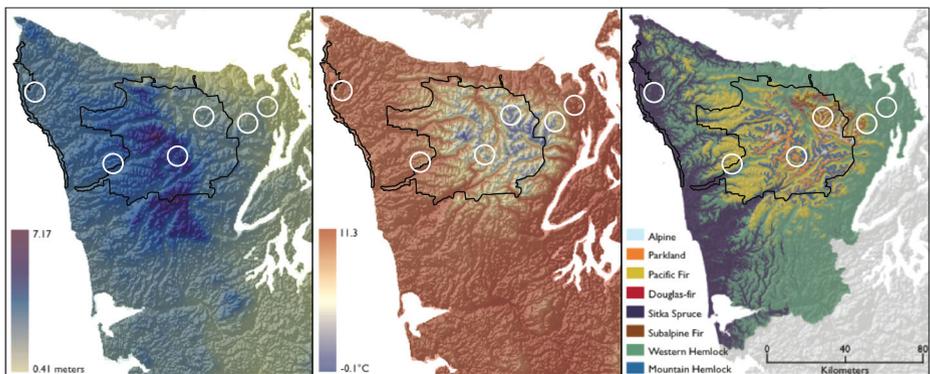


Fig. 1 Environmental gradients of the Olympic Peninsula, Washington (USA). **a**) Mean annual precipitation and **b**) mean annual temperature from PRISM (Daly et al. 2008); **c**) Potential Natural Forest Zones from (Henderson et al. 2011). White circles represent the six study landscapes, national park boundaries are outlined in black. Figure modified from Gavin and Brubaker (2015)

interactions between tree species in 30×30 m grid cells. Tree establishment and growth in each grid cell are determined by species-specific bioclimatic thresholds and life-history parameters (Table S2). Mortality is induced by stress, disturbance (fire and windthrow), and maximum longevity. A detailed description of the LANDCLIM model is given in the Supplementary Material. Several studies have utilized LANDCLIM to understand the local and regional responses of vegetation to climate change and to explore ecosystem dynamics in different environments around the world (Schumacher et al. 2006; Henne et al. 2012; Schwörer et al. 2014; Thrippleton et al. 2014).

2.3 Species parameterization

We defined and parameterized 15 of the common, dominant tree species on the Olympic Peninsula (Table S2). Rare species and species associated with certain microsites (e.g. western white pine [*Pinus monticola*], whitebark pine [*Pinus albicaulis*], Engelmann spruce [*Picea engelmannii*] and slide alder [*Alnus viridis* subsp. *Sinuata*]) were not included in these experiments because their occurrence is controlled by local factors such as avalanche disturbances and topographic influences on moisture availability (Franklin and Dyrness 1988; Burns and Honkala 1990a), which are not represented in LANDCLIM.

2.4 Snow accumulation-and-melt module

It was necessary to customize LANDCLIM to take into account the hydrological effects of snowpack on mountain forests. In the mountain ranges of Western North America, spring snowpack provides a major source of moisture during the dry summer months (Mote et al. 2005). Previous versions of LANDCLIM treated all precipitation as rain, with surplus water that is not needed by the vegetation leaving the grid cell as runoff. We therefore implemented the simple snow accumulation-and-melt model of McCabe and Wolock (2009) into the monthly calculation of the water balance for the LANDCLIM drought index. Precipitation that falls above a monthly mean air temperature of $3\text{ }^{\circ}\text{C}$ is recorded as rain, whereas precipitation below $-1\text{ }^{\circ}\text{C}$ is recorded as snow (i.e. as snow water equivalent (SWE) in mm). Between the two temperature thresholds, the proportion of snow and rain changes linearly. Snowmelt is a function of monthly air temperature and occurs if temperatures are above the snow temperature threshold of $-1\text{ }^{\circ}\text{C}$. Snow can accumulate over the months and melt again if temperatures are warm enough (McCabe and Wolock 2009). As a result, much of the winter precipitation at higher elevation is stored and released in spring and early summer.

2.5 Environmental inputs

LANDCLIM is forced by monthly means of temperature and precipitation. To examine a range of possible paleoclimates, we used two climate scenarios. The AOGCM-scenario is based on climate data from the TraCE-21 ka project (Liu et al. 2009), which simulated global climatic variation over the past 21 ka. For the proxy-scenario, we used an independent, chironomid-inferred Holocene (12.5–0.5 ka) July temperature reconstruction from southern British Columbia (Chase et al. 2008).

Other environmental input data include soil characteristics and topographical information. Please see the Supplementary Material for a full description of the climate and environmental input data.

2.6 Simulation protocol

LANDCLIM was run with the AOGCM-scenario from 16 ka to present and with the proxy-scenario from 13 ka to 0.5 ka at all six study sites. To evaluate model results, we first compared simulated biomass from the AOGCM-scenario averaged over the last 150 years to vegetation survey data from a broad network of ecological plots placed in undisturbed forest on the Olympic Peninsula (ECOSHARE 2015). We then compared the entire paleo-simulations at each site with corresponding pollen and macrofossil data from the sediment record. Pollen and macrofossils represent different spatial scales due to different source areas. Most of the pollen deposited in small lakes in mountainous terrain comes from plants growing a few kilometers around the lake (Gavin et al. 2005). Macrofossils on the other hand represent local vegetation (Tinner 2007). We therefore compared the simulated total biomass of all species in the entire study landscape to pollen percentages and the simulated biomass up to 250 m around each lake to the macrofossil record.

To explore the role of snowpack, we simulated forest dynamics with and without the snow accumulation-and-melt module. This allowed us to examine the performance of the module as well as the hydrological effect of the snowpack on moisture availability and species composition.

3 Results

3.1 Present-day elevational species distributions

LANDCLIM produced moderately realistic present-day species compositions with respect to elevation and precipitation gradients (Figs. 2 a,c,d,f and S1). The model correctly simulates forests dominated by western hemlock, Sitka spruce and western redcedar at low elevations and a transition to Pacific silver fir and mountain hemlock with increasing elevation on the west side. On the east side, the model correctly simulates abundant Douglas-fir together with western hemlock and western redcedar at low and predominantly subalpine fir and Pacific silver fir at high elevation. However, the model failed to simulate Douglas fir at low elevations in the west and western hemlock at elevations >1000 m in the east.

3.2 Sensitivity to snow at the middle and high elevation sites

Simulations without the snow module reveal the sensitivity of total biomass and species composition to snowpack at mid to high elevations (Fig. 2b,e). In the western part of the peninsula, simulations without the snow module result in forests composed of Pacific silver fir, Douglas-fir and Alaska yellow cedar between 1000 and 1300 m a.s.l. and subalpine fir at higher elevations. On the east side, model runs without the snow module show forests dominated by subalpine fir and lodgepole pine at mid to high elevations, with notably low biomass values. Moreover, there is a drastic reduction in total biomass above ca. 1000 m a.s.l., with a lowering of timberline in the east by ca. 300 m due to lower moisture availability and increased drought stress during the growing season (Figs 2 and 3). Since there is hardly any snow below ca. 800 m a.s.l. low elevation forests on the east and west side show no sensitivity to the inclusion of the snow module.

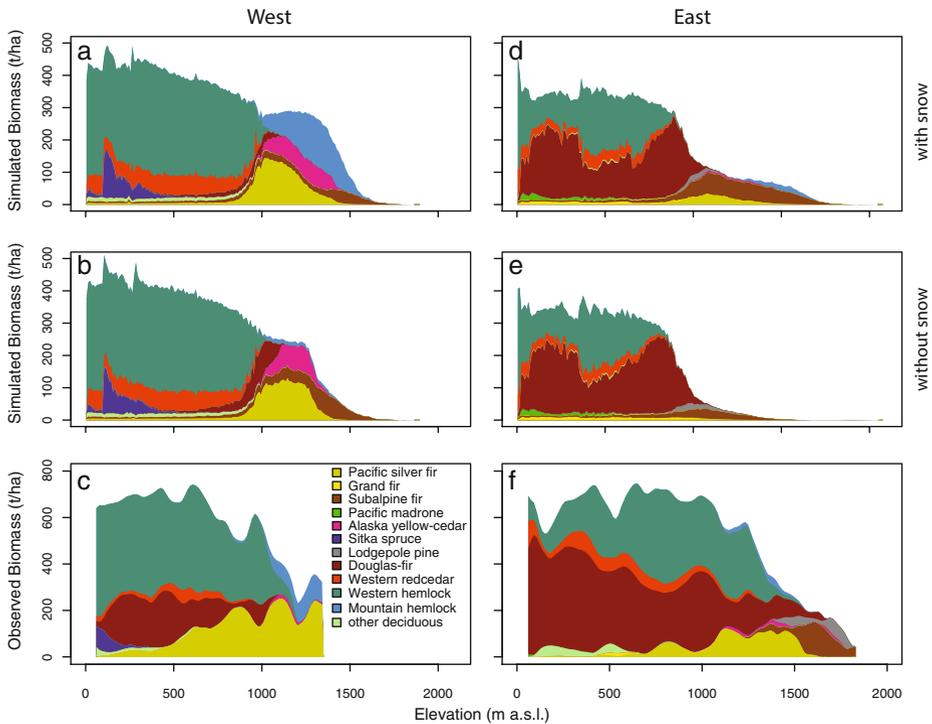


Fig. 2 Elevational distribution and abundance of simulated and observed tree species. **a)** simulated biomass of individual tree species averaged over the last 150 years. **b)** same as **a)** but without the snow accumulation-and-melt module. **c)** Percent cover of tree species in 639 ecological plots in the Olympic National Forest (ECOSHARE), multiplied by average species-specific values of aboveground biomass (Smith et al. 1984; Burns and Honkala 1990a; Burns and Honkala 1990b). Note that there are no plots above 1400 m a.s.l. on the west side. **d, e,** and **f** same as **a, b** and **c**, but for the east side of the peninsula

3.3 Vegetation simulations

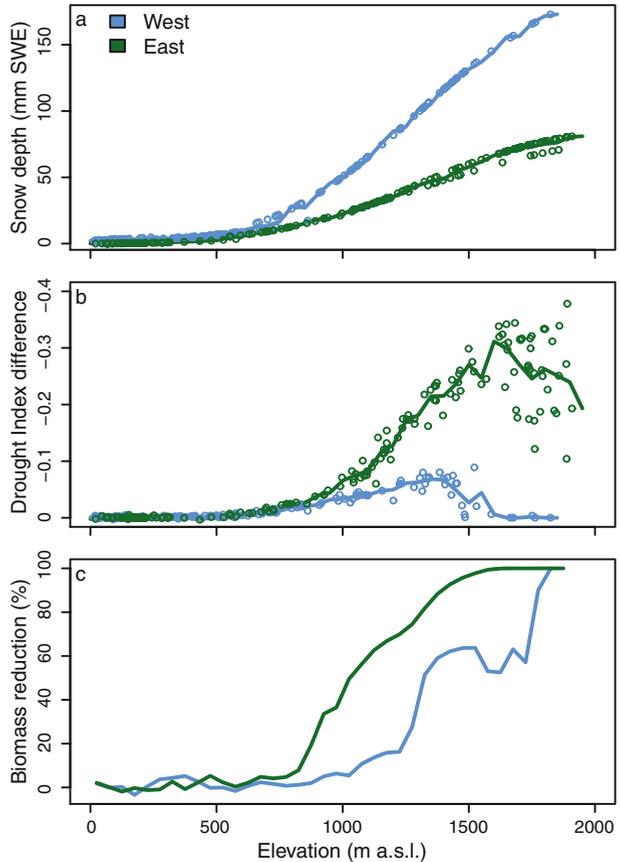
LANDCLIM simulations run with the two climate scenarios (Fig. 4) generally agree with pollen and macrofossil records for the five sites on the regional and local species composition and post-glacial vegetation dynamics (Figs. 5 and 6).

At the low-west site (Wentworth Lake), both simulations show forests dominated by western hemlock and western redcedar for most of the Holocene with the addition of Sitka spruce in the proxy-scenario (Fig. 5g,h). The pollen record shows forests characterized by abundant red alder and Sitka spruce in the Early Holocene and the establishment of the present-day forest type with Sitka spruce, western hemlock and western redcedar around 6 ka (Fig. 5i). The same pattern can be found on the local scale (Fig. 6 h-i).

At the mid-west site (Yahoo Lake), both simulations show a nearly identical progression as at the low-west site (Fig. 5d,e). The pollen and macrofossil records indicate a diverse subalpine forest with Sitka spruce as well as mountain hemlock and Pacific silver fir during the Late-glacial. At the beginning of the Holocene, red alder and Douglas-fir increase, before the present-day Western Hemlock Zone establishes (Fig. 5f).

At the high-west site (Martins Lake), both climate scenarios result in forests characterized by fir and mountain hemlock during the Late-glacial, with the addition of western hemlock, western

Fig. 3 Effect of snowpack on simulated bioclimatic variables and biomass at the west (blue line) and east (green line) side of the Olympic Peninsula. Circles are individual values from randomly selected gridcells in the study areas and solid lines show LOESS smoothed data. **a)** mean snow depth in March for the last 150 years on the west and east side of the Olympic Peninsula; **b)** difference in the LANDCLIM drought Index between simulations with and without the snow accumulation-and-melt module; **c)** relative reduction in simulated biomass in the model run without the snow module. A biomass reduction of 100 % means trees could not establish in the model. SWE = Snow Water Equivalent



redcedar and Douglas-fir during the Holocene (Fig. 5a,b), which is in agreement with the pollen record (Fig. 5c). In contrast to the simulations however, the macrofossil record indicates very open conditions with timberline below the lake until ca. 7.8 ka (Fig. 6c). Otherwise, the simulations at the local as well as regional scale match the paleobotanical records moderately well.

At the low-east site (Crocker Lake), simulated forests are dominated by Douglas-fir with some western hemlock under both climate scenarios for the entire simulation period (Figs. 5o,p and 6o,p). Both simulations show frequent disturbances that cause short-term changes in the total biomass (Figs. 5o,p and S2). The paleobotanical records differ from the simulations, showing a non-analog vegetation type in the Late-glacial with open parkland consisting of Sitka spruce, lodgepole pine and subalpine fir (Figs. 5q and 6q). With the beginning of the Holocene, pollen percentages of red alder and Douglas-fir increase, before western redcedar dominates the record.

At the mid-east site (Sink Lake), the simulation run with the AOGCM-scenario shows forests with mainly Douglas-fir and true firs (Fig. 5m). The simulation using the proxy-scenario is similar, but with a more diverse species composition after ca. 6 ka, which reflects the altitudinal zonation in this steep landscape (Fig. 5n). Unfortunately there is no paleobotanical record from the mid-east side of the Olympic Peninsula for comparison.

At the high-east site (Moose Lake), low simulated forest biomass reflects the high abundance of non-forested grid cells in the landscape (Fig. 5i, Fig. S1). Under the proxy-scenario,

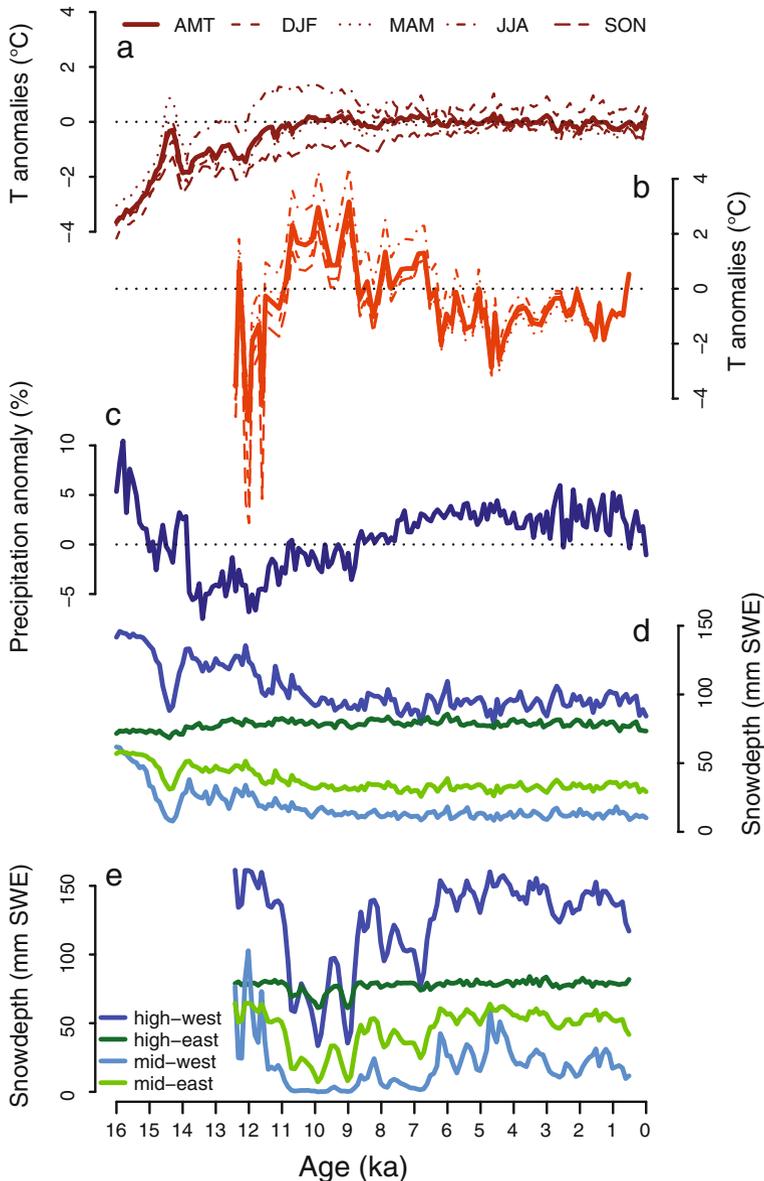


Fig. 4 Time-series of climatic input parameters for the AOGCM and proxy scenario as well as simulated snowpack for the high- and mid-elevation sites. **a**) AOGCM-derived temperature anomalies for annual (AMT) as well as seasonal mean temperatures (dashed lines: DJF = winter, MAM = spring, JJA = summer, SON = fall). **b**) mean annual and seasonal temperature anomalies used in the proxy scenario, derived from a chironomid-inferred July-temperature reconstruction (Chase et al. 2008) adjusted for changes in insolation according to Schwörer et al. (2014). Dashed lines show seasonal values. **c**) AOGCM-derived precipitation anomaly. For the proxy scenario, we used twentieth century mean values since there is no regional quantitative reconstruction of precipitation for the studied time period. **d**) Simulated snow depths in March for the AOGCM-scenario at the study sites at middle and high elevations. **e**) Same as **d**) but for the proxy-scenario

simulated forests were dominated by true firs with the addition of Douglas-fir in the early to mid-Holocene and mountain hemlock in the Late Holocene (Fig. 5k). The paleobotanical

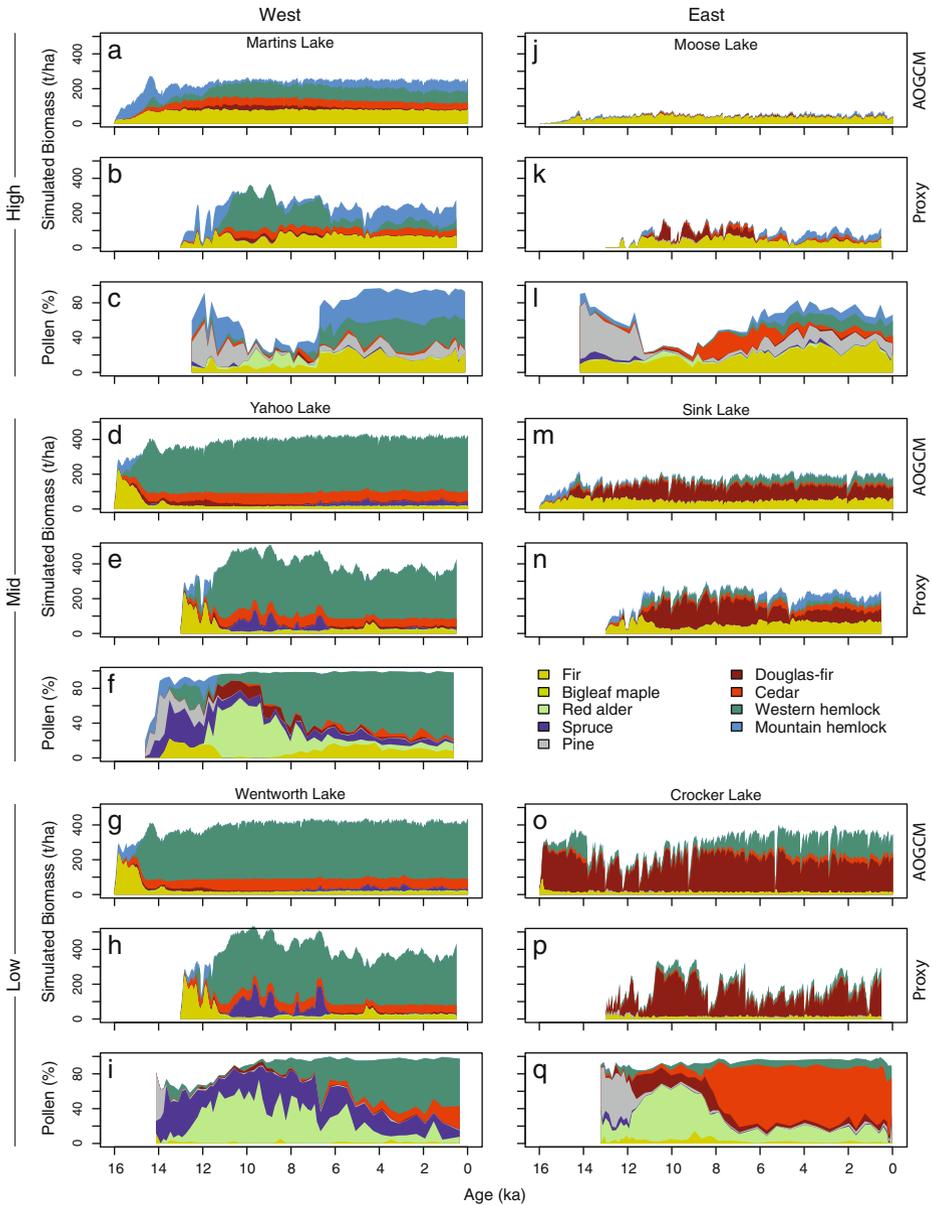


Fig. 5 Simulated biomass of all tree species around Martins Lake for the **a**) AOGCM- and **b**) proxy-scenario, compared to **c**) the pollen record from Martins Lake. Pollen data is given as percentage of the terrestrial pollen sum. The AOGCM simulation was run from 16 ka to present, whereas the proxy-scenario was run from 13 ka to 0.5 ka. Simulated biomass of certain tree species has been pooled to facilitate comparison with the taxonomic resolution of the pollen records. The other panels (**d–q**) are according to **a**, **b**, **c**) but for Yahoo Lake (**d**, **e**, **f**), Wentworth Lake (**g**, **h**, **i**), Moose Lake (**j**, **k**, **l**), Sink Lake (**m**, **n**) and Crocker Lake (**o**, **p**, **q**). Note that there is no pollen record available from Sink Lake

records indicate that timberline reached the site at the beginning of the Holocene with forests consisting mainly of subalpine fir (Fig. 6l). The timing as well as the species composition is

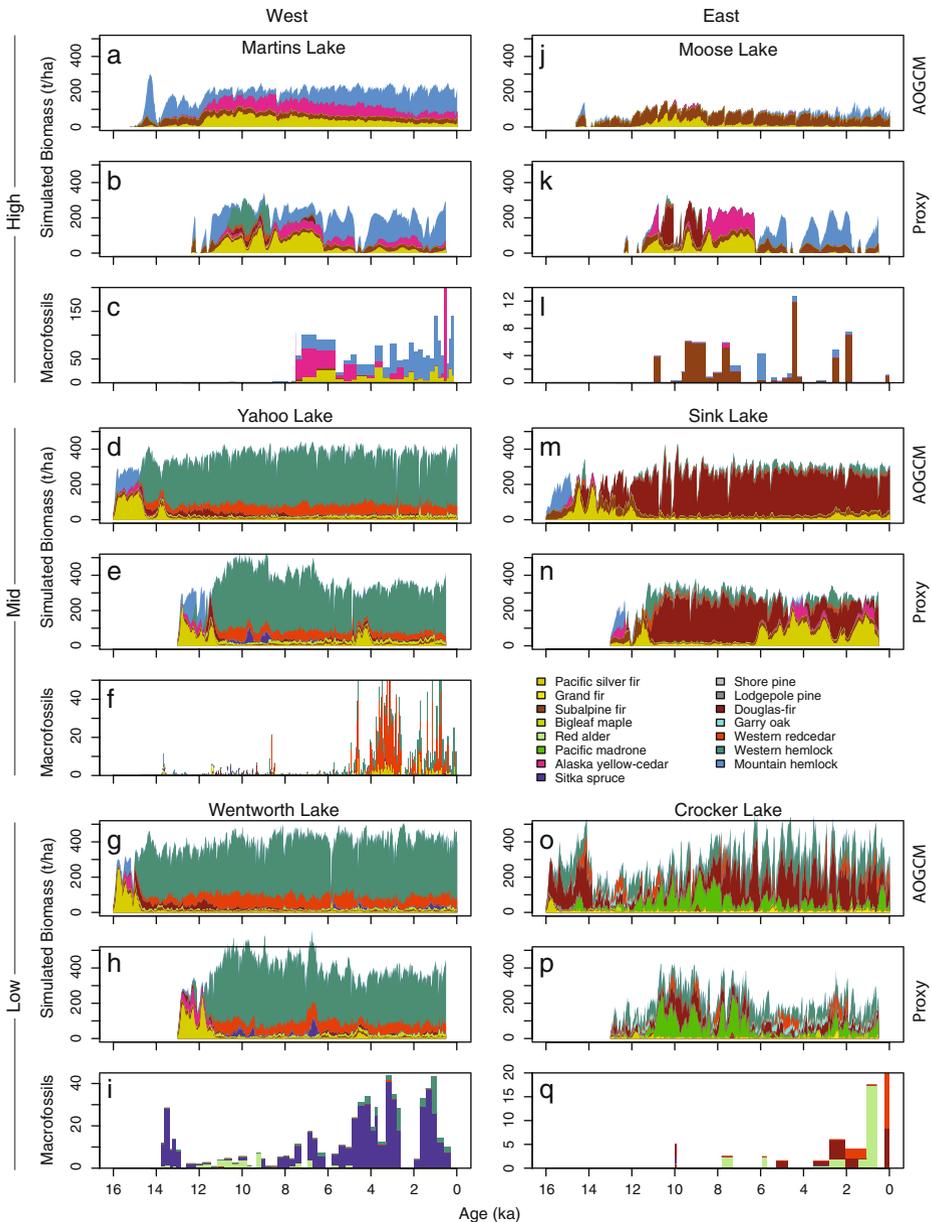


Fig. 6 Simulated biomass of all tree species within a 250 m radius of Martins Lake for the **a**) AOGCM- and **b**) proxy-scenario, compared to **c**) the macrofossil record from Martins Lake. The AOGCM simulation was run from 16 ka to present, whereas the proxy-scenario was run from 13 ka to 0.5 ka. The other panels (**d–q**) are according to **a**, **b**, **c**) but for Yahoo Lake (**d**, **e**, **f**), Wentworth Lake (**g**, **h**, **i**), Moose Lake (**j**, **k**, **l**), Sink Lake (**m**, **n**) and Crocker Lake (**o**, **p**, **q**). Note that there is no macrofossil record available from Sink Lake. Macrofossil data is given as concentrations (pieces 100 cm^{-3}) except **f** (pieces 5 cm^{-3})

simulated remarkably well by the proxy-scenario, whereas the AOGCM-scenario simulates timberline reaching the elevation of Moose Lake already at ca. 14.5 ka (Fig. 6o,p).

4 Discussion

4.1 Comparison of simulated biomass to the paleobotanical record

Generally, LANDCLIM is able to partially simulate realistic species composition at each study site, reflecting 1) the spatial pattern of forest types on the Olympic Peninsula and 2) major changes during the last 16 ka. Mismatches between the simulations and observed species patterns (Figs. 2 and S1) can be explained by mismatches in the location of the plot data and the simulation landscapes as well as model limitations. For example, Douglas-fir is simulated with low abundances in the west, whereas high values in the observed data reflect its presence on recently burned south aspects that are abundant on the south-west side of the Olympic Peninsula (Agee 1996). The lower limit of Pacific silver fir is simulated at ca. 800 m a.s.l. on the west side. This species, however, is also observed at lower elevations due to a competitive advantage in cold air drainages and where the snowpack causes physical damage to western hemlock (Gavin and Brubaker 2015). LANDCLIM captures neither of those processes. Similarly on the east side, western hemlock and Douglas-fir have higher upper-elevational limits than were simulated, possibly due to topographic effects on temperature such as warm south-facing slopes.

Most of the discrepancies between the pollen records and LANDCLIM simulations can be explained by the fact that some taxa are highly over-represented or under-represented in the pollen record. Tree taxa with high pollen productivity such as alder and pine dominate most pollen records during the Late-glacial and Early Holocene, even though they probably account for only a small portion of the tree biomass in the landscape. This effect is even more pronounced by low pollen influx from the local vegetation, where the lake is not surrounded by forest (e.g. at Moose Lake). Expressing the pollen data as influx (grains $\text{cm}^{-2} \text{yr}^{-1}$) may seem to be a more robust comparison with the simulation results (Miller et al. 2008). However, at these sites pollen influx appears to be confounded by changing basin morphometry and fluvial inputs (Gavin and Brubaker 2015).

Another cause of the mismatch between the simulated biomass and the pollen and macrofossil diagrams is the over-representation of tree species occurring in riparian and wetland settings. Sitka spruce, red alder and western redcedar grow preferentially in water-logged soils at the edge of the lake or inflowing streams and therefore contribute a higher amount of plant remains and pollen to the sediment records. Moreover, waterlogging is not represented in LANDCLIM. This could explain the dominance of Cupressaceae pollen (i.e. western redcedar) at the low east site throughout the mid- to Late Holocene. Indeed, other pollen records from southern Vancouver Island indicate that the regional landscape was dominated by Douglas-fir in dry and western hemlock in wetter areas (Brown and Hebda 2002), which agrees well with our simulations.

The comparison between the simulation outputs and the paleobotanical data also point to limitations of the species parameterization. Sitka spruce, for example, was an important part of low- to mid-elevation forests during the Late-glacial on the west and to a smaller extent also on the east side. This is not simulated by the model, since the species has a relatively high temperature threshold (Table S2). The climatic parameters for all tree species have been originally obtained by overlaying maps of bioclimatic variables onto species distribution maps from Oregon and Washington only (Bugmann and Solomon 2000). However, using the climatic parameters of the species' entire range would give unrealistic results, with Sitka spruce growing at unreasonably high elevations (Gutierrez et al. submitted). The problem here is that Sitka spruce requires high humidity created by moist maritime air and summer fog, which is not represented in LANDCLIM.

Results from this study corroborate conclusions drawn from earlier process-based and statistical model studies that explain climate-vegetation relationships in the PNW (Woodward et al. 1995; Zolbrod and Peterson 1999; Nakawatase and Peterson 2006; Littell et al. 2010; Fisher 2013). From the Late-glacial to the Holocene, simulated biomass follows the pattern of the temperature input data, suggesting that temperature or indeed growing season length is limiting total biomass. However, the east side has consistently lower total biomass, suggesting growing season soil moisture is a limiting factor in the rainshadow (Fig. 5, Fig. S3). This is especially evident in the AOGCM-scenario at the low-east site, where biomass follows precipitation rather than temperature (Figs. 4c and 5o). The drier conditions on the east side also resulted in larger simulated forest fires (Fig. S2), which agrees with present day observations (Agee 1996). Our results support previous studies that suggest that in the PNW, climate components related to growing season length and intensity are positively correlated with growth on windward slopes, and climate components related to summertime moisture availability are positively correlated with growth on leeward slopes (McKenzie et al. 2003; Nakawatase and Peterson 2006). Lastly, our results suggest a role of inertia in response of vegetation to climate change. Specifically, at the macrofossil spatial scale (Fig. 6) vegetation changes are abrupt and more variable due to the role of disturbances, while greater vegetation-climate equilibrium occurs at the landscape scale, as found by Gavin et al. (2013).

4.2 Differences between simulated and reconstructed climate input data

By comparing the simulation output of different climate scenarios with the paleobotanical record, we can also test the accuracy of the climate input data. There is for instance some disagreement between the AOGCM and proxy temperature data, regarding both the magnitude and variability of temperatures since the end of the last Ice Age. The chironomid-inferred temperature reconstruction from Windy Lake (Chase et al. 2008) that we used for the proxy-scenario as well as other temperature reconstructions based on chironomid assemblages from the region (Palmer et al. 2002; Rosenberg et al. 2004), indicate a colder (ca. 2–4 °C) Younger Dryas (i.e. 12.9–11.5 ka) and a significantly warmer (up to 4 °C) Early Holocene than today (Fig. 4b). Even though the AOGCM-temperature data also shows warmer summers during the Early Holocene, the magnitude is significantly lower than in the proxy data (Fig. 4a). All of the pollen records show drastic changes in the local vegetation assemblage during the Younger Dryas – Holocene transition, in contrast to the simulations with the AOGCM-scenario. The timing of the observed changes is in agreement with the simulation output of the proxy-scenario, indicating that the AOGCM-temperature data might be underestimating the amplitude of temperature change during this time period. Other paleoclimate indicators such as alkenone-inferred sea surface temperatures (SST) from the Northern Californian Coast and off Vancouver Island also indicate a temperature increase of up to 5 °C at the beginning of the Holocene (Kienast and McKay 2001; Barron et al. 2003). There is also widespread evidence of higher-than-present treelines during the Early Holocene in Western North America (e.g. Clague et al. 1992; Mensing et al. 2012; Jiménez-Moreno and Anderson 2013). This is in agreement with the simulation driven by the proxy climate scenario, which shows timberlines ca. 200 m higher than present in the Early Holocene (Fig. S3). The higher temperature variability of the proxy scenario has a bigger effect on the simulated forests on the west side of the peninsula (Fig 5). This is in agreement with the hypothesis that forests on the wet west side are limited by temperature or more specifically by the length of the growing season, whereas forests on the dry east side are more susceptible to changes in moisture availability (Peterson and Peterson 2001).

A limitation of the climate data is that modeled and reconstructed temperature anomalies have been uniformly applied to all sites. This downscaling therefore cannot account for differences in magnitude of Holocene temperature changes among the individual sites. The maritime west side of the Olympic Peninsula probably had a smaller amount of temperature change than the east side, which is reflected in the absence of subalpine species during the Late-glacial in the paleobotanical record at the low-west site. Stability from the Late-glacial through the Holocene in hypermaritime areas of the Pacific Northwest has long been noted by paleoecologists (e.g., Hansen 1947).

4.3 Hydrological effects of snow on subalpine forests

Our results demonstrate the important control of persistent snowpack on species composition and abundance. Without the additional moisture provided by melting snow in the dry summer months, simulated conditions are too dry for mountain hemlock at the high-west site. In the rainshadow at the high-east site, the absence of snow causes a decrease in total biomass with a lowering of timberline by ca. 300 m. Evidently, conditions are too dry at higher elevations to support tree growth due to coarse talus substrates and slow soil accumulation over the millennia. This finding has important implications for the future of subalpine forests in the PNW, since climate change is projected to lead to a rise in the snowline due to warmer winters (Mote et al. 2005). Even though a total loss of winter snowpack as simulated seems unrealistic, our results still suggest dramatic changes in species composition a few hundred meters above the present snowline (ca. 800 m a.s.l.). This is also supported by the proxy-scenario, where up to 2 °C warmer winter temperatures during the Early Holocene, caused a decrease in snowpack at high elevations (Fig. 4e), which resulted in the nearly complete replacement of mountain hemlock. These simulation results are in agreement with the paleoecological records, which show a drastic decrease in mountain hemlock pollen and an absence of macrofossils during this time period (Figs. 5 and 6). Thus, reduction in snowpack in combination with shallow soils might explain the late tree establishment at the high-west site.

An effect of a changing snowpack that is not implemented in the LANDCLIM model is the impact on seedling establishment due to different growing season lengths. The twentieth century encroachment of subalpine meadows by subalpine fir and mountain hemlock in the Olympic Mountains has been attributed to a longer growing season as well as changes in snowpack (Kuramoto and Bliss 1970; Woodward et al. 1995; Ettinger et al. 2011). Also, previous modeling efforts indicate that mountain forests are sensitive to snowpack-mediated changes in growing season length (Fisher 2013). However, we feel that this process is already implicitly incorporated in the model with the current species-specific minimum requirements for growing degree-days. This is evident in that the model somewhat underestimates the present upper species limits (Figs. 2 and S1). Additionally, our results suggest that moisture availability in the dry summer months and not growing season length will be the main driver of treeline dynamics in the future.

5 Conclusions

This study affirms the importance of exploring the effects of climate change on forests with methods that consider species interactions, transient dynamics, and functional components of the climate. By comparing paleobotanical records with process-based vegetation models we

can validate the model and gain valuable insights into the drivers of species-level change in forest communities at local to regional scales. On centennial-to-millennial timescales, the main driver of forest dynamics on the wet, west side of the peninsula is temperature, whereas on the dry, east side moisture availability is more important. Generally, the dynamic vegetation model is able to simulate realistic forest dynamics under past climate change such as the frequent fire disturbance in the dry rainshadow sites and the altitudinal shift of forest zones in response to temperature changes. Discrepancies between observed and simulated vegetation serve to highlight areas of limited understanding and focus future research efforts.

About 60 % of the snow-covered area on the Olympic Peninsula has been deemed “at-risk” because minimal amounts of winter warming could convert much precipitation from snow to rain (Nolin and Daly 2006). Our results suggest that this would have pronounced effects on the species composition and distribution of mountain forests in the PNW, with a change to more drought-adapted species or even dry meadows on shallow alpine soils. Simulations of forest dynamics with future climate scenarios could assess climate change impacts, providing valuable context for the recent and ongoing changes in forest composition.

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