Published in final edited form as:

Ecol Monogr. 2017 November ; 87(4): 665–684. doi:10.1002/ecm.1272.

The impact of future forest dynamics on climate: interactive effects of changing vegetation and disturbance regimes

Dominik Thom¹, Werner Rammer, and Rupert Seidl

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

Abstract

Currently, the temperate forest biome cools the earth's climate and dampens anthropogenic climate change. However, climate change will substantially alter forest dynamics in the future, affecting the climate regulation function of forests. Increasing natural disturbances can reduce carbon uptake and evaporative cooling, but at the same time increase the albedo of a landscape. Simultaneous changes in vegetation composition can mitigate disturbance impacts, but also influence climate regulation directly (e.g., via albedo changes). As a result of a number of interactive drivers (changes in climate, vegetation, and disturbance) and their simultaneous effects on climate-relevant processes (carbon exchange, albedo, latent heat flux) the future climate regulation function of forests remains highly uncertain. Here we address these complex interactions to assess the effect of future forest dynamics on the climate system. Our specific objectives were (1) to investigate the long-term interactions between changing vegetation composition and disturbance regimes under climate change, (2) to quantify the response of climate regulation to changes in forest dynamics, and (3) to identify the main drivers of the future influence of forests on the climate system. We investigated these issues using the individual-based forest landscape and disturbance model (iLand). Simulations were run over 200 yr for Kalkalpen National Park (Austria), assuming different future climate projections, and incorporating dynamically responding wind and bark beetle disturbances. To consistently assess the net effect on climate the simulated responses of carbon exchange, albedo, and latent heat flux were expressed as contributions to radiative forcing. We found that climate change increased disturbances (+27.7% over 200 yr) and specifically bark beetle activity during the 21st century. However, negative feedbacks from a simultaneously changing tree species composition (+28.0% broadleaved species) decreased disturbance activity in the long run (−10.1%), mainly by reducing the host trees available for bark beetles. Climate change and the resulting future forest dynamics significantly reduced the climate regulation function of the landscape, increasing radiative forcing by up to +10.2% on average over 200 yr. Overall, radiative forcing was most strongly driven by carbon exchange. We conclude that future changes in forest dynamics can cause amplifying climate feedbacks from temperate forest ecosystems.

¹E-mail: dominik.thom@boku.ac.at.
Corresponding Editor: Anthony W. D'Amato.

Keywords

albedo; bark beetles; carbon sequestration; climate change; evapotranspiration; forest dynamics; iLand; Kalkalpen National Park; latent heat flux; radiative forcing; simulation modelling; wind disturbance

Introduction

Current rates of anthropogenic climate change are at the upper bounds of the scenario envelope of the latest climate change projections (Moss et al. 2010, Smith et al. 2016). The major driver of the ongoing changes in the climate system is CO₂ emissions (e.g., from industry, transportation, or deforestation; IPCC 2007). Altogether, CO₂ is responsible for 76% of the global greenhouse gas emissions, with fossil fuels and industrial processes being the most important source of greenhouse gasses (65%), followed by methane (16%), as well as deforestation and other land use change (11%; IPCC 2014). Globally, forests store ~45% of the terrestrial carbon (Bonan 2008), and take up ~33% of the carbon emitted from fossil fuels and land-use change (IPCC 2007). Without this mitigating effect of forests the ongoing climate change would be even more severe than observed.

In addition to carbon exchange with the atmosphere, albedo and latent heat flux are important for climate regulation (see, e.g., Bonan 2008, Beck et al. 2011, Naudts et al. 2016). Albedo is the fraction of short wave incoming solar radiation that is immediately reflected and not absorbed by the surface, while latent heat flux refers to the energy that is bound by the evapotranspiration of water. The climate effect of changes in albedo can be significant, especially in boreal forests, whereas the effect of latent heat flux is particularly pronounced in the tropical biome (Bonan 2008). While the overwhelming majority of studies on the role of forests in the context of climate change mitigation have focused on carbon, other climate regulating functions have been rarely addressed and remain highly uncertain (Bright et al. 2015, Thom and Seidl 2016).

The contribution of forest ecosystems to mitigate climate change is of growing interest (Locatelli et al. 2015, Keenan et al. 2016), yet, how to increase the climate change mitigation function of forests remains an active debate among scientists, practitioners, and policy makers. While forest management has been promoted as a driver for active climate change mitigation (Canadell and Raupach 2008, Lundmark et al. 2014), Naudts et al. (2016) recently suggested that past management in Europe's forests has not mitigated climate change. Another strategy discussed to mitigate climate change is to cease forest management altogether, as this will increase the carbon stored in the ecosystem (Seidl et al. 2007, Nunery and Keeton 2010). However, the rate of carbon uptake may decrease over time (Kashian et al. 2013), and a non-intervention strategy to raise carbon stocks increases the risk of carbon losses by natural disturbances (Hurteau et al. 2008). Disturbances release carbon from the biosphere to the atmosphere via fast (biomass combustion) and slow (decomposition) processes, and alter the ability of forests to take up carbon (Stuart-Haëntjens et al. 2015). For instance, fire has decreased the net carbon gain of global terrestrial ecosystems by 1.0 Pg C/yr on average over the 20th century (Li et al. 2014). Recent bark beetle infestations in the

western United States and Central Europe were found to release even more carbon than fire in these regions (Hicke et al. 2013, Seidl et al. 2014a).

Changes in climatic conditions strongly alter forest dynamics, particularly disturbance and species assembly, complicating the prediction of the future contribution of forests to climate regulation. For instance, in many temperate forest ecosystems a change from conifer-dominated ecosystems toward broadleaf-dominated ecosystems is expected (Hanewinkel et al. 2012, Thom et al. 2017a). This change not only affects the capacity of forests to store carbon but also impacts climate regulation through changes in albedo and latent heat flux. Furthermore, natural disturbances such as bark beetles (Wermelinger 2004) or wildfire (Littell et al. 2009) are sensitive to changes in temperature and precipitation, and are expected to change significantly in the future (Balshi et al. 2009, Temperli et al. 2013). Increasing disturbances will affect the climate regulation function, for instance, through a strong release of carbon (Kurz et al. 2008, Seidl et al. 2014a). However, tree species changes can dampen disturbance activity, reducing the negative effect of disturbances. Also, disturbances generally increase the albedo of a forest ecosystem and thus also have a cooling effect. The net effect of disturbance changes on climate regulation, resulting from the combined positive and negative effects on C storage, latent heat flux, and albedo, remains poorly understood to date (e.g., Landry et al. 2016), with high uncertainty about the future contribution of forests to climate regulation (see also Bonan 2008). Will forest ecosystems increase their climate regulating function when climate (and consequently tree species and disturbance regimes) are changing, or are processes such as increasing disturbances counteracting the regulating functions of forests and lead to positive climate feedbacks and a further amplification of climate change through changes in forest dynamics?

Simulation models are prime tools for studying the complex interactions between climate, vegetation, and disturbance at the landscape scale. However, in order to obtain robust projections of future trajectories under dynamically changing conditions, models need to be based on first principles, explicitly considering the mechanisms that govern ecosystem and their interactions (Gustafson 2013). Here we explore this question using a high-resolution, process-based, forest landscape model that is able to account for the dynamic interactions between climate change, tree species composition, and disturbance, in order to assess their effects on the climate system. In particular, our objectives were (1) to investigate the long-term effects of climate and vegetation change on forest disturbance regimes, (2) to quantify the response of climate regulating services to climate-mediated changes in forest ecosystem dynamics, and (3) to identify the main drivers of the future influence of forests on the climate system. Addressing these objectives is challenging, as disturbances and tree species composition (both affecting the climate regulating function of forests) interact dynamically, and are both sensitive to changing climatic conditions (Fig. 1). Following previous research we hypothesized an amplification of disturbance activity under climate change (Seidl et al. 2014a, Millar and Stephenson 2015). Furthermore, we expected an increasing share of warm-adapted broadleaved species as a result of climate change (Manusch et al. 2014), with increasing disturbances catalyzing compositional turnover (Thom et al. 2017a). As broadleaved trees are generally less prone to disturbances in Central Europe (Schelhaas et al. 2003, Thom et al. 2013), a negative, dampening feedback from compositional changes on disturbances can be expected over longer time scales (Temperli et al. 2013). Considering the

dynamic interactions between climate, disturbances, and tree species composition, we tested the hypothesis that the amplifying effect of climate change on disturbance regimes is greater than the dampening feedbacks through tree species change, expecting a net increase in disturbance activity. Subsequently, we investigated the effects of these dynamic interactions on the climate regulation function of forests. Increasing disturbances alter the carbon storage (decrease), albedo (increase), and latent heat flux (decrease) of forest ecosystems (hypothesized relationships in parenthesis; Thom and Seidl 2016). Simultaneous changes in the tree species composition toward broad-leaved forest types likewise alter climate regulation, however, considerable uncertainties remain (see also Landry et al. 2016). Generally, we expected an increase in albedo and latent heat flux as broadleaves reflect radiation more effectively (Hollinger et al. 2010), and their evapotranspiration is higher (Schume et al. 2004) compared to conifers. As our investigation focuses on a temperate forest ecosystem we expected the strongest climate change mitigation effect of forests from carbon storage, with only moderate effects from evaporative cooling and albedo (Bonan 2008). Considering the large expected impact of disturbances on carbon storage, we hypothesized that disturbances are the most important driver of the future climate regulating function. Moreover, we assumed that the carbon and evaporative cooling effect will decrease in the future, and that this decrease is only partly compensated by an increase in albedo (Fig. 1). Overall, we expected the climate regulating function of forests to decrease under climate change. All the hypotheses and effects addressed are summarized in Fig. 1.

Materials and Methods

Study area

The Kalkalpen National Park (KANP) is located in the northern front range of the Alps and covers a total area of 20,850 ha (Fig. 2). The complex terrain extends across elevations between 385 and 1963 m above sea level, and temperature and precipitation vary considerably with topography. Mean annual temperature ranges from 3.6° to 9.0°C, with mean annual precipitation sum varying between 1,205–1,741 mm (Bogner et al. 2002). The dominant soil types are shallow Lithic and Rendzic Leptosols as well as Chromic Cambisols over calcareous bedrock (Kobler 2004). KANP is accredited by the IUCN under category II (National Park), and management ceased in its core zone (89% of the total landscape area) in 1997. KANP is currently the largest contiguous forest area under strict protection in Austria. The prevailing forest types are highly representative of large parts of Central Europe, and include European beech (*Fagus sylvatica* [L.]) dominated forests at low elevations, mixed forests of Norway spruce (*Picea abies* [K.]), silver fir (*Abies alba* [Mill.]), and European beech in mid-elevations, and Norway-spruce-dominated forests in the high elevation portions of the landscape.

Simulation model

We employed iLand (the individual-based forest landscape and disturbance model) to account for dynamic feedbacks between climate (change), tree vegetation, and disturbance regimes over time. iLand is a high-resolution process-based model, designed to dynamically simulate forest landscapes. The main entities of the simulation are individual trees, and the entirety of the tree population on the landscape is modelled explicitly. The simulated forest

dynamics emerges from the interactions between trees and the underlying environmental conditions. iLand is a multi-scale model, and processes are simulated at temporal scales from days to millennia and spatial scales from 10^0 to 10^8 m² (e.g., forest floor light conditions are modeled at 2×2 m spatial resolution integrated over the year, while soil water availability, and the resulting constraints on plant growth, is updated daily at a spatial resolution of 100×100 m). Processes at the stand and landscape scale constrain the dynamics of individual trees in a hierarchical multiscale framework, and thus allow for a robust scaling of trees to large areas (Seidl et al. 2012a). For each individual tree the three main demographic processes of growth, mortality, and regeneration are simulated.

Growth—Light is the central energy source for plant growth. Competition for light is modeled based on ecological field theory in iLand (Wu et al. 1985), where the influence of a tree on its neighborhood is defined via the spatial extent and intensity of its competitive effect. This “field of light influence” depends on dynamically simulated attributes of the individual tree, such as tree species, height, and leaf area. Based on the positions of neighbors and their individual light influence a wall-to-wall index of light use is calculated for the landscape (Seidl et al. 2012a), determining the contribution of each individual tree to the absorbed photosynthetically active radiation (APAR). APAR is calculated on a grid of 100-m resolution as the fraction of global radiation that is absorbed by a stands’ leaf area following Beers law (see also Landsberg and Waring 1997, Medlyn et al. 2003). The utilizable fraction of APAR is subsequently determined by environmental constraints representing the limiting effects of climate (temperature, vapor pressure deficit) and soil conditions (soil water and nutrient availability). The contribution of each individual tree to utilizable APAR is based on its shading status (depending on tree size and local neighborhood), leaf area, and potential to utilize light (i.e., whether a tree is shade tolerant or light demanding).

Climate variables are considered on a daily time step. A process-based water balance is simulated at the stand level, considering precipitation, interception and evapotranspiration, snow storage and melting, as well as runoff of excess water. Interception is modelled following the approach of Landsberg and Gower (1997) and accounts for species-specific differences in canopy water storage potential (Seidl et al. 2005). Evapotranspiration is calculated based on the Penman-Monteith equation (Monteith 1965). Snow storage and melting follows the approach presented by Running and Coughlan (1988). The water-holding capacity of the soil is determined by effective soil depth and soil texture (Cosby et al. 1984, Schwalm and Ek 2004). As an indicator for nutrient limitation iLand uses plant-available nitrogen and applies phenomenological species-specific response functions of tree growth response to nitrogen limitation (Pastor and Post 1985). Primary production is calculated from the utilizable APAR following a light-use efficiency approach (Landsberg and Waring 1997), with the atmospheric CO₂ concentration modifying production (calculated based on a Michaelis-Menten type CO₂ response as described in Friedlingstein et al. (1995), and accounting for interactions with nitrogen and water limitations). Allocation of assimilated C to tree compartments is based on allometric relationships, and assumes priority of leaves and fine roots over stem growth. Besides environmental constraints, compartment-specific turnover rates (e.g., the senescence of needles and fine roots)

determine maintenance respiration. Furthermore, trees adapt their growth strategy dynamically to their environment, investing more resources into root growth under water- and/ or nutrient-limited conditions, and favoring height growth over diameter growth under strong competition for light.

Mortality and regeneration—The probability that an individual tree will die is linked to stress in iLand, as indicated by a tree's C balance. If a tree suffers C starvation (i.e., the respiratory demands cannot be met by the C gains from photosynthesis and the available non-structural carbohydrate reserves) its mortality probability increases (Seidl et al. 2012a). C starvation can result from harsh environmental conditions, but can also be the outcome of intense competition for resources among trees. In addition to stress-related mortality, a fraction of trees (determined based on life history traits) dies stochastically every year (Keane et al. 2001), assuming that, even in the absence of stress, only a small subset of the population is able to reach the species-specific maximum age. iLand includes process-based sub-modules for the simulation of wildfire, bark beetles, and wind disturbances. Since wind and bark beetles dominate the current (Thom et al. 2013) and future (Seidl et al. 2014a) disturbance regimes of Central Europe we here focused on these two disturbance agents and their interactions with changing climate and tree vegetation.

Wind disturbance is simulated on a spatial resolution of individual trees (Seidl et al. 2014b). iLand modifies the exposure to wind according to upwind gap size and local shelter from neighboring trees, considers soil frost as a factor improving the anchorage of trees, and includes species-specific parameters for critical wind speeds of uprooting and stem breakage. During a wind event, a sequence of steps is executed to dynamically simulate wind disturbance: (1) canopy edges are detected via height differences among grid cells with 10-m horizontal resolution, (2) the vertical wind profile is calculated at each edge, (3) gap size in the upwind direction is computed to estimate the individual tree turning coefficient, (4) critical wind speeds for uprooting and breakage are calculated, and (5) new gaps are created from uprooting or breakage of trees. These steps are repeated until the maximum event duration is reached, allowing for dynamic vegetation–disturbance feedbacks within a single event (e.g., through a growing upwind gap size or a reduced shelter from neighbors as trees are killed by wind). As gaps generally increase, the probability of wind disturbance in neighboring forests, other disturbances (such as bark beetles) potentially influence wind disturbances in the simulations. Climate change affects the simulated wind disturbances directly and indirectly via an altered soil frost regime, changes in tree species composition and forest structure, and by increased gap formation caused by other sources of tree mortality.

The bark beetle module simulates the impact of the European spruce bark beetle (*Ips typographus*) on Norway spruce (Seidl and Rammer 2016). *I. typographus* is the by far most important bark beetle species in terms of area affected and timber volume disturbed in Europe (Schelhaas et al. 2003, Seidl et al. 2009a). The module accounts for bark beetle phenology and development, determines temperature-dependent emergence and swarming, and calculates the number of beetle generations and sister broods developed per year. Dispersal of beetles from host trees is simulated spatially, with beetles actively searching for suitable hosts. Colonization considers defense capacity of trees, which is a function of the

dynamically simulated nonstructural carbohydrate reserves of the attacked tree. Beetle mortality is dependent on the time since outbreak (assuming a lagged response of the antagonist community) and on temperature limitation in winter. Outbreaks are initiated randomly via a climate-sensitive background probability, or develop from areas recently disturbed by wind, which provide large quantities of defenseless breeding material (i.e., fresh downed Norway spruce trees). Climate change has direct and indirect effects on bark beetle disturbance in iLand. Processes with a direct link to climate are, for instance, winter mortality of beetles as well as the number of generations and sister broods developing during a year. Indirect effects arise from changing tree species composition, the stress level of individual host trees and the amount of windthrown trees.

Tree regeneration depends on the availability of seeds, which are distributed through the landscape from individual mature trees via seed dispersal kernels (20×20 m horizontal resolution). Long-distance dispersal is explicitly considered in the parameterization of dispersal kernels. Environmental filters (e.g., light availability, thermal requirements) determine the probability of establishment once seeds are available at a site (Seidl et al. 2012a,b). Light availability on the forest floor is simulated at 2×2 m horizontal resolution in iLand. After successful establishment the growth and mortality of saplings up to 4 m in height is simulated in height-based tree cohorts. iLand is freely available under a GNU open source license.² The website also contains in-depth model documentation in the form of a model wiki.

Model applicability and evaluation—In the context of our research, questions about the dynamic interactions between climate (change), vegetation, and disturbances are of particular importance. iLand is well suited to address these interactions, as it considers both direct and indirect vegetation responses to climate change. For instance, temperature increases directly affect processes such as leaf phenology and the length of vegetation period, the efficiency of photosynthesis (modeled using a state acclimation approach following Mäkelä et al. 2008), and the availability of water in the soil (via altered evapotranspiration rates). Similarly, rising CO₂ levels directly affect net primary production via CO₂ fertilization. Thus, climate change might affect growth of one species differently than that of another species (direct effect), leading to a change in forest competition and structure (indirect effect). Growth changes in the simulation subsequently influence the susceptibility to wind (e.g., taller trees are increasingly at risk from blowdown) as well as the defense capacity of trees against bark beetles (via the non-structural carbohydrates available for defense).

A second crucial aspect for the current analysis is the simulation of the forest carbon cycle. iLand tracks live carbon stocks in stem, branch, foliage, coarse root and fine root pools, and also considers the C stored in tree regeneration. A closed carbon cycle is simulated by tracking C in detritus and soil pools, where the model distinguishes between decomposition of young (such as leaf and fine root litter) and old (i.e., humified organic matter) carbon components (Kätterer and Andrén 2001). Both temperature and humidity modify decomposition rates. Snags and the transition from snags to downed woody debris are

²<http://iLand.boku.ac.at>

simulated explicitly. iLand is thus well suited to address the complex and interactive effects of vegetation changes on the carbon balance of forests.

iLand is currently parameterized for 29 Central European tree species. The traits of each species are quantified via 60 species-specific parameters. Interspecific trait variability is assumed to be more important than intraspecific trait variability (Burton et al. 2017), hence homogeneous traits are assumed for trees of the same species in iLand. The model and its current parameterization were thoroughly tested in previous studies of Central European forest ecosystems. Following a pattern-oriented approach to model evaluation (Grimm et al. 2005), we compared a variety of observed patterns such as individual tree dimensions, stand-level productivity, mortality, tree responses to disturbance, and simulated potential natural vegetation composition against independent observational data (Silva Pedro et al. 2015, Seidl et al. 2017a, Thom et al. 2017b). For the specific context of the current study area, we successfully evaluated the model's capability to reproduce observed tree productivity, sensitivity to interannual climate variation, and potential natural vegetation composition at the landscape scale (see Thom et al. 2017b for details). Furthermore, specific tests were conducted to evaluate the performance of the process-based disturbance modules employed within the iLand framework. The wind disturbance module was successfully tested against independent data for storm events in Sweden (Seidl et al. 2014b) and Austria (Seidl and Rammer 2016). Furthermore, the iLand bark beetle module was successfully evaluated for the KANP by comparing simulations to independent data for a recent outbreak in the landscape (Seidl and Rammer 2016).

iLand is currently parameterized for 29 Central European tree species. The traits of each species are quantified via 60 species-specific parameters. Interspecific trait variability is assumed to be more important than intraspecific trait variability (Burton et al. 2017), hence homogeneous traits are assumed for trees of the same species in iLand. The model and its current parameterization were thoroughly tested in previous studies of Central European forest ecosystems. Following a pattern-oriented approach to model evaluation (Grimm et al. 2005), we compared a variety of observed patterns such as individual tree dimensions, stand-level productivity, mortality, tree responses to disturbance, and simulated potential natural vegetation composition against independent observational data (Silva Pedro et al. 2015, Seidl et al. 2017a, Thom et al. 2017b). For the specific context of the current study area, we successfully evaluated the model's capability to reproduce observed tree productivity, sensitivity to interannual climate variation, and potential natural vegetation composition at the landscape scale (see Thom et al. 2017b for details). Furthermore, specific tests were conducted to evaluate the performance of the process-based disturbance modules employed within the iLand framework. The wind disturbance module was successfully tested against independent data for storm events in Sweden (Seidl et al. 2014b) and Austria (Seidl and Rammer 2016). Furthermore, the iLand bark beetle module was successfully evaluated for the KANP by comparing simulations to independent data for a recent outbreak in the landscape (Seidl and Rammer 2016).

Landscape initialization and drivers

iLand requires inputs for climate, soil, and vegetation to simulate landscape dynamics. Data for climate and soil vary at the level of 100×100 m cells. We selected the period 1950–2010 as climatic baseline for our analyses, randomly sampling years with replacement to obtain a 200 yr time series for simulation. Three different combinations of global and regional circulation models under SRES A1B forcing (IPCC 2000) were used to represent transiently changing climatic conditions until the end of the 21st century, including CNRM-RM4.5 (Radu et al. 2008) driven by the global climate models (GCM) ARPEGE, and MPI-REMO (Jacob 2001), as well as ICTP-RegCM3 (Pal et al. 2007) driven by the GCM ECHAM5. Recent tests showed that these scenarios are well within the envelope of the more recent RCP scenario families, and that ecological differences between SRES and RCP scenarios were small for our study area (Thom et al. 2017a). All climate data were bias corrected by means of quantile mapping (Déqué 2007) at 1×1 km resolution using the INCA data set (Haiden et al. 2011), and statistically downscaled to 100 m cells using daily weather gradients within the study area. Beyond the year 2099, we assumed a stabilization of the climate system (Nazarenko et al. 2015), and resampled years from the period 2080–2099 with replacement to obtain a 200-yr time series (i.e., multi-year climate episodes were not explicitly considered in this extension of the climate time series beyond 2099). The period of 2080–2099 represents a temperature change of between $+3.1^\circ$ and $+3.3^\circ\text{C}$, and a precipitation change of between -89 mm and $+141$ mm relative to the baseline period.

Modelling peak wind events in climate models still remains challenging (Rockel and Woth 2007). Consequently we simulated the occurrence of strong winds probabilistically. We fitted a Gumbel distribution to past storm data for the landscape (see e.g., Cheng and Yeung 2002, Rajabi and Modarres 2008), assuming that the storm event “Kyrill” in 2007 represented the 90th percentile of peak wind speeds in the area. Subsequently, annual peak wind speeds were drawn from this distribution and used in the simulations. This approach assumes a large number of minor wind events, but also includes infrequent heavy storms (see, e.g., Gardiner et al. 2010, Panayotov et al. 2011). At the landscape scale, peak wind speeds were further modified by the effects of local topography using the Austrian Wind Atlas (Krenn et al. 2011). For each wind event the main wind direction was determined probabilistically, with 75% of the events distributed over the current main wind directions (southwest–northwest), and the remaining 25% drawn from other directions. Also the day of the year of storm occurrences was determined probabilistically mimicking past storms, with a large majority of events (75%) occurring in autumn and winter.

We utilized a 300×300 m inventory grid over KANP to quantify soil conditions on the landscape. Based on this inventory grid wall-to-wall estimates for soil depth and soil type ($n = 710$ and $n = 688$, respectively), were previously derived by Kobler (2004) using linear and logistic regression models. Soil texture surveys ($n = 622$) were aggregated by soil type and resampled over the landscape. Based on the same inventory grid, also the amount of deadwood ($n = 1,172$) in the initial year of the simulation was determined. Plant available nitrogen and initial carbon pools for litter and soil organic matter were derived from the Austrian National Forest Inventory ($n = 557$) (Seidl et al. 2009b), and imputed on the study

area by means of stratified sampling by ecoregion (as classified by Kilian et al. 1994), elevation, soil depth, aspect, and slope.

Various data source were used to obtain the current state of the vegetation at KANP as initial values for our simulations. First, we defined stand polygons (median stand size 1.4 ha) in which tree vegetation was fairly homogenous with regard to species composition and structure using aerial photography (spatial grain 10×10 m). The dominant tree height per stand polygon was derived from airborne LiDAR (Light Detection And Ranging) data (resolution 1×1 m). Subsequently, we used terrestrial inventory data for KANP ($n = 1,122$ sample plots) to determine species composition, and to estimate diameter at breast height (dbh) as well as the number of trees within each stand polygon. Whenever fewer than three sample plots were available for a stand polygon, additional plots were sampled from areas with similar species composition and dominant height. Stand age was derived from forest inventory and planning data. Moreover, LiDAR and forest inventory data were utilized to estimate the stockable area within each stand polygon, accounting for rocky areas and water bodies permanently unsuitable for tree vegetation. LiDAR data was subsequently used to determine the position of each individual tree within a stand polygon, faithfully representing the structural diversity of the current vegetation in the initial conditions for simulation. In total, we initialized more than 2×10^6 trees from 17 different species on 13,865 ha of stockable forest area. For details on the approach and data used, we refer to Thom et al. (2017a,b). The data sources used to describe vegetation conditions pertained to the late 1990s and early 2000s, with 1999 determined as the year of initialization. To accommodate recent severe disturbance events at KANP (most notably the storm Kyrill in 2007), we simulated the forest landscape from 1999 to 2013, imposing observed disturbances as documented in the spatially explicit disturbances records of KANP. Ultimately, 2013 represents the initial year for all scenario analyses presented here. To allow the migration of tree species not currently present at the landscape, we assumed a small background probability of seed dispersal from neighboring forests, with species shares determined by the forest types expected in adjacent areas.

Simulation design

Starting from the year 2013, we simulated forest development for 200 yr under the four alternative climate scenarios. As we were specifically interested in the effect of disturbances on the climate regulation function of forests (Fig. 1) we simulated three different disturbance scenarios under each climate scenario, i.e., a control scenario without disturbances (undisturbed), a scenario simulating wind and bark beetle disturbances dynamically under historic wind conditions as described above (disturbed), and an alternative disturbance scenario simulating wind and beetle dynamics assuming an increase in wind speeds by 10% in the future (disturbed+). This latter scenario reflects the finding of previous research that wind speeds could increase in Central Europe in a warming world (Beniston et al. 2007, Rockel and Woth 2007). In all disturbance scenarios, wind and bark beetle disturbances were simulated mechanistically employing the respective iLand disturbance modules. To account for stochasticity in our simulations, we ran 20 replicates per scenario combination. In total, our study encompassed 240 simulation runs (4 climate scenarios $\times$ 3 disturbance scenarios $\times$ 20 replicates). No management interventions (e.g., regular harvesting, salvage

logging) were simulated throughout the 200-yr study period. All simulations were executed on the Vienna Scientific Cluster.

Climate change impacts on disturbance regimes and forest composition

The application of a fully dynamic simulation approach allowed us to investigate the long-term impacts of climate change on natural disturbance regimes and forest composition over space and time. The ecological significance of disturbances depends on the extent and severity of disturbances as well as on the recovery rate of ecosystems (Turner et al. 1993). Consequently, we here report disturbance impacts in terms of forest area and growing stock, and used the ratio between disturbance rate (percent of growing stock disturbed) and volume increment as a measure of recovery capacity.

We attributed the overall effect of climate change to direct effects (i.e., unmediated responses of ecological processes to changes in temperature and precipitation) and indirect effects (i.e., changes in processes that are brought about by climate influencing other processes, which in turn alter the focal process; Bentz et al. 2010, Liu and Wimberly 2016, Seidl et al. 2017b). Specifically, we assessed the direct impact of climate change on the extent of disturbed area and tree species composition, respectively. Subsequently, we also quantified indirect effects resulting from their interactions (e.g., an increased species turnover due to increased disturbance activity, and/ or a reduction in disturbances due to a decreasing share of disturbance-prone conifers, cf. Fig. 1). Using the undisturbed scenario as control allowed us to quantify the effect of disturbances on tree species change directly. However, the reciprocal effect, i.e., how tree species change affects disturbance activity, cannot be directly inferred from our simulations, as climate change affects species composition and disturbances simultaneously in iLand. We thus used machine learning to quantify this effect, fitting a random forest (Breiman 2001) to the simulation data in order to synthesize the effect of changing shares of broadleaved species on disturbance activity. We used disturbed area as response variable in this analysis, and broadleaved share, climate variables (temperature, precipitation, wind speed, and the number of wind events) as well as basal area (as a proxy for stand developmental stage) as predictors, acknowledging that drivers other than tree species composition also influence the disturbance regime. Random forest is a powerful, non-parametric, supervised learning technique for identifying key variables and explaining complex ecological processes (Cutler et al. 2007). It combines a group of weak learners (individual classification trees) in an ensemble approach to form a strong learner (a random forest based on all classification trees). We used the R language and environment for statistical computing (R Development Core Team 2016), and specifically employed the `tuneRF()` function of the `randomForest` package (Breiman and Cutler 2015) to determine the best model. We then fitted the model incorporating 2000 regression trees. Subsequently, the random forest model was used to quantify the effect of an increase in broadleaved trees on disturbances under climate change, while controlling for changes in other covariates of disturbance change.

Radiative forcing

Forests play an important role in the regulation of the world's climate, not only by storing and releasing large amounts of carbon, but also via biophysical processes that alter the

energy balance of the Earth's surface. Despite their very different physical foundations, the three climate regulating functions considered here can be converted to a common currency, referred to as radiative forcing (RF). RF describes a change in the planetary energy budget, i.e., the difference between the incoming insolation absorbed by the earth's surface and the outgoing energy reflected back to space (Hansen et al. 1997). The convention used here is that positive values of RF describe a net positive energy balance at the surface of the earth resulting in a warming effect, while negative values refer to a cooling effect.

We analyzed the climate regulating function of the forests at KANP by quantifying the effect of changes in carbon stocks, surface albedo, and latent heat flux on radiative forcing. An important difference between these three factors is that the effect of albedo and latent heat flux are effective locally and in the short-term, whereas the carbon effect on the atmosphere is global and long-term: Due to atmospheric mixing and long residence times CO₂ is an effective greenhouse gas even years after the initial emission.

We derived the total radiative forcing R_T by additively combining the contributions of changing carbon stocks (R_C), surface albedo (R_A), and latent heat flux (R_L) for each year in each simulation run ($n = 240$; see Eqs. 2–6 for definitions of R_C , R_A , and R_L)

$$R_T = \Delta R_C + R_A + R_L \quad (1)$$

Carbon—The carbon effect is based on the net exchange of carbon between the forest and the atmosphere and can be derived from first principles (Kirschbaum et al. 2011). Absorbed or released carbon alters the CO₂ concentration in the atmosphere and causes a change in radiative forcing. The radiative forcing for changes in atmospheric carbon R_M per day and square meter ground surface (J·m⁻²·d⁻²) can be expressed as follows:

$$\Delta R_M = 86,400 \times 5.35 \times \ln \left(1 + \frac{\Delta C_t / 2.123 \times 10^9}{\text{CO}_2} \right) \quad (2)$$

with C_t the absolute difference in atmospheric carbon at year t (Mg C), CO₂ the background atmospheric CO₂ concentration (ppm), 2.123×10^9 the conversion of C to ppm CO₂, 5.35 the conversion factor from CO₂ to radiative forcing (W/m²), and 86,400 the number of seconds per day.

In order to calculate the total radiative forcing effect in GJ/yr, R_M needs to be multiplied with the surface area of the Earth and the number of days per year

$$\Delta R_C = \Delta R_M \times 510 \times 10^{12} \times 365/10^9 \quad (3)$$

where R_C is the total radiative forcing of additional atmospheric carbon (GJ/yr), 510×10^{12} m² is the surface area of the Earth, 365 is the number of days per year, and 10^9 the conversion between J and GJ. Based on Eq. 3 the total annual radiative forcing of one

additional ton of carbon in the atmosphere is approximately $104 \text{ GJ} \cdot \text{Mg C}^{-1} \cdot \text{yr}^{-1}$ (Kirschbaum et al. 2011).

We derived the net exchange of carbon between the biosphere and the atmosphere from the net ecosystem carbon balance (NECB) simulated by iLand. NECB is the total net change across all carbon pools of the ecosystem, i.e., NECB includes changes in above- and below-ground carbon of living and dead biomass (Chapin et al. 2006). Since negative NECB designates a net flux of carbon toward the atmosphere, the total stock change in atmospheric carbon originating from the study area can be calculated by summing up NECB over time

$$\Delta C_t = - \sum_{i=1}^t \text{NECB}_i \quad (4)$$

with C_t the cumulative change of atmospheric carbon at year t (Mg C/ha), and NECB_i the net ecosystem carbon balance (Mg C/ha) of the year i .

Albedo—A reduction in albedo, e.g., by extending the snow-free period in winter or by a change in the tree species composition from broadleaves to conifers, leads to higher levels of absorbed energy (i.e., a decrease in negative radiative forcing from albedo). We used crown cover (at 10 m horizontal resolution) and species composition simulated dynamically in iLand to derive the effective albedo of the landscape. We accounted for canopy gaps, open areas from disturbance, and species-specific differences in albedo using the parameters suggested by Shuman et al. (2011) and Kuusinen et al. (2013; Table 1). We did not differentiate the albedo of the vegetation by season, as differences in parameters between seasons are generally small (Kuusinen et al. 2013), and a predetermined differentiation between seasons is of limited value under climate change, as the length of the growing season changes in response to climate. Rather, we explicitly accounted for days when snow covers tree crowns or the forest floor, as snow cover increases albedo considerably (Table 1). iLand dynamically simulates snow pack at 100 m horizontal resolution, and albedo parameters were changed from vegetation to snow whenever the simulated snowpack was >0 cm.

To convert the albedo effect into an average radiative forcing per hectare, we adopted the approach of Kirschbaum et al. (2011)

$$R_A = - (1 - 0.2) \cdot 10,000 \cdot \sum_{i=1}^{365} \text{rad}_i \times \begin{cases} \text{sp} > 0 : A_S \\ \text{sp} = 0 : A_V \end{cases} \quad (5)$$

where R_A is the radiative forcing from albedo ($\text{GJ} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$), rad_i is the incoming shortwave radiation ($\text{GJ} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$), 0.2 is the proportion of short-wave radiation absorbed by the atmosphere, 10,000 is the number of square meters in a hectare, sp the height of the snowpack (cm), and A_V and A_S are the albedo parameters for days without (A_V) and with snow (A_S), respectively. Please note that R_A is always negative, since the reflection of radiation reduces the energy balance of the surface.

Latent heat flux—Latent heat flux arises from the evapotranspiration of the canopy or the ground surface of forest ecosystems, and constitutes an energy flux from the surface to the atmosphere (evaporative cooling), resulting in a negative radiative forcing (Bonan 2008). iLand calculates evapotranspiration per hectare at daily time step using the Penman-Monteith equation (Monteith 1965) and we here used annual aggregates to convert evapotranspiration to radiative forcing

$$R_L = - \left(ET \times \frac{2.45}{1,000} \right) \quad (6)$$

where R_L is the radiative forcing from the latent heat flux ($\text{GJ} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$) per year, ET is the evapotranspiration ($\text{mm} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$), 2.45 MJ/kg is the latent heat of vaporization of water (e.g., Pereira 2004, Grodsky et al. 2009), and $1,000$ is the factor to convert MJ to GJ .

In addition to the effect of evaporative cooling, water in the atmosphere also has other effects on the climate system. For instance, atmospheric water vapor influences cloud formation, which can have both warming (via absorption of long wave radiation emitted from the surface and reflection back to the surface) and cooling (due to reflection of incoming solar radiation) effects (Kiehl and Trenberth 1997). Such complex indirect effects of water vapor on the earths' energy balance were not considered here.

Drivers of radiative forcing—In addition to quantifying radiative forcing under different future climate and disturbance scenarios, we were interested in attributing changes in R_T to the main drivers influencing the climate regulation function of forests. Based on Eq. 1–6, we expected that tree species composition (and specifically the share of broadleaved trees), disturbed area, and the number of days with snow cover all influence R_T . The contribution of each factor is, however, again affected by the complex interactions between climate, vegetation, and disturbance (Fig. 1). The net ecosystem productivity (NEP) of broadleaf-dominated temperate forests is generally lower than that of conifer-dominated forest (Bonan 2008), but broadleaves are associated with higher albedo (Hollinger et al. 2010) and higher evapotranspiration (Schume et al. 2004). Disturbances release carbon from the biosphere to the atmosphere (Kurz et al. 2008) and reduce evapotranspiration, but also increase albedo (Beck et al. 2011). Snow cover strongly increases albedo (Hollinger et al. 2010), but changes dynamically with climate change.

We assumed a linear relationship between radiative forcing and its explanatory variables. In order to consistently attribute changes in radiative forcing to individual drivers while controlling for multicollinearity, we used principle component regression (PCR). Each explanatory variable was standardized by subtracting the mean and dividing by the standard deviation. The standardized variables ($n = 240$) were used in a principal component analysis (PCA), which transforms predictors into orthogonal factors. Subsequently, the factors were regressed onto the response variable (here the average R_T over the 200-yr study period). In order to prevent overfitting, we reduced the number of principal components by applying the Kaiser criterion (Ford et al. 1986). Consequently, the final model contained only one principal component, which was subsequently regressed against R_T . The loadings of the

PCA were used to re-transform the regression coefficients of the PCR into the original units of each variable. The thus-obtained regression coefficients can be interpreted as the sensitivity of R_T to standardized changes (i.e., changes in units of standard deviation) in the covariates.

Results

Trajectories of forest development under climate change

All scenarios resulted in an increase in growing stock at KANP during the first 60–90 yr of the simulation (Fig. 3), as the landscape recovered from past forest management (prior to the establishment of the national park in 1997) and recent strong disturbance events (most notably the storm Kyrill in 2007 and the following bark beetle outbreak). The growing stock at the end of the simulation period was on average highest under the hypothetical reference scenario, assuming baseline climate and undisturbed forest development (609.8 m³/ha), and lowest under climate change (mean over all climate change projections) and increased peak wind speeds (484.8 m³/ha). Climate change and disturbances generally had a negative impact on growing stock in all simulated scenarios. Growing stock decreased by –40.4 m³/ha (–6.6%) on average as a result of climate change. Disturbances induced a reduction in growing stock ranging from –83.2 m³/ha (disturbed scenario) to –123.1 m³/ha (disturbed+ scenario) under baseline climate (–13.6% to –20.2%), and from –66.1 m³/ha to –84.6 m³/ha under scenarios of climate change (–11.6% to –14.9%).

Decreasing levels of growing stock under climate change were accompanied by an increase in European beech at the expense of Norway spruce. In all scenarios except the baseline runs, European beech became the most prevalent tree species at KANP. The speed of species turnover from Norway spruce to European beech was accelerated by natural disturbances. Tree species other than European beech and Norway spruce are currently present only on a relatively minor portion of the landscape, and a projection period of 200 yr was not sufficient for those species to greatly increase their abundance (see also Thom et al. 2017a). However, trends in species change were also visible for species beyond spruce and beech. While European larch (an early-seral species favored by past forest management) decreased in all scenarios, silver fir (a late-seral species negatively affected by past forest management) increased. Moreover, with climate change Scots pine and sessile oak became more prominent, especially when disturbances were considered in the simulation.

Spatiotemporal trajectories of disturbance

Our simulations revealed diverging disturbance activity under baseline climate and changed climatic conditions (Fig. 4). While the total cumulative area affected by wind disturbance remained relatively stable during the first century of the analysis regardless of scenario, changes in forest composition and structure resulted in decreasing wind disturbance activity in the second century of the simulation under climate change. This trend was most distinctive for the disturbed+ scenario, which also experienced the largest turnover of species (Fig. 3). Consequently, in the disturbed+ scenario, the cumulative area disturbed by wind over 200 yr of baseline climate exceeded the area disturbed by wind under climate change conditions by +42.6% (+1,280.5 ha; Fig. 4). A negative vegetation feedback on

disturbances under climate change was also evident for bark beetles, where the amount of disturbed area first increased strongly, but then leveled off after approximately 150 simulated years. However, the total area disturbed by bark beetles was +90.2% (+2,158.6 ha; disturbed) and +63.4% (+2,045.4 ha; disturbed+) higher under climate change compared to baseline climate conditions. While the net effect of climate change on the total amount of disturbed area was between +29.0% (+1413.4 ha; disturbed) and +10.2% (+764.9 ha; disturbed+) after 200 yr, an increase in peak wind speeds (disturbed+) had an even more pronounced impact on disturbance activity with an increase of +54.0% (+2,632.9 ha; baseline climate) and +31.5% (+1,984.4 ha; climate change) compared to simulations with current wind speeds (scenario disturbed). The combined effects of disturbances from wind and bark beetles correspond to a disturbance rate of 0.18% per yr (disturbed) and 0.23% per yr (disturbed+) of the landscape under baseline climate, and 0.27% per yr (disturbed) as well as 0.30% per yr (disturbed+) on average over the climate change scenarios.

While disturbance activity markedly differed between baseline climate and climate change scenarios, the spatial distribution of disturbances on the landscape remained similar, with only a weak indication for an upward shift in elevation of disturbances (Fig. 5). This conservation of spatial patterns was, however, the result of diverging and compensatory trends in disturbances from the two agents, with bark beetles shifting upward in elevation while wind disturbances decreasing in exposed higher elevation areas (Fig. 5, Appendix S1: Figs. S1, S2). Bark beetles are thermally limited in their development in the higher reaches of KANP under baseline climate, and largely affect low- to mid-elevation zones, where they are limited by host availability, as spruce share increases with elevation. Under climate change, the thermal limitations for beetle development are alleviated and an expansion into spruce-dominated higher elevation reaches of the landscape is possible. Wind disturbance, on the other hand, generally decreased with climate change, as a result of the most wind-prone tree species Norway spruce being outcompeted by other species (Fig. 3), or being killed by the expanding bark beetles. Changes in peak wind speeds did not alter the spatial distribution of disturbances from both agents (Fig. 5, Appendix S1: Figs. S1, S2).

Disturbance severity was less strongly affected by climate change than the overall area disturbed. Sites with high disturbance severity (>50% of growing stock killed by wind or bark beetles) were generally rare, and decreased under climate change. Under baseline climate they amounted to 0.3% of the landscape area in the disturbed scenario (1.4% in the disturbed+ scenario), and decreased to 0.1% (0.4%) under climate change. However, the area only marginally affected by disturbances (severity of <1%) also decreased under climate change, from 9.8% of the landscape under baseline climate (5.3% in the disturbed+ scenario) to 6.7% (4.7%) under climate change. The median disturbance severity over the entire landscape was 5.9% (disturbed) and 10.6% (disturbed+) under baseline climate, and increased with climate change to 7.8% (disturbed) and 11.1% (disturbed+).

Disturbance impacts not only depend on the extent and severity of disturbance but also on the ability of the system to recover. In this regard, our simulations showed that hotspots of disturbance impacts, i.e., areas where the regrowth is low relative to the amount of disturbed growing stock, are located particularly at high elevations (Appendix S1: Fig. S3). These patterns of disturbance effects remained consistent also in a changing climate, indicating that

changes in the relation between disturbance patterns and the capacity to recovery did not differ substantially across climate scenarios.

Dynamic feedbacks between species composition and disturbances under climate change

We disentangled the direct (e.g., temperature, precipitation, CO₂) and indirect effects (i.e., feedbacks between disturbance activity and tree species composition) of climate change on forest dynamics at KANP based on simulation modeling and random forest analysis (Fig. 6, upper panel). In total, at the end of the 200-yr simulation period, the direct effect of climate change on the natural disturbance regime resulted in an increase in disturbed area of +1,716.9 ha (+27.7% relative to baseline climate). This climate-induced increase in disturbances also caused the share of broadleaved tree species to increase by +13.3 percentage points. This indirect climate change effect on species composition via disturbance change was of similar magnitude as the direct effect of climate on the share of broadleaves (+14.7 percentage points). In turn, the change in tree species composition mitigated 36.6% of the direct climate change effect on disturbances. However, even when accounting for the dampening feedbacks from tree species change, the cumulative area disturbed increased by +17.6% (+1,089.1 ha) under climate change, relative to baseline climate.

Changing provisioning of climate regulation services

Climate-induced changes in forest dynamics affected the provisioning of climate regulation services via multiple pathways. On average over the 200 yr of simulation, the share of broadleaved trees increased between +6.3 (undisturbed) and +8.3 (disturbed+) percentage points. The area disturbed also increased under climate change, on average by +11.1% (disturbed+) to +27.8% (disturbed) compared to baseline climate conditions. Conversely, the number of days with snow cover per year was reduced by 53 d (Table 2). These changes had a distinct impact on the climate regulating functions of forests (Table 3). On average over the simulation period, climate change reduced NECB between −19.8% (disturbed+) and −28.7% (undisturbed), resulting in a reduction of carbon stocks at the end of the simulation period of between −3.9% (disturbed+) and −7.3% (undisturbed) compared to simulations under baseline climate (Appendix S1: Figs. S4, S5). Climate change decreased albedo on the landscape by between −11.9% (disturbed) and −12.4% on average over the simulation period. At the same time evapotranspiration increased by +16.4% (undisturbed) to +20.5% (disturbed+). Relative to the undisturbed reference run disturbances increased albedo only slightly by +1.7% (disturbed) and +2.8% (disturbed+) under historic climate, and by +2.2% (disturbed) and +3.1% (disturbed+) under climate change. Disturbance impacts on evapotranspiration followed a similar pattern, increasing the latent heat flux by between +4.0% (baseline climate, disturbed) and +9.7% (climate change, disturbed+) over the 200-yr simulation period.

Aggregating the individual changes in NECB, albedo, and latent heat flux into the net climate regulation effect as expressed by radiative forcing (Table 3), our results indicate a cooling effect of future forest development at NPKA (i.e., a decrease in radiative forcing) in all scenarios studied (Fig. 7). This decrease in radiative forcing mainly resulted from a distinct increase in carbon stocks during the first decades of the study period (Appendix S1:

Fig. S4). Climate change impacts on forest dynamics have an amplifying effect on climate change, as indicated by an increase in radiative forcing by between $+1,564.4 \text{ GJ}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ (disturbed+) and $+1,765.2 \text{ GJ}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ (undisturbed) on average over the simulation period compared to baseline climate. The relative increase in radiative forcing as a result of climate change varied between $+9.4\%$ (disturbed+) and $+10.2\%$ (disturbed). Similarly, disturbances reduced the cooling effect of forests and increased radiative forcing by $+847.3 \text{ GJ}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ (disturbed) and $+1,446.2 \text{ GJ}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ (disturbed+) under baseline climate ($+4.9\%$ and $+8.7\%$, respectively), as well as by $+842.9 \text{ GJ}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ (disturbed) and $+1,245.4 \text{ GJ}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ (disturbed+) under climate change ($+5.4\%$ and $+8.2\%$, respectively). Although changing climate and disturbance regimes had a net negative effect on the climate regulation function of forests (i.e., caused an increase in radiative forcing), the underlying factors contributing to changes in radiative forcing varied considerably (Fig. 6, lower panel, and Appendix S1: Fig. S6). While changes in carbon stocks and albedo increased mean radiative forcing as a result of climate change ($+1,441.1$ and $+725.1 \text{ GJ}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$, respectively), latent heat flux reduced radiative forcing under climate change ($-469.5 \text{ GJ}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$), and thus compensated 21.7% of the changes in carbon and albedo. Disturbances decreased the radiative forcing from both albedo and latent heat flux (-138.1 and $-189.9 \text{ GJ}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$), but increased radiative forcing from NECB ($+1,397.9 \text{ GJ}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$). Consequently, disturbance-induced changes in albedo and latent heat flux compensated 23.5% of the radiative forcing effects of NECB losses.

We subsequently analyzed the drivers of changes in radiative forcing by means of PCR to determine the relative influence of different factors (Table 4). Overall, PCR explained 54.5% of the variance in radiative forcing. The share of broadleaved trees was found to be the most important driver of changes in radiative forcing (22.1% of variance explained), followed by the area disturbed (18.6% of variance explained), and days with snow cover (13.8% of variance explained). An increase in the share of broadleaved trees by one unit of standard deviation (i.e., 5.2 percentage points) alters radiative forcing by $+396.1 \text{ GJ}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$. An increase in disturbed area by one unit of standard deviation (i.e., $+0.12\%$ of the total area) has a slightly lower positive impact on radiative forcing by $+332.0 \text{ GJ}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$, while an equivalent increase in snow cover days (i.e., 25.1 d) reduced radiative forcing by $-247.7 \text{ GJ}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$.

Discussion

Forest disturbance dynamics in a changing world

Our analysis revealed strong alterations of the current species composition and disturbance regime under climate change, with implications for the provisioning of climate regulating services and the potential for amplifying climate feedback. Our results generally support the hypothesized climate change-induced increase in disturbance activity (Bentz et al. 2010, Liu et al. 2010, Weed et al. 2013, Seidl et al. 2014a, 2017b, Millar and Stephenson 2015), but also revealed dynamic downregulation of disturbance changes over time. Increasing disturbances during the first century of the simulation were mainly driven by amplified bark beetle activity. Warming increases the number of generations and decreases winter mortality, boosting beetle population dynamics (Wermelinger 2004, Kausrud et al. 2012). However, bark beetle disturbances were reduced over the second century of the simulation (Fig. 3),

with changes in the tree species composition causing a decrease in host availability on the landscape. Additionally, tree species changes dampened the pronounced interaction effect between wind and bark beetle disturbances (Pasztor et al. 2014, Seidl and Rammer 2016). Changes in climatic conditions not only modified the amount but also the spatial distribution of bark beetle disturbances, shifting beetle activity toward high elevational zones of the National Park (Appendix S1: Fig. S1). This is consistent with previous research, suggesting that disturbances from *Ips typographus* will substantially shift in elevation and latitude under climate change (Jönsson et al. 2009, Hlásny et al. 2011).

Conversely, changes in temperature and precipitation did not significantly affect wind disturbance, which primarily responded to different peak wind speeds (scenarios disturbed and disturbed+). While there was a negligible direct effect of warming on wind during the first century, decreasing shares of Norway spruce during the second century dampened the susceptibility of forests toward wind (see also Valinger and Fridman 2011, Pasztor et al. 2015). Overall, we found amplifying direct effects of climate change to dominate the disturbance regime over the coming decades, with long-term dampening via indirect climate change effects of tree species change (Fig. 6, upper panel; see also Seidl et al. 2017b). This suggests a long-term adaptation of forest ecosystems to changing disturbance regimes, and underlines the importance of accounting for both direct and indirect effects in the prediction of future trajectories of forest disturbance (see also Temperli et al. 2013). However, it has to be noted that we here focused on the agents dominating the current disturbance regime and did not consider the emergence of new disturbance agents. Climate change could, for instance, increase the importance of wildfires also in Central Europe (Zumbrunnen et al. 2012), or could facilitate the spread of invasive alien pest species (Walther et al. 2009), which could both substantially alter future disturbance regimes.

Climate feedbacks from altered forest dynamics

Following Bonan (2008), we expected a strong climate change mitigation effect from increasing carbon storage, a moderate mitigating effect from greater evaporative cooling, and a moderate amplifying effect from reduced albedo in temperate forest under global warming. Our results support these expectations for evapotranspiration and albedo change, but we found an opposing trend with regard to carbon uptake under climate change. Overall, our study does not support the hypothesis of an increased climate regulation function of temperate forests under climate change as a result of increasing productivity (Bonan 2008). Instead we found positive climate–vegetation feedbacks, i.e., climate effects amplifying climate change through a reduction in the mitigating effect of forest vegetation. Both direct and indirect effects of climate change had a net amplifying effect on climate change at the end of the simulation period, due to decreases in NECB (+28.7% in radiative forcing of undisturbed and +44.1% in the disturbed scenarios) and albedo (+16.3% in radiative forcing of the undisturbed and +13.4% in the disturbed scenarios; Fig. 6, lower panel). Only increasing latent heat flux indicated a stronger cooling effect of the atmosphere under climate change compared to baseline climate (−12.5% in radiative forcing of the undisturbed and −18.7% in the disturbed scenarios). As the effects of C exchange between the vegetation and the atmosphere strongly dominated the alteration of the climate regulation function at KANP, we found a net increase in the radiative forcing as a result of climate change. This

finding of the overarching importance of the carbon cycle for the variation of the climate regulation function of temperate forest ecosystems is in line with previous findings (Schwaab et al. 2015, Landry et al. 2016), but contrasts with recent analyses suggesting a high importance of albedo and latent heat flux in Europe's forests (De Wit et al. 2014, Naudts et al. 2016). Overall, the amplifying effect of climate change via a reduced climate regulation function of forests found here may imply that current climate models underestimate the rate of climate change, as they do not account for the climate change feedbacks from changing forest dynamics (Moss et al. 2010, Carvalhais et al. 2014).

Our study demonstrates the potential of applying a high-resolution process-based model to account for the complex feedbacks between climate, vegetation, and disturbance. Approaches such as dynamic global vegetation models (Bonan 2008) or species distribution models (Hanewinkel et al. 2012) often neglect important processes and feedbacks such as the dampening effect from changing vegetation on disturbance impacts over time (see also Seidl et al. 2017b), which could bias the assessment of future forest ecosystems and associated benefits to society. However, detailed and fully dynamic approaches such as the one applied here are currently not able to address extended spatial scales from the continent to the globe. Future efforts should thus focus on new approaches to scaling ecosystem dynamics (see, e.g., Luo and Weng 2011), in order to account for complex feedbacks and interactions between climate, vegetation, and disturbance also at the large scales of relevance for the global climate system. A limitation of our study in this latter context was the exclusion of complex atmospheric processes, i.e., we did not account for fluctuating residence times of carbon (Carvalhais et al. 2014) or cloud formation as a result of increasing moisture in the atmosphere (Maness et al. 2013). Furthermore, challenges also remain for understanding the climate regulating function of forests at the local scale. For instance, we found that changes in days with snow cover had a stronger impact on forest albedo than climate-change-induced modifications of the tree species composition. However, forest structure and composition is itself affecting the distribution and duration of snow cover (Musselman et al. 2008, Varhola et al. 2010), an effect that was not explicitly included here. More research is thus needed to develop a comprehensive understanding of how forests interact with climate (Bonan 2008, Becknell et al. 2015).

Overall, radiative forcing from our study system was negative under all scenarios, i.e. the landscape is likely to counteract climate change over the next 200 yr. Largely responsible for this effect was the ongoing long-term recovery from past land-use, which is reflected in the large amounts of carbon uptake during the first decades of the simulation. As many European forests, both managed and unmanaged, are currently bouncing back from past exploitation (e.g., Bebi et al. 2017) this finding has at least two major implications for climate regulation studies in forest ecosystems: (1) the chosen reference condition (here: the state of the forest in the year 2013) is of decisive importance for the sign and strength of the climate regulation effect (see also Nabuurs et al. 2013, Naudts et al. 2016), and (2) historical land-use and disturbances need to be considered explicitly in future works to disentangle legacy effects of the past from emerging effects of future climate and disturbance regimes (see also Bürgi et al. 2017).

Implications for climate change mitigation

The improvement of climate regulation services is of increasing interest in forest ecosystem management and forest policy, but has largely focused on the carbon effect of forests to date (Bright et al. 2015). Increasingly, the effects of changes in albedo and latent heat flux are also considered in scientific analyses (see e.g., O'Halloran et al. 2012, Rydsaa et al. 2015, Naudts et al. 2016), yet high uncertainty remains regarding their relative importance, and their sensitivity to changing climate and disturbance regimes. Our dynamic long-term simulations confirm the importance of changes in carbon storage for temperate forest ecosystems, but also indicate that albedo and latent heat flux need to be considered in order to obtain a comprehensive assessment of radiative forcing from forest ecosystems (see also Bonan 2008). Understanding the relative contributions of these forest functions on climate regulation is important to develop optimal solutions for climate change mitigation. Ideally, forests would sequester and store high amounts of carbon, reflect solar radiation, and sustain a high rate of evapotranspiration at the same time. As these functions cannot be maximized simultaneously, it is important to quantify trade-offs, and understand the effects of the underlying processes of forest dynamics (which can be altered via management, such as modifying species composition and disturbance risk). In contrast to our expectation, disturbances were only the second most important driver of changes in radiative forcing, with changes in forest composition having an even greater influence on climate regulation.

The dense, conifer-dominated forests that are currently wide-spread in Central Europe store large amounts of carbon, which, based on our analyses, are likely to overcompensate their lower albedo and evapotranspiration relative to forest types dominated by broadleaved trees. Past increases in conifers in the area might thus have contributed to climate change mitigation. However, as demonstrated in our simulations, these forests are also highly susceptible to disturbances, particularly from bark beetles (see also Seidl et al. 2011, Thom et al. 2013), and future extreme events could quickly release large amounts of the stored carbon back to the atmosphere (Körner 2003). An option that balances the trade-offs between capacity and risk and optimizes forest functions regarding climate regulation could be mixed forests of coniferous and broadleaved trees. Species-rich mixed forests have recently been shown to be more productive than forests dominated by only a few number of tree species (Liang et al. 2016). At KANP, for example, mixed spruce–fir–beech forest types are the current natural vegetation in mid elevations. These ecosystems are among the most productive ones in Central Europe and can store high amounts of carbon (Erb 2004), while their considerable share of beech and other broadleaved species can increase albedo and evapotranspiration (see, e.g., Bonan 2008, Kuusinen et al. 2013). Mixed forests have also been shown to reduce the susceptibility to bark beetle outbreaks (Overbeck and Schmidt 2012), and mitigate the impact of disturbances on the C cycle (Silva Pedro et al. 2015). In conclusion, our findings suggest that a careful combination of site- and climate-adapted tree species in mixed forests has the potential to minimize the trade-offs between carbon storage and sequestration, albedo, and evapotranspiration, and thus to maximize the climate regulating function of forests in the future.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

This study was supported by the Austrian Science Fund FWF (grants P 25503-B16 and Y895-B25), and the Austrian Climate and Energy Fund ACRP (grant KR14AC7K11960). The simulations presented here were conducted at the Vienna Scientific Cluster (VSC). We thank two anonymous reviewers for helpful comments on an earlier version of this work.

Literature Cited

- Balshi MS, McGuire AD, Duffy P, Flannigan M, Walsh J, Melillo J. Assessing the response of area burned to changing climate in western boreal North America using a Multivariate Adaptive Regression Splines (MARS) approach. *Global Change Biology*. 2009; 15:578–600.
- Bebi P, Seidl R, Motta R, Fuhr M, Firm D, Krumm F, Conedera M, Ginzler C, Wohlgemuth T, Kulakowski D. Changes of forest cover and disturbance regimes in the mountain forests of the Alps. *Forest Ecology and Management*. 2017; 388:43–56. [PubMed: 28860675]
- Beck PSA, Goetz SJ, Mack MC, Alexander HD, Jin Y, Randerson JT, Lorant MM. The impacts and implications of an intensifying fire regime on Alaskan boreal forest composition and albedo. *Global Change Biology*. 2011; 17:2853–2866.
- Becknell JM, et al. Assessing interactions among changing climate, management, and disturbance in forests: A macrosystems approach. *BioScience*. 2015; 65:263–274.
- Beniston M, et al. Future extreme events in European climate: An exploration of regional climate model projections. *Climatic Change*. 2007; 81:71–95.
- Bentz BJ, Régnière J, Fettig CJ, Hansen EM, Hayes JL, Hicke JA, Kelsey RG, Negrón JF, Seybold SJ. Climate change and bark beetles of the western United States and Canada: direct and indirect effects. *BioScience*. 2010; 60:602–613.
- Bogner M, Lehner T, Mahringer G. Das meteorologische Messnetz im Nationalpark Kalkalpen, Oberösterreich. Flächendeckende Erfassung und Auswertung von Niederschlag, Temperatur und Strahlung / Le réseau de mesures météorologiques dans le Parc national des Kalkalpen, Haute Autriche. Précipitations, températures, rayonnement: répartition spatiale et évaluation. *Revue de Géographie Alpine*. 2002; 90:61–72.
- Bonan GB. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science*. 2008; 320:1444–1449. [PubMed: 18556546]
- Breiman L. Random forests. *Machine Learning*. 2001; 45:5–32.
- Breiman, L., Cutler, A. Package randomForest; 2015. p. 1–27. <https://www.stat.berkeley.edu/~breiman/RandomForests/>
- Bright RM, Zhao K, Jackson RB, Cherubini F. Quantifying surface albedo and other direct biogeophysical climate forcings of forestry activities. *Global Change Biology*. 2015; 21:3246–3266. [PubMed: 25914206]
- Bürgi M, Östlund L, Mladenoff DJ. Legacy effects of human land use: Ecosystems as time-lagged systems. *Ecosystems*. 2017; 20:94–103.
- Burton JJ, Perakis SS, McKenzie SC, Lawrence CE, Puettmann KJ. Intraspecific variability and reaction norms of forest understory plant species traits. *Functional Ecology*. 2017; doi: 10.1111/1365-2435.12898
- Canadell JG, Raupach MR. Managing forests for climate change mitigation. *Science*. 2008; 320:1456–1457. [PubMed: 18556550]
- Carvalhais N, et al. Global covariation of carbon turnover times with climate in terrestrial ecosystems. *Nature*. 2014; 514:213–217. [PubMed: 25252980]
- Chapin FS, et al. Reconciling carbon-cycle concepts, terminology, and methods. *Ecosystems*. 2006; 9:1041–1050.

- Cheng E, Yeung C. Generalized extreme gust wind-speeds distributions. *Journal of Wind Engineering and Industrial Aerodynamics*. 2002; 90:1657–1669.
- Cosby BJ, Hornberger GM, Clapp RB, Ginn TR. A statistical exploration of the relationships of soil moisture characteristics to the physical properties of soils. *Water Resources Research*. 1984; 20:682–690.
- Cutler DR, Edwards TC, Beard KH, Cutler A, Hess KT, Gibson J, Lawler JJ. Random forests for classification in ecology. *Ecology*. 2007; 88:2783–2792. [PubMed: 18051647]
- De Wit HA, Bryn A, Hofgaard A, Karstensen J, Kvælevåg MM, Peters GP. Climate warming feedback from mountain birch forest expansion: Reduced albedo dominates carbon uptake. *Global Change Biology*. 2014; 20:2344–2355. [PubMed: 24343906]
- Déqué M. Frequency of precipitation and temperature extremes over France in an anthropogenic scenario: Model results and statistical correction according to observed values. *Global and Planetary Change*. 2007; 57:16–26.
- Erb K-H. Land use related changes in aboveground carbon stocks of Austria's terrestrial ecosystems. *Ecosystems*. 2004; 7:563–572.
- Ford JK, MacCallum RC, Tait M. The application of exploratory factor analysis in applied psychology: a critical review and analysis. *Personnel Psychology*. 1986; 39:291–314.
- Friedlingstein P, Fung I, Holland E, John J, Brasseur G, Erickson D, Schimel D. On the contribution of CO₂ fertilization to the missing biospheric sink. *Global Biogeochemical Cycles*. 1995; 9:541–556.
- Gardiner, B., et al. Destructive storms in European forests: Past and forthcoming impacts. Final Report to European Commission-DG Environment. European Forest Institute; 2010. p. 138
- Grimm V, Revilla E, Berger U, Jeltsch F, Mooij WM, Railsback SF, Thulke H-H, Weiner J, Wiegand T, DeAngelis DL. Pattern-oriented modeling of agent-based complex systems: Lessons from ecology. *Science*. 2005; 310:987–991. [PubMed: 16284171]
- Grodsky SA, Bentamy A, Carton JA, Pinker RT. Intraseasonal latent heat flux based on satellite observations. *Journal of Climate*. 2009; 22:4539–4556.
- Gustafson EJ. When relationships estimated in the past cannot be used to predict the future: Using mechanistic models to predict landscape ecological dynamics in a changing world. *Landscape Ecology*. 2013; 28:1429–1437.
- Haiden T, Kann A, Wittmann C, Pistotnik G, Bica B, Gruber C. The integrated nowcasting through comprehensive analysis (INCA) system and its validation over the Eastern Alpine Region. *Weather and Forecasting*. 2011; 26:166–183.
- Hanewinkel M, Cullmann DA, Schelhaas M-J, Nabuurs G-J, Zimmermann NE. Climate change may cause severe loss in the economic value of European forest land. *Nature Climate Change*. 2012; 3:203–207.
- Hansen J, Sato M, Ruedy R. Radiative forcing and climate response. *Journal of Geophysical Research*. 1997; 102:6831–6864.
- Hicke JA, Meddens AJH, Allen CD, Kolden CA. Carbon stocks of trees killed by bark beetles and wildfire in the western United States. *Environmental Research Letters*. 2013; 8 035032.
- Hlásky T, Zajířková L, Turčáni M, Holuša J, Sitková Z. Geographical variability of spruce bark beetle development under climate change in the Czech Republic. *Journal of Forest Science*. 2011; 57:242–249.
- Hollinger DY, et al. Albedo estimates for land surface models and support for a new paradigm based on foliage nitrogen concentration. *Global Change Biology*. 2010; 16:696–710.
- Hurteau MD, Koch GW, Hungate BA. Carbon protection and fire risk reduction: Toward a full accounting of forest carbon offsets. *Frontiers in Ecology and the Environment*. 2008; 6:493–498.
- Nakicenovic, N., Swart, R., editors. IPCC. Emissions scenarios. Special report on emission scenarios. Contribution of Working Group III of the Intergovernmental Panel on Climate Change. Cambridge University Press; Cambridge, UK: 2000. p. 1-570.
- Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K., Tignor, M., Miller, H., editors. IPCC. Climate Change 2007: The Physical Science Basis. Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press; Cambridge, UK: 2007. p. 1-996.

- Edenhofer, OR. Pichs-Madruga, R. Sokona, Y. Farahani, E. Kadner, S. Seyboth, K. Adler, A. Baum, I. Brunner, S. Eickemeier, P. Kriemann, B., et al., editors. IPCC. Climate Change 2014: Mitigation of Climate Change. Climate Change 2014: Mitigation of Climate Change. Contribution of Working Group III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press; Cambridge, UK and New York, NY, USA: 2014. p. 1-1435.
- Jacob D. A note to the simulation of the annual and inter-annual variability of the water budget over the Baltic Sea drainage basin. *Meteorology and Atmospheric Physics*. 2001; 77:61–73.
- Jönsson AM, Appelberg G, Harding S, Barring L. Spatio-temporal impact of climate change on the activity and voltinism of the spruce bark beetle, *Ips typographus*. *Global Change Biology*. 2009; 15:486–499.
- Kashian DM, Romme WH, Tinker DB, Turner MG, Ryan MG. Postfire changes in forest carbon storage over a 300-year chronosequence of *Pinus contorta*-dominated forests. *Ecological Monographs*. 2013; 83:49–66.
- Kätterer T, Andrén O. The ICBM family of analytically solved models of soil carbon, nitrogen and microbial biomass dynamics—descriptions and application examples. *Ecological Modelling*. 2001; 136:191–207.
- Kausrud K, Økland B, Skarpaas O, Grégoire J-C, Erbilgin N, Stenseth NC. Population dynamics in changing environments: the case of an eruptive forest pest species. *Biological Reviews*. 2012; 87:34–51. [PubMed: 21557798]
- Keane RE, Austin M, Field C, Huth A, Lexer MJ, Peters D, Solomon A, Wyckoff P. Tree mortality in gap models: Application to climate change. *Climatic Change*. 2001; 51:509–540.
- Keenan TF, Prentice IC, Canadell JG, Williams CA, Wang H, Raupach M, Collatz GJ. Recent pause in the growth rate of atmospheric CO₂ due to enhanced terrestrial carbon uptake. *Nature Communications*. 2016; 7 13428.
- Kiehl JT, Trenberth KE. Earth's annual global mean energy budget. *Bulletin of the American Meteorological Society*. 1997; 78:197–208.
- Kilian W, Müller F, Starlinger F. Die forstlichen Wuchsgebiete Österreichs. Eine Naturraumgliederung nach waldökologischen Gesichtspunkten. FBVA-Berichte. 1994; 82:1–60.
- Kirschbaum MUF, Whitehead D, Dean SM, Beets PN, Shepherd JD, Ausseil AGE. Implications of albedo changes following afforestation on the benefits of forests as carbon sinks. *Biogeosciences*. 2011; 8:3687–3696.
- Kobler, J. Risikokarten als Planungsgrundlage für Flächenbewirtschaftung und Tourismuslenkung im Nationalpark Kalkalpen Oberösterreich. Faculty of Earth Sciences, Geography and Astronomy, University of Vienna; Vienna, Austria: 2004.
- Körner C. Slow in, rapid out—Carbon flux studies and Kyoto targets. *Science*. 2003; 300:1242–1243. [PubMed: 12764181]
- Krenn, A., Winkelmeier, J., Tiefgraber, C., Cattin, R., Müller, S., Truhetz, H., Biberacher, M., Gadocha, S. Endbericht Windatlas und Windpotentialstudie Österreich. Klima- und Energiefonds des Bundes; Friedburg, Austria: 2011.
- Kurz WA, Stinson G, Rampley GJ, Dymond CC, Neilson ET. Risk of natural disturbances makes future contribution of Canada's forests to the global carbon cycle highly uncertain. *Proceedings of the National Academy of Sciences USA*. 2008; 105:1551–1555.
- Kuusinen N, Tomppo E, Berninger F. Linear unmixing of MODIS albedo composites to infer subpixel land cover type albedos. *International Journal of Applied Earth Observation and Geoinformation*. 2013; 23:324–333.
- Landry J-S, Parrott L, Price DT, Ramankutty N, Matthews HD. Modelling long-term impacts of mountain pine beetle outbreaks on merchantable biomass, ecosystem carbon, albedo, and radiative forcing. *Biogeosciences*. 2016; 13:5277–5295.
- Landsberg, JJ., Gower, ST. Applications of physiological ecology to forest management. Academic Press; San Diego, California, USA: 1997.
- Landsberg JJ, Waring RH. A generalised model of forest productivity using simplified concepts of radiation-use efficiency carbon balance and partitioning. *Forest Ecology and Management*. 1997; 95:209–228.

- Li F, Bond-Lamberty B, Levis S. Quantifying the role of fire in the Earth system - Part 2: Impact on the net carbon balance of global terrestrial ecosystems for the 20th century. *Biogeosciences*. 2014; 11:1345–1360.
- Liang J, et al. Positive biodiversity-productivity relationship predominant in global forests. *Science*. 2016; 354 aaf8957.
- Littell JS, McKenzie D, Peterson DL, Westerling AL. Climate and wildfire area burned in western U. S. ecoregions, 1916–2003. *Ecological Applications*. 2009; 19:1003–1021. [PubMed: 19544740]
- Liu Z, Wimberly MC. Direct and indirect effects of climate change on projected future fire regimes in the western United States. *Science of the Total Environment*. 2016; 542:65–75. [PubMed: 26519568]
- Liu Y, Stanturf J, Goodrick S. Trends in global wildfire potential in a changing climate. *Forest Ecology and Management*. 2010; 259:685–697.
- Locatelli B, Pavageau C, Pramova E, Di Gregorio M. Integrating climate change mitigation and adaptation in agriculture and forestry: opportunities and trade-offs. *Wiley Interdisciplinary Reviews: Climate Change*. 2015; 6:585–598.
- Lundmark T, Bergh J, Hofer P, Lundström A, Nordin A, Poudel BC, Sathre R, Taverna R, Werner F. Potential roles of Swedish forestry in the context of climate change mitigation. *Forests*. 2014; 5:557–578.
- Luo Y, Weng E. Dynamic disequilibrium of the terrestrial carbon cycle under global change. *Trends in Ecology and Evolution*. 2011; 26:96–104. [PubMed: 21159407]
- Mäkelä A, Pulkkinen M, Kolari P, Lagergren F, Berbigier P, Lindroth A, Loustau D, Nikinmaa E, Vesala T, Hari P. Developing an empirical model of stand GPP with the LUE approach: analysis of eddy covariance data at five contrasting conifer sites in Europe. *Global Change Biology*. 2008; 14:92–108.
- Maness H, Kushner PJ, Fung I. Summertime climate response to mountain pine beetle disturbance in British Columbia. *Nature Geoscience*. 2013; 6:65–70.
- Manusch C, Bugmann H, Wolf A. The impact of climate change and its uncertainty on carbon storage in Switzerland. *Regional Environmental Change*. 2014; 14:1437–1450.
- Medlyn B, Barrett D, Landsberg JJ, Sands P, Clement R. Conversion of canopy intercepted radiation to photosynthesis: review of modeling approaches for regional scales. *Functional Plant Biology*. 2003; 30:153–169.
- Millar CI, Stephenson NL. Temperate forest health in an era of emerging megadisturbance. *Science*. 2015; 349:823–826. [PubMed: 26293954]
- Monteith LJ. Evaporation and environment. *Symposia of the Society for Experimental Biology*. 1965; 19:205–224. [PubMed: 5321565]
- Moss R, et al. The next generation of scenarios for climate change research and assessment. *Nature*. 2010; 463:747–756. [PubMed: 20148028]
- Musselman KN, Molotch NP, Brooks PD. Effects of vegetation on snow accumulation and ablation in a mid-latitude sub-alpine forest. *Hydrological Processes*. 2008; 22:2767–2776.
- Nabuurs G-J, Lindner M, Verkerk PJ, Gunia K, Deda P, Michalak R, Grassi G. First signs of carbon sink saturation in European forest biomass. *Nature Climate Change*. 2013; 3:792–796.
- Naudts K, Chen Y, McGrath MJ, Ryder J, Valade A, Otto J, Luyssaert S. Europe's forest management did not mitigate climate warming. *Science*. 2016; 351:597–600. [PubMed: 26912701]
- Nazarenko L, et al. Future climate change under RCP emission scenarios with GISS ModelE2. *Journal of Advances in Modeling Earth Systems*. 2015; 7:244–267.
- Nunery JS, Keeton SW. Forest carbon storage in the northeastern United States: Net effects of harvesting frequency, post-harvest retention, and wood products. *Forest Ecology and Management*. 2010; 259:1363–1375.
- O'Halloran TL, et al. Radiative forcing of natural forest disturbances. *Global Change Biology*. 2012; 18:555–565.
- Overbeck M, Schmidt M. Modelling infestation risk of Norway spruce by *Ips typographus* (L.) in the Lower Saxon Harz Mountains (Germany). *Forest Ecology and Management*. 2012; 266:115–125.

- Pal JS, et al. Regional climate modeling for the developing world: The ICTP RegCM3 and RegCNET. *Bulletin of the American Meteorological Society*. 2007; 88:1395–1409.
- Panayotov M, Kulakowski D, Laranjeiro Dos Santos L, Bebi P. Wind disturbances shape old Norway spruce-dominated forest in Bulgaria. *Forest Ecology and Management*. 2011; 262:470–481.
- Pastor, J., Post, WM. Development of a linked forest productivity-soil process model. United States Department of Energy; Washington D.C., USA: 1985. ORNL/TM-9519
- Pasztor F, Matulla C, Rammer W, Lexer MJ. Drivers of the bark beetle disturbance regime in Alpine forests in Austria. *Forest Ecology and Management*. 2014; 318:349–358.
- Pasztor F, Matulla C, Zuvela-Aloise M, Rammer W, Lexer MJ. Developing predictive models of wind damage in Austrian forests. *Annals of Forest Science*. 2015; 72:289–301.
- Pereira AR. The Priestley-Taylor parameter and the decoupling factor for estimating reference evapotranspiration. *Agricultural and Forest Meteorology*. 2004; 125:305–313.
- R Development Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing; Vienna, Austria: 2016. <http://R-project.org>
- Radu R, Déqué M, Somot S. Spectral nudging in a spectral regional climate model. *Tellus A*. 2008; 60:898–910.
- Rajabi MR, Modarres R. Extreme value frequency analysis of wind data from Isfahan, Iran. *Journal of Wind Engineering and Industrial Aerodynamics*. 2008; 96:78–82.
- Rockel B, Woth K. Extremes of near-surface windspeed over Europe and their future changes as estimated from an ensemble of RCM simulations. *Climatic Change*. 2007; 81:267–280.
- Running SW, Coughlan JC. A general model of forest ecosystem processes for regional applications. I. Hydrological balance, canopy gas exchange and primary production processes. *Ecological Modelling*. 1988; 42:125–154.
- Rydsaa JH, Stordal F, Tallaksen LM. Sensitivity of the regional European boreal climate to changes in surface properties resulting from structural vegetation perturbations. *Biogeosciences*. 2015; 12:3071–3087.
- Schelhaas MJ, Nabuurs G-J, Schuck A. Natural disturbances in the European forests in the 19th and 20th centuries. *Global Change Biology*. 2003; 9:1620–1633.
- Schume H, Jost G, Hager H. Soil water depletion and recharge patterns in mixed and pure forest stands of European beech and Norway spruce. *Journal of Hydrology*. 2004; 289:258–274.
- Schwaab J, Bavay M, Davin E, Hagedorn F, Hüsler F, Lehning M, Schneebeli M, Thürig E, Bebi P. Carbon storage versus albedo change: Radiative forcing of forest expansion in temperate mountainous regions of Switzerland. *Biogeosciences*. 2015; 12:467–487.
- Schwalm CR, Ek A. A process-based model of forest ecosystems driven by meteorology. *Ecological Modelling*. 2004; 179:317–348.
- Seidl R, Rammer W. Climate change amplifies the interactions between wind and bark beetle disturbances in forest landscapes. *Landscape Ecology*. 2016; doi: 10.1007/s10980-016-0396-4
- Seidl R, Lexer MJ, Jäger D, Hönninger K. Evaluating the accuracy and generality of a hybrid forest patch model. *Tree Physiology*. 2005; 25:939–951. [PubMed: 15870060]
- Seidl R, Rammer W, Jäger D, Currie WS, Lexer MJ. Assessing trade-offs between carbon sequestration and timber production within a framework of multi-purpose forestry in Austria. *Forest Ecology and Management*. 2007; 248:64–79.
- Seidl R, Schelhaas M-J, Lindner M, Lexer MJ. Modelling bark beetle disturbances in a large scale forest scenario model to assess climate change impacts and evaluate adaptive management strategies. *Regional Environmental Change*. 2009a; 9:101–119.
- Seidl R, Rammer W, Lexer MJ. Schätzung von Bodenmerkmalen und Modellparametern für die Waldöko-systemsimulation auf Basis einer Großbrauminventur. *Allgemeine Forstund Jagdzeitung*. 2009b; 180:35–44.
- Seidl R, Schelhaas M-J, Lexer MJ. Unraveling the drivers of intensifying forest disturbance regimes in Europe. *Global Change Biology*. 2011; 17:2842–2852.
- Seidl R, Rammer W, Scheller RM, Spies TA. An individual-based process model to simulate landscape-scale forest ecosystem dynamics. *Ecological Modelling*. 2012a; 231:87–100.

- Seidl R, Spies TA, Rammer W, Steel EA, Pabst RJ, Olsen K. Multi-scale drivers of spatial variation in old-growth forest carbon density disentangled with Lidar and an individual-based landscape model. *Ecosystems*. 2012b; 15:1321–1335.
- Seidl R, Schelhaas M-J, Rammer W, Verkerk PJ. Increasing forest disturbances in Europe and their impact on carbon storage. *Nature Climate Change*. 2014a; 4:806–810.
- Seidl R, Rammer W, Blennow K. Simulating wind disturbance impacts on forest landscapes: Tree-level heterogeneity matters. *Environmental Modelling & Software*. 2014b; 51:1–11.
- Seidl R, Vigl F, Rössler G, Neumann M, Rammer W. Assessing the resilience of Norway spruce forests through a model-based reanalysis of thinning trials. *Forest Ecology and Management*. 2017a; 388:3–12. [PubMed: 28860674]
- Seidl R, et al. Forest disturbances under climate change. *Nature Climate Change*. 2017b; doi: 10.1038/nclimate3303
- Shuman JK, Shugart HH, O'Halloran TL. Sensitivity of Siberian larch forests to climate change. *Global Change Biology*. 2011; 17:2370–2384.
- Silva Pedro M, Rammer W, Seidl R. Tree species diversity mitigates disturbance impacts on the forest carbon cycle. *Oecologia*. 2015; 177:619–630. [PubMed: 25526843]
- Smith P, et al. Biophysical and economic limits to negative CO₂ emissions. *Nature Climate Change*. 2016; 6:42–50.
- Stuart-Haëntjens EJ, Curtis PS, Fahey RT, Vogel CS, Gough CM. Net primary production exhibits a threshold response to increasing disturbance severity in a temperate deciduous forest. *Ecology*. 2015; 96:2478–2487. [PubMed: 26594704]
- Temperli C, Bugmann H, Elkin C. Cross-scale interactions among bark beetles, climate change, and wind disturbances: A landscape modeling approach. *Ecological Monographs*. 2013; 83:383–402.
- Thom D, Seidl R. Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. *Biological Reviews*. 2016; 91:760–781. [PubMed: 26010526]
- Thom D, Seidl R, Steyrer G, Krehan H, Formayer H. Slow and fast drivers of the natural disturbance regime in Central European forest ecosystems. *Forest Ecology and Management*. 2013; 307:293–302.
- Thom D, Rammer W, Seidl R. Disturbances catalyze the adaptation of forest ecosystems to changing climate conditions. *Global Change Biology*. 2017a; 23:269–282. [PubMed: 27633953]
- Thom D, Rammer W, Dirnböck T, Müller J, Kobler J, Katzensteiner K, Helm N, Seidl R. The impacts of climate change and disturbance on spatio-temporal trajectories of biodiversity in a temperate forest landscape. *Journal of Applied Ecology*. 2017b; 54:28–38. [PubMed: 28111479]
- Turner MG, Romme WH, Gardner RH, O'Neill RV, Kratz TK. A revised concept of landscape equilibrium: Disturbance and stability on scaled landscapes. *Landscape Ecology*. 1993; 8:213–227.
- Valinger E, Fridman J. Factors affecting the probability of windthrow at stand level as a result of Gudrun winter storm in southern Sweden. *Forest Ecology and Management*. 2011; 262:398–403.
- Varhola A, Coops NC, Weiler M, Moore RD. Forest canopy effects on snow accumulation and ablation: An integrative review of empirical results. *Journal of Hydrology*. 2010; 392:219–233.
- Walther GR, et al. Alien species in a warmer world: risks and opportunities. *Trends in Ecology and Evolution*. 2009; 24:686–693. [PubMed: 19712994]
- Weed AS, Ayres MP, Hicke JA. Consequences of climate change for biotic disturbances in North American forests. *Ecological Monographs*. 2013; 83:441–470.
- Wermelinger B. Ecology and management of the spruce bark beetle *Ips typographus*—a review of recent research. *Forest Ecology and Management*. 2004; 202:67–82.
- Wu H-I, Sharpe PJH, Walker J, Penridge LK. Ecological field theory: A spatial analysis of resource interference among plants. *Ecological Modelling*. 1985; 29:215–243.
- Zumbrunnen T, Menéndez P, Bugmann H, Conedera M, Gimmi U, Bürgi M. Human impacts on fire occurrence: A case study of hundred years of forest fires in a dry alpine valley in Switzerland. *Regional Environmental Change*. 2012; 12:935–949.

Fig. 1.

Hypothesized climate change effects on the climate regulating function of forest ecosystems as mediated by changes in forest dynamics, particularly changing tree species composition and disturbance regimes. A plus sign indicates a hypothesized increase in the focal variable, a minus sign represents an expected decrease, and a tilde represents small and/or variable effects.

Fig. 2. Location (lower left panel), topography (central panel), and major forest types (right panels) in Kalkalpen National Park, Austria (KANP). The main forest types are (a) European beech dominated forests in low elevations (<800 m above sea level [asl]), (b) mixed forests of Norway spruce, silver fir, and European beech in mid elevations (800–1,200 m asl), and (c) Norway spruce-dominated forests in high elevations (>1,200 m asl).

Fig. 3.

Development of growing stock by tree species over time, aggregated at the landscape level and averaged per hectare. Columns contrast baseline climate (i.e., representing the climatic conditions of the period 1950–2010) with trajectories under climate change (here the mean over three climate warming scenarios). Rows contrast undisturbed forest development (top row) with two scenarios accounting for disturbances by wind and bark beetles (disturbed, assuming a continuation of past peak wind speeds and return intervals; disturbed+, assuming a 10% increase in peak wind speeds). All scenario combinations are the means over all

replicated simulations. For clarity, only species with a growing stock of $>10 \text{ m}^3/\text{ha}$ at the end of the simulated period are shown explicitly. Species are *Fagus sylvatica*, *Quercus petraea*, *Abies alba*, *Larix decidua*, *Picea abies*, and *Picea sylvestris*.

Fig. 4.

Cumulative area disturbed for the 13,865-ha landscape over the 200-yr simulation period. Presented are means (darker hues) of baseline climate (blue) and climate change scenarios (red), as well as individual simulation runs (lighter hues) for disturbance from wind, bark beetles, and total disturbed area under scenarios of historic (left column) and increased wind speed (right column).

Fig. 5.

Spatial distribution of disturbances at KANP. Presented is the average amount of growing stock disturbed by wind and bark beetles under (a) baseline climate and (b) climate change, as well as the relative share of bark beetles on the total disturbance under (c) baseline climate and (d) climate change scenarios over the 200-yr simulation period. A bark beetle share of zero indicates that the disturbance effect is solely attributable to wind. Elevational gradients are presented as isolines.

Fig. 6.

Climate change impacts on forest dynamics and climate regulating functions at KANP. Presented are direct impacts of climate change (blue arrows and bars) and indirect effects of climate change (gray arrows) via feedbacks between tree species composition and disturbances (upper panel). Banded blue and gray bars give the net total effect of direct and indirect climate change effects. Note that changes in tree species composition refer to percentage points while changes in disturbances indicate relative differences. Climate change (yellow) and climate change + disturbance (brown) induced impacts on radiative forcing from changing net ecosystem carbon balance (NECB), albedo, and latent heat flux (LHF) are presented in the lower panel of the figure. All values are averages over all climate change scenarios studied, reported relative to baseline climate. Values from changes in composition, disturbances and NECB pertain to the cumulative effect after 200 yr of simulation, while changes in the radiative forcing from albedo and latent heat flux refer to the average over the last 20 yr of the simulation in order to account for yearly variation.

Fig. 7.

The radiative forcing of KANP, resulting from the combined effects of changes in NECB, albedo, and latent heat flux. Shown are averages over the respective scenario combinations. Heavy lines represent running means over 10 contiguous years, and fine lines visualize the simulation result of each individual year. Negative values indicate a cooling effect of the forest to the atmosphere.

Table 1

Albedo of vegetation (A_V) and snow cover (A_S).

Species	A_V	A_S	Source
<i>Betula pendula</i>	0.137	0.375	Kuusinen et al. (2013)
<i>Larix</i> spp.	0.120	0.270	Shuman et al. (2011)
<i>Picea abies</i>	0.102	0.285	Kuusinen et al. (2013)
<i>Picea sylvestris</i>	0.110	0.301	Kuusinen et al. (2013)
Other conifers	0.092	0.236	Kuusinen et al. (2013)
Other broadleaves	0.137	0.331	Kuusinen et al. (2013)
Bare ground	0.132	0.492	Kuusinen et al. (2013)

Note: Snow cover albedo values were considered for days with snowpack > 0 cm.

Table 2

Scenario effects on forest dynamics and snow cover at Kalkalpen National Park, Austria (KANP).

Drivers of climate regulating functions	Baseline climate						Climate change					
	Undisturbed		Disturbed		Disturbed+		Undisturbed		Disturbed		Disturbed+	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Broadleaf trees (%)	42.0	1.5	47.1	2.6	50.5	4.1	48.3	4.9	55.4	7.7	58.0	8.1
Disturbed area (% per yr)	–	–	0.18	0.32	0.27	0.50	–	–	0.23	0.28	0.30	0.42
Snow days (d/yr)	137	28	136	28	136	29	83	35	83	35	83	35

Note: Presented are means and standard deviations (SD) for baseline climate and climate change (including all three climate change scenarios) under three disturbance scenarios (in total 240 runs were simulated over 200 yr).

Table 3

Scenario effects on climate regulation functions at KANP.

Factors	Baseline climate						Climate change					
	Undisturbed		Disturbed		Disturbed+		Undisturbed		Disturbed		Disturbed+	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Functions in original units												
NECB (Mg C-ha ⁻¹ ·yr ⁻¹)	0.62	1.11	0.48	2.12	0.41	3.09	0.44	1.33	0.36	1.85	0.33	2.39
Albedo (dim.)	0.162	0.014	0.165	0.014	0.167	0.015	0.142	0.014	0.145	0.013	0.147	0.013
Evapotranspiration (mm/yr)	252.7	20.1	256.7	19.0	258.3	18.4	269.1	29.5	276.7	29.4	278.8	29.3
Functions in radiative forcing												
NECB	-6043	1543	-4996	1299	-4288	1185	-4599	1833	-3453	1638	-2951	1587
Albedo	-5919	556	-6018	567	-6088	576	-5190	521	-5306	513	-5353	513
Latent heat flux	-6190	492	-6289	466	-6328	452	-6596	722	-6784	719	-6836	717

Notes: Presented are means and standard deviations (SD) for baseline climate and climate change (including all three climate change scenarios) under three disturbance scenarios (in total 240 runs were simulated over 200 yr). The upper part of the table describes the investigated climate regulating functions in their original units, whereas the lower part presents the net climate regulation effect as expressed by radiative forcing. NECB, net ecosystem carbon balance; dim., dimensionless.

Table 4

Sensitivity of radiative forcing ($\text{GJ}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) to underlying drivers derived by means of principal component regression (PCR; $R^2 = 0.545$).

Driver	Coefficient ($\text{GJ}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$)	SD	<i>P</i>	Variance explained (%)
Broadleaf trees	396.1	23.5	<0.001	40.6
Disturbed area	332.0	19.7	<0.001	34.0
Snow days	-247.7	14.7	<0.001	25.4

Notes: The coefficients indicate the average radiative forcing change in response to a change in the respective explanatory variable by one standard deviation. The variance explained indicates the relative contribution of each variable on the total variance explained by the PCR.