Legacies of past land use have a stronger effect on forest carbon exchange than future climate change in a temperate forest landscape

Running head: "Land use legacies determine C exchange"

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Abstract

Forest ecosystems play an important role in the global climate system, and are thus intensively discussed in the context of climate change mitigation. Over the past decades temperate forests were a carbon (C) sink to the atmosphere. However, it remains unclear to which degree this C uptake is driven by a recovery from past land use and natural disturbances or ongoing climate change, inducing high uncertainty regarding the future temperate forest C sink. Here our objectives were (i) to investigate legacies within the natural disturbance regime by empirically analyzing two disturbance episodes affecting the same landscape 90 years apart, and (ii) to unravel the effects of past land use and natural disturbances as well as future climate on 21st century forest C uptake by means of simulation modelling. We collected historical data from archives to reconstruct the vegetation and disturbance history of a forest landscape in the Austrian Alps from 1905 to 2013. The effects of legacies and climate were disentangled by individually controlling for past land use, natural disturbances, and future scenarios of climate change in a factorial simulation study. We found only moderate spatial overlap between two episodes of wind and bark beetle disturbance affecting the landscape in the early 20th and 21st century, respectively. Our simulations revealed a high uncertainty about the relationship between the two disturbance episodes, whereas past land use clearly increased the impact of the second disturbance episode on the landscape. The future forest C sink was strongly driven by the cessation of historic land use, while climate change reduced forest C uptake. Compared to land use change the two past episodes of natural disturbance had only marginal effects on the future carbon cycle. We conclude that neglecting legacies can substantially bias assessments of future forest dynamics.

Key words: bark beetles, climate change, forest history, forest management, Kalkalpen National Park, legacy effects, net ecosystem exchange, wind

Copyright statement

1. Introduction

Carbon dioxide (CO_2) is responsible for 76% of the global greenhouse gas emissions, and is thus the single most important driver of anthropogenic climate change (IPCC 2014). Forest ecosystems take up large quantities of CO_2 from the atmosphere, and play a key role in mitigating climate change (IPCC 2007). During the period 1990 – 2007, established and regrowing forests were estimated to have taken up 60% of the cumulative fossil carbon emissions (Pan et al., 2011). This carbon (C) sink strength of forests has further increased in recent years (Keenan et al., 2016), resulting from multiple drivers: On the one hand, possible factors contributing to an increasing sink strength of the biosphere are CO_2 (Drake et al., 2011) and nitrogen (Perring et al., 2008) fertilization, in combination with extended vegetation periods resulting from climate warming (Keenan et al., 2014). On the other hand, the accelerated carbon uptake of forests might be a transient recovery effect of past carbon losses from land use and natural disturbances (Erb, 2004; Loudermilk et al., 2013).

For the future, dynamic Global Vegetation Models (DGVMs) frequently suggest a persistent forest carbon sink (Keenan et al., 2016; Sitch et al., 2008). However, while DGVMs are suitable for tracking the direct effects of global change, they frequently neglect the effects of long-term legacies of the past. Both natural disturbances (e.g., wind storms and bark beetle outbreaks) and land use have decreased the amount of carbon currently stored in forest ecosystems (Erb et al., 2018; Goetz et al., 2012; Harmon et al., 1990; Seidl et al., 2014a). The legacy effects of past disturbances and land use have the potential to significantly influence forest dynamics and alter the trajectories of carbon uptake in forest ecosystems over time frames of decades and centuries (Gough et al., 2007; Landry et al., 2016; Seidl et al., 2014b). This is of particular importance for the forests of Central Europe, which have been markedly affected by forest management and natural disturbances over the past centuries (Naudts et al., 2016; Svoboda et al., 2012). The importance of an improved understanding of past disturbance dynamics and its impacts on the future carbon cycle is further underlined by the expectation that climate change will amplify natural disturbance regimes in the future (Seidl et al., 2017). In this context the role of temporal autocorrelation within disturbance regimes is of particular relevance, i.e., the influence that past disturbances and land use have on future disturbances at a given site. Are past disturbances and land use increasing or decreasing the propensity and severity for future disturbances? And are such temporal autocorrelations influencing the future potential of forests to take up carbon? The propensity and effect of such interactions between disturbances and land use across decades remain understudied to date, largely due to a lack of long-term data on past disturbances and land use.

Here we investigate the effect of long-term disturbance and land use legacies on forest ecosystem dynamics, in order to better understand the drivers of future forest carbon uptake, and thus aid the development of effective climate change mitigation strategies. In particular, our first objective was to investigate the temporal interaction of two major episodes of natural disturbance affecting the same Central European forest landscape 90 years apart (i.e., 1917 – 1923 and 2007 – 2013). We hypothesized a temporal autocorrelation of the two major disturbance episodes, and specifically an amplifying effect from the earlier disturbance episode on the later disturbance episode(see e.g., Schurman et al., 2018). Our hypothesis was based on the importance of landscape topography for wind and bark beetle disturbances (Senf and Seidl, 2018; Thom et al., 2013), and the fact that susceptibility to these agents generally increases with stand age, and is usually high after 90 years of stand development (Overbeck and Schmidt, 2012; Valinger and Fridman, 2011). In addition, we tested the effect of land use on the more recent natural disturbance episode, following the hypothesis that land use increased natural disturbance risk in Central Europe by promoting homogeneous structures and single-species plantations (Seidl et al., 2011; Silva Pedro et al., 2015). Our second goal was to quantify the contribution of past natural disturbance and land use on the future C uptake of the landscape under a number of climate change scenarios using simulation modelling. We were particularly interested in the relative effects of past disturbance, land use, and future climate on the future forest C sink strength. To that end we reconstructed the vegetation history of the landscape from 1905 to 2013 using historical sources and remote sensing. We subsequently determined the effect of past disturbance and land use on 21st century C dynamics by simulating forests from the early 20th century to the end of the 21st century, experimentally altering past disturbance and land use regimes in a factorial simulation experiment. These analyses were run under multiple climate scenarios for the 21st century, and focused on Net Ecosystem Exchange (NEE) (i.e., the net C exchange of the ecosystem with the atmosphere, which is the inverse of Net Ecosystem Productivity, NEP) as the response variable. We hypothesized that the legacies of past disturbance and land use are of paramount importance for the future carbon sink (Gough et al., 2007; Thom et al., 2017a), expecting a saturation of carbon uptake as the landscape recovers from past disturbance and land use (i.e., a negative but decreasing NEE through the 21st century). Moreover, we hypothesized a negative impact of future climate change on carbon uptake as a result of less favorable conditions for carbon-rich spruce dominated forests (Kruhlov et al., 2018; Thom et al., 2017a).

2. Materials and Methods

2.1 Study area

We selected a 7,609 ha forest landscape located in the northern front range of the Alps as our study area (Fig. 1). Focusing on the landscape scale allowed us to mechanistically capture changes in forest structure and C stocks by jointly considering large scale processes such as disturbances as well as fine scale processes such as competition between individual trees. The focal landscape is particularly suited to address our research questions as it (i) was affected by two major episodes of natural disturbance (driven by wind and bark beetles) in the past century, and (ii) has a varied land use history, with intensive management up until 1997, and then becoming a part of Kalkalpen National Park (KANP), the largest contiguous protected forest area in Austria. The steep elevational gradient of the study landscape, ranging from 414 m to 1637 m a.s.l., results in considerable variation in environmental conditions. For instance, temperatures range from 4.3 – 9.0°C and mean annual precipitation sums vary between 1179 – 1648 mm across the landscape. Shallow Lithic and Renzic Leptosols as well as Chromic Cambisols over calcareous bedrock are the prevailing soil types (Kobler 2004). The most prominent natural forest types on the landscape are European beech (*Fagus sylvatica* [L.]) forests at low elevations, mixed forests of Norway spruce (*Picea abies* [K.]), silver fir (*Abies alba* [Mill.]) and European beech at mid-elevations, and Norway spruce forests at high elevations. These forest types are among the most common ones in Europe, and are highly valuable to society also from a socio-economic perspective (Hanewinkel et al., 2012).

2.2 Simulation model

We employed the individual-based forest landscape and disturbance model (iLand) to simulate past and future forest dynamics at our study landscape. iLand is a high-resolution process-based forest model, designed to simulate the dynamic feedbacks between vegetation, climate, management and disturbance regimes (Seidl et al., 2012a, 2012b). It simulates processes in a hierarchical multi-scale framework, i.e., considering processes at the individual tree (e.g., growth, mortality as well as competition for light, water, and nutrients), stand (e.g., water and nutrient availability), and landscape (e.g., seed dispersal, disturbances) scale as well as their cross-scale interactions. Competition for resources among individual trees is based on ecological field theory (Wu et al., 1985). Resource utilization is modelled employing a light use efficiency approach (Landsberg and Waring, 1997), incorporating the effects of temperature, solar radiation, vapor pressure deficit as well as soil water and nutrient availability on a daily basis. Resource use efficiency is further modified by variation in the atmospheric CO_2 concentration. Seeds are dispersed via species-specific dispersal kernels (20 × 20 m horizontal resolution) around individual mature trees. The establishment success of tree regeneration is constrained by environmental filters (e.g., temperature and light availability). Mortality of trees is driven by stress-induced carbon starvation and also considers a stochastic probability of tree death depending on life-history traits.

Climate change affects tree growth and competition in iLand in several ways (Seidl et al., 2012a, 2012b). For instance, an increase in temperature modifies leaf phenology and the length of the vegetation period, but also reduces soil water availability due to increased evapotranspiration. Net primary production is further influenced by climate change-induced alterations in precipitation, atmospheric CO_2 levels, and solar radiation. Trees respond differently to changes in climate in iLand based on their species-specific traits. Climate change thus not only alters biogeochemical processes in the model but also modifies the competitive strength of tree species, and consequently forest composition and structure (Thom et al. 2017a).

iLand currently includes three submodules to simulate natural disturbances, i.e., wind (Seidl et al., 2014c), bark beetles (Seidl and Rammer 2017), and wildfire (Seidl et al., 2014b). As wind and bark beetles are of paramount importance for the past and future disturbance regimes of Central Europe's forests (Seidl et al., 2014a; Thom et al., 2013), we employed only these two process-based disturbance submodules in our simulations. The impact of wind disturbance in iLand depends on species- and size-specific susceptibility (e.g., critical wind speeds of uprooting and stem breakage), vertical forest structure (e.g., gaps), and storm characteristics (e.g., maximum wind speeds). The bark beetle module simulates the impact of *Ips typographus* (L.) on Norway spruce, and thus addresses the effects of the most important bark beetle species in Europe with respect to area affected and timber volume disturbed (Kautz et al., 2017; Seidl et al., 2009). The model *inter alia* accounts for insect abundance, phenology and development, as well as emergence and dispersal. It computes the number of beetle generations and sister broods developed per year as well as winter survival rates based on the prevailing climate and weather conditions, and considers individual tree defense capacity and susceptibility (simulated via the non-structural carbohydrates pool of individual trees). Thus the model accounts for inter-annual variation in the interactions between trees and bark beetles. Interactions between wind and bark beetle disturbances arise from a high infestation probability and low defense capacity of freshly downed trees after wind disturbance, while newly formed gaps (e.g., by bark beetles) increase the exposure of surrounding forests to storm events. Seidl and Rammer (2017) found that iLand is well able to reproduce these interactions for Kalkalpen National Park.

In addition to the submodules of natural disturbance we used the agent-based forest management module (ABE) in iLand (Rammer and Seidl, 2015) to simulate past forest management. ABE enables the dynamic application of generalized stand treatment programs, including planting, tending, thinning, and harvesting activities. The dynamically simulated management agent observes constraints at the stand and landscape scales, such as maximum clearing sizes and sustainable harvest levels. Besides silvicultural treatments, we used ABE to emulate the past management practice of salvage logging after bark beetle outbreaks.

iLand simulates a closed carbon cycle, tracking C in both aboveground (stem, branch, foliage, tree regeneration) and belowground live tree compartments (coarse and fine roots). Decomposition rates of detrital pools are modified by temperature and humidity to allow for the simulation of C dynamics under changing climatic conditions. Detrital pools include litter (i.e., dead material from both leaf and fine root turnover) and soil organic matter (Kätterer and Andrén, 2001) as well as snags and downed coarse woody debris.

iLand has been extensively evaluated against independent data from forest ecosystems of the northern front range of the Alps using a pattern-oriented modeling approach (Grimm et al., 2005). The patterns for which simulations were compared against independent observations include tree productivity gradients and natural vegetation dynamics (Thom et al., 2017b), wind and bark beetle disturbance levels and distribution (Seidl and Rammer 2017), as well as management trajectories (Albrich et al., 2018). A comprehensive documentation of iLand can be found online at http://iLand.boku.ac.at, where also the model executable and source code are freely available under a GNU GPL open source license.

2.3 Reconstructing forest disturbance and land use history

The study area has a long history of intensive timber harvesting for charcoal production, mainly driven by a local pre-industrial iron-producing syndicate. This syndicate was active until 1889, when the land was purchased by the k.k. ("kaiserlich und königlich") Ministry for Agriculture. During the 20th century, the majority of the landscape was managed by the Austrian Federal Forests, and only limited areas within the landscape were still under the ownership of industrial private companies (Weichenberger, 1994, 1995; Weinfurter, 2005). Forest management in the late 19th and early 20th century was strongly influenced by the emerging industrialization. The substitution of wood by mineral coal for heating, but especially for industrial energy supply, changed the focus of forest management from fuel wood to timber production. At the same time, an increase in agricultural productivity (also triggered by an input of fossil resources and artificial fertilizer) allowed for the abandonment of less productive agricultural plots, often followed by afforestation or natural regrowth of forest vegetation. Consequently, growing stocks increased in many parts of Europe throughout the 20th century as the result of increases in both forest extent and density (Bebi et al., 2017). In our study system, the shifting focus from fuel wood to timber production around 1900 was accompanied by the introduction of systematic stand delineation for spatial management planning (Fig. S1) as well as decadal inventories and forest plan revisions. These documents are preserved in the archives of the Austrian Federal Forests, and were used here to reconstruct past forest vegetation as well as management and disturbance history (see Section S1, Fig. S1 and S2 in the Supplementary Material for details).

The oldest historic vegetation data available for the landscape were from an inventory conducted between the years 1898 and 1911 and comprised growing stock and age classes for 11 tree species at the level of stand compartments for the entire landscape; we subsequently used the year 1905 (representing the area-weighted mean year of this initial inventory) as the temporal starting point for our analyses (Fig. 2). A major challenge for managers was to extract resources from remote and inaccessible parts of the topographically highly complex landscape. The most important means of timber transportation in the early 20th century was drifting (i.e., flushing logs down creeks and streams after artificially damming them). However, this transportation technique was not feasible for heavy hardwood timber such as beech (Grabner et al., 2004). Consequently, managers harvested trees selectively, and mainly focused on accessible areas (i.e., stands close to streams). This resulted in some parts of the landscape holding young, recently cut forests, while others containing stands of >160 years of age (Fig. S3).

In addition to deriving the state of the forest in 1905, we reconstructed management activities (thinnings, final harvests, artificial regeneration) and natural disturbances (wind and bark beetle outbreaks) until 2013. From 1905 to 1917 timber extraction was fairly low. Between 1917 and 1923, however, a major disturbance episode by wind and bark beetles hit the region. Resulting from a lack of labor force (military draft, malnutrition) in the last year of World War I a major windthrow in 1917 could not be cleared, and the resulting bark beetle outbreak affected large parts of the landscape. Overall, wind and bark beetles disturbed approximately one million cubic meters of timber in the region between 1917 and 1923 (based on archival sources; Soyka, 1936; Weichenberger, 1994). Consequently, a railroad was installed to access and salvage the disturbed timber. After the containment of the bark beetle outbreak in 1923 forest management resumed at low intensity and no major natural disturbances were recorded. Following World War II, a network of forest roads was built in order to gradually replace timber transportation by railroads. The introduction of motorized chain saws (Fig. 2) further contributed to an intensification of harvests. By 1971, forest railroads were completely replaced by motorized transportation on forest roads, resulting in a further increase in the timber extracted from the landscape. Timber removals from management as well as natural disturbances by wind and bark beetles between 1905 and 1997 were reconstructed from annual management reviews available from archival sources. With the landscape becoming part of KANP forest management ceased in 1997. A second major natural disturbance episode affected the landscape from 2007-2013, when a large bark beetle outbreak followed three storm events in 2007 and 2008. This second disturbance episode was reconstructed from disturbance records of KANP in combination with remote sensing data (Seidl and Rammer, 2016; Thom et al., 2017b).

2.4 Landscape initialization and drivers

The vegetation data for the year 1905 were derived from historical records for 2079 stands with a median stand size of 1.7 ha. On average over the landscape, the growing stock was 212.3 m^3 ha^{-1} in 1905. The most common species were Norway spruce (with a growing stock of on average 116.3 m^3 ha^{-1}), European beech (68.0 m^3 ha^{-1}), and European larch (*Larix decidua* [Mill.], 21.5 m^3 ha^{-1}). With an average growing stock of 4.2 m^3 ha^{-1} silver fir was considerably underrepresented on the landscape relative to its role in the potential natural vegetation composition, resulting from historic clear-cut management and high browsing pressure from deer (see also Kučeravá et al., 2012). Despite these detailed records on past vegetation not all information for initializing iLand were available from archival sources, e.g., diameters at breast height (dbh) and height of individual trees, as well as tree positions, regeneration and belowground carbon-pools had to be reconstructed by other means. To that end we developed a new method for initializing vegetation and carbon pools in iLand, combining spin-up simulations with empirical reference data on vegetation state, henceforth referred to as "legacy spin-up".

Commonly, spin-ups run models for a certain amount of time or until specified stopping criteria are reached (e.g., steady-state conditions). The actual model-based analysis is then started from the thus spun-up vegetation condition (Thornton and Rosenbloom, 2005). This has the advantage that the model-internal dynamics (e.g., the relationships between the different C and N pools in an ecosystem) are consistent when the focal analysis starts. However, the thus derived initial vegetation condition frequently diverges from the vegetation state observed at a given point in time (e.g., due to not all processes being represented in the applied model), and does not account for the legacies of past management and disturbance. The legacy spin-up approach developed here aims to reconstruct an (incompletely) known reference state of the vegetation (e.g., the species composition, age, and growing stock reconstructed from archival sources for the current analysis) from simulations (Fig. S4). To this end, iLand simulates long-term forest development for each stand under past management and disturbance regimes. During the simulations, the emerging forest trajectory is periodically compared to the respective reference values, and the assumed past management is adapted iteratively in order to decrease the difference between simulated vegetation states and observed reference values. This procedure is executed in parallel for all stands on the landscape over a long period of time (here: 1000 years). The simulated vegetation state best corresponding to the reference values is stored individually for each stand (including individual tree properties, regeneration, and carbon pools), and later used to initialize model-based scenario analyses. A detailed description of the legacy spin-up approach is given in the Supplementary Material Section S2.

In simulating 20th century forest dynamics we accounted for the abandonment of cattle grazing and litter raking in forests (Glatzel, 1991) as well as an increasing atmospheric deposition of nitrogen (Dirnböck et al., 2014; Roth et al., 2015). Specifically, we dynamically modified the annual plant available nitrogen in our simulations based on data of nitrogen deposition in Austria between 1880 and 2010, with nitrogen input peaking in the mid 1980s, followed by a decrease and a stabilization after 2000 (Dirnböck et al., 2017). Besides edaphic factors also an increase in temperature has led to more favorable conditions of tree growth (Pretzsch et al., 2014). Detailed observations of climate for our study region reach back to 1950. Climate data were statistically downscaled to a resolution of 100 × 100 m by means of quantile mapping, accounting for topographic differences in climate conditions (Thom et al., 2017b).The lack of detailed climate information before 1950 required an extension of the climate time series for the years 1905 to 1949. To that end, we extracted data from the nearest weather station covering the period from 1905 to present (i.e., Admont, located approximately 20 km south of our study area), and used its temperature and precipitation record to sample years with corresponding conditions from the observational record for our study landscape.

After using the legacy spin-up to generate tree vegetation and carbon pools in 1905, simulations were run from 1905 until 2099, considering four different climate scenarios for the period 2013 – 2099. Climate change was represented by three combinations of global circulation models (GCM) and regional climate models (RCM) under A1B forcing, including CNRM-RM4.5 (Radu et al., 2008) driven by the GCM ARPEGE, and MPI-REMO (Jacob, 2001) as well as ICTP-RegCM3 (Pal et al., 2007), both driven by the GCM ECHAM5. The A1B scenario family assumes rapid economic growth with global population peaking mid-century and declining thereafter, and a balanced mix of energy sources being used (IPCC 2000). With average temperature increases of between +3.1°C and +3.3°C and changing annual precipitation sums of -87.0 mm to +135.6 mm by the end of the 21st century, the scenarios studied here are comparable to the changes expected under the representative concentration pathways RCP4.5 and RCP6.0 for our study region (Thom et al., 2017c). In addition to the three scenarios of climate change a historic baseline climate scenario was simulated. The years 1950 – 2010 were used to represent this climatic baseline, and were randomly resampled to derive a stationary climate time series until 2099.

2.5 Analyses

First, we evaluated the ability of iLand to reproduce the empirical data gathered for the studied landscape. Following a pattern-oriented modeling approach (Grimm et al., 2005) we evaluated a suit of different processes such as tree growth and competition, natural disturbances and forest management. Specifically, we compared model outputs for different aspects of landscape development (e.g., species composition, harvested and disturbed growing stock) at various points in time against empirically derived historical data.

To address our first objective, i.e. investigating the spatio-temporal interactions of natural disturbances, we used the empirically derived stand-level records of the two historic disturbance episodes (1917 – 1923 and 2007 – 2013). We discretized the information (disturbed/ undisturbed) and rasterized the stand polygon data to a grid of 10 × 10 m. Subsequently, we used this grid to calculate an odds ratio for the probability that the two disturbance events affected the same locations on the landscape (i.e., the odds that areas disturbed in the first episode were disturbed again in the second episode). We calculated the 95% confidence interval of the odds ratio using the vcd package in R (Meyer et al., 2016).

To gain further insights into the drivers of the second disturbance period we ran simulations under a combination of different land use and disturbance histories. Specifically, we investigated the effect of two factors on the growing stock disturbed during the second disturbance episode by controlling for their effects individually and in combination, resulting in four simulated scenarios. The two factors considered were (i) the first episode of natural disturbance (1917-1923), and (ii) forest management between 1923 (the end of the first disturbance episode) and 1997 (the foundation of Kalkalpen National Park) (Fig. 2). Differences among scenarios were compared by means of permutation-based independence tests using the coin package (Hothorn et al., 2017).

To address our second objective, i.e., evaluating the impact of past land use and natural disturbance as well as future climate on the 21st century carbon sink strength, we extended our factorial simulation design to also account for the second disturbance episode and different future climate scenarios. Hence, a third factor considered in the simulated landscape history was the second natural disturbance episode (2007-2013) (Fig. 2). The factorial combination of elements representing the actual history of our study landscape was chosen as a reference for assessing the effects of past disturbance and land use on future C uptake. After 2013 four different climate scenarios were simulated for all alternative disturbance histories, to assess the impacts of climate change on the future NEE of the landscape.

All simulations were started from the landscape conditions in 1905, determined by means of the legacy spin-up procedure described above. From 1905 to 1923 management and natural disturbances were implemented in the simulation as recorded in the stand-level archival sources. After 1923, natural disturbances were simulated dynamically using the respective iLand disturbance modules. For the second disturbance episode (2007 – 2013) the observed peak wind speeds for the storms Kyrill (2007), Emma (2008) and Paula (2008) were used in the simulation (see Seidl and Rammer 2017 for details). Beyond 2013, natural disturbances were dynamically simulated with iLand, however, we excluded high intensity wind disturbance events to control for confounding effects with past disturbance events. Specifically, we randomly sampled annual peak wind speeds from the distribution of years before 2006, and simulated the wind and bark beetle dynamics emerging on the landscape (see also Thom et al., 2017a).

Management interventions from 1924 to 1997 were simulated using ABE. The individual silvicultural decisions were thus implemented dynamically by the management agent in the model, based on generic stand treatment programs of past management in Austria's federal forests and the emerging state of the forest. The advantage of this approach was that management was realistically adapted to different forest states in the simulations, e.g., with harvesting patterns differing in the runs in which the disturbance episode 1917 – 1923 was omitted. Moreover, in line with the technical revolutions of the 20th century (Fig. 2) the simulated management agent was set to account for an intensification of forest management over time (e.g., a higher number of thinnings and shorter rotation periods). In summary, our simulation design consisted of 32 combinations of different land use and disturbance histories and climate futures (first disturbance episode (yes/no) × management (yes/no) × second disturbance episode (yes/no) × 4 climate scenarios). In order to account for the stochasticity of iLand (e.g., with regard to bark beetle dispersal distance and direction, uprooting and breakage probability during storm events etc.) we replicated each scenario combination 20 times (i.e., in total 640 simulation runs) for the years 1905 – 2099 (195 years).

We evaluated the ability of iLand to reproduce past natural disturbance and land use as well as the resultant forest vegetation dynamics on the landscape by comparing simulations of the baseline scenario (i.e., including historic climate, as well as reconstructed natural disturbance and land use) with independent empirical data for different time periods: The simulated amount of timber extracted was compared to historical records for three time periods signifying major technical system changes during the 20th century (Fig. 2). Simulated impacts of the second disturbance episode (2007 – 2013) on growing stock were compared against empirical records from KANP. Model outputs for species shares and total growing stock were compared against historical records for the year 1905, testing the ability of the legacy spin-up to recreate the initial vegetation state. Furthermore, simulated species shares and growing stocks were related to observations for 1999, i.e., testing the capacity of iLand to faithfully reproduce forest conditions after 95 years of vegetation dynamics. The results of all these tests can be found in the Supplement Sections S2 and S3.

We used simulation outputs to investigate the changes in NEE over time and across different scenarios. NEE denotes the net C flux from the ecosystem to the atmosphere, with negative values indicating ecosystem C gain (Chapin et al., 2006). To determine the impact of past disturbance and land use as well as future climate on the 21st century carbon balance of the landscape, we first computed the cumulative NEE over the period 2014 – 2099 for each simulation. Next, the effects of past disturbance and land use as well as future climate were determined from mean differences between the different factor combinations in the simulation experiment with regard to their cumulative NEE in 2099. P-values were computed by means of independence tests (Hothorn et al., 2017). All analyses were performed using the R language and environment for statistical computing (R Development Core Team 2017).

3. Results

3.1 Reconstructing historic landscape dynamics

Using iLand, we were able to successfully reproduce historic vegetation dynamics on the landscape. The results from the legacy spin-up revealed a good match with the species composition and growing stock expected from the historic records for the year 1905 (see Section S2 including Fig. S5, Fig. S6). Furthermore, the iLand management module ABE was well able to reproduce the intensification of forest management over the 20th century (Fig. S7). Only the first evaluation period (1924 – 1952) resulted in a small overestimation of simulated harvests. Further, the simulated wind and bark beetle disturbances between 2007 and 2013 corresponded well to the expected values derived from KANP inventories (Fig. S8). Our dynamic simulation approach adequately reproduced the tree species composition and growing stock at the landscape scale after 95 years of simulation (Fig. S9). Despite an intensification of harvests until 1997 and the occurrence of a major disturbance event in 1917 – 1923, the average growing stock on the landscape doubled between 1905 and 2013 (Fig. S10). At the same time total ecosystem carbon increased by 40.9% (Fig. S11). European beech dominance increased over the 20th century, in particular at lower elevations (Fig. S10, Fig. 1e and 1f). Further details on historic landscape development can be found in the Supplement in Sections S2 and S3 (Fig. S4-S11).

3.2 Long-term drivers of natural disturbances

We used the empirically derived spatial footprint of two episodes of natural disturbance 90 years apart to investigate the long-term temporal interactions between disturbances. Both disturbance episodes were found to have a similar impact on growing stock (117,441 m^3 and 93,084 m^3 of growing stock disturbed, respectively), whereas the first episode affected an area more than twice the size of the second episode (2334 ha and 1116 ha, respectively). Only 9.2% of the area disturbed during the first episode was also affected by the second episode (Fig. 3). Whereas the first disturbance episode mainly affected the central and southern reaches of the study area, the effects of the second disturbance episode were most pronounced in the northern parts of the landscape. The odds ratio of 0.49 ($p<0.001$) revealed a lower probability that the same location of the first disturbance episode is affected by the second disturbance episode on the landscape compared to the odds that a previously undisturbed area is disturbed by the second disturbance episode. Based on our simulations we found only a moderate positive effect of the first disturbance episode on the volume disturbed during the second episode (+8,181 m^3, $p=0.401$). In contrast, land use had a considerable impact on the second disturbance episode. On average, land use increased the volume disturbed by +28.927 m^3 ($p<0.001$).

3.3 The effect of past disturbance and land use as well as future climate on 21st century carbon sequestration

Our simulations revealed a considerable impact of past land use on the current state of total ecosystem carbon (Table 1). On average over all scenarios, the cessation of land use resulted in an increase in carbon stocks of +39.7 tC ha^{-1} (+9.2%) in 2013. The two episodes of natural disturbance had a limited effect on current carbon stocks. The omission of both natural disturbance episodes increased carbon stocks in 2013 by only +4.2 tC ha^{-1} (+0.9%). Conversely, past land use initiated a strong and continuous positive legacy effect on the future cumulative carbon uptake of the landscape beyond 2013 (Table 1, Fig. 4), resulting from a persistent recovery of growing stocks (Table 2). Notably, past land use caused a cumulative decrease in future NEE of -41.8 tC ha^{-1} ($p<0.001$) until 2099 on average over all scenarios. The second disturbance episode resulted in an initial release of carbon (positive NEE) lasting for several years after the event, followed by a reversal of the trend towards a negative NEE effect (Fig. 4). Its overall impact on cumulative NEE at the end of the simulation period was -3.1 tC ha^{-1} ($p=0.191$), i.e. over the 21st century the recent disturbance period had an overall positive effect on forest C sequestration. The first disturbance episode (1917-1923) had almost no effect on the forest carbon dynamics in the 21st century (NEE effect of -0.6 tC ha^{-1}, $p=0.792$).

Climate change weakened the carbon sink strength on the landscape, mainly as a result of a climate-mediated alteration of successional trajectories (Table 2). Also, climate change effects on NEE were more variable compared to disturbance legacy effects, with increasing uncertainty over time as a result of differences in climate scenarios (Fig. 4). On average, climate change increased the cumulative NEE until 2099 by +22.9 tC ha^{-1} ($p<0.001$), and thus reduced the carbon uptake of the landscape relative to a continuation of historic climate (Fig. 4).

4. Discussion

4.1 Human and natural disturbance interactions

Based on previous studies assessing the spatial and temporal autocorrelation of disturbances in Europe (Marini et al., 2012; Schurman et al., 2018; Stadelmann et al., 2013; Thom et al., 2013) we hypothesized that a disturbance episode in the early 20th century influenced disturbances in the early 21st century. However, our analysis revealed a low probability for the same area to be affected by two consecutive disturbance episodes of the same disturbance agents (Fig. 3). Moreover, our simulations only indicate a weak correlation between the two consecutive disturbance episodes on the landscape. Hence, our data do not support the hypothesis of amplified disturbance interactions and long-term cyclic disturbance in Central European forests. Our initial assumption was based on the expectation of uniform recovery after the first disturbance episode, with large parts of the landscape reaching high susceptibility to wind and bark beetles simultaneously. However, disturbances can also have negative, dampening effects on future disturbance occurrence, e.g., when they lead to increased heterogeneity (Seidl et al., 2016) and trigger autonomous adaptation of forests to novel environmental conditions (Thom et al., 2017c). The low overlap between the two disturbance episodes reported here could thus be an indication for such a dampening feedback between disturbances in parts of the landscape, yet further tests are needed to substantiate this hypothesis for Central European forest ecosystems. An alternative explanation for the diverging spatial patterns of the two disturbance episodes might be a different wind direction in the storm events initiating the two respective episodes, affecting different parts of the highly complex mountain forest landscapes. Also the legacy effects from past land use were different for each episode. The more open structure within stands resulting from heavy exploitation before 1900 may, for instance, have increased wind susceptibility in the central and southern reaches of the landscape.

In contrast to our finding regarding interactions between natural disturbances, our simulations supported our expectation of an amplifying effect of past land use on recent disturbance activity. This finding is congruent with other analyses suggesting past forest management as a driver of current natural disturbance regimes (Hanewinkel et al., 2014; Schelhaas, 2008; Seidl et al., 2011). Past forest management in Central Europe has, for instance, strongly promoted Norway spruce, which is one of the most vulnerable species to natural disturbances in the region (Hanewinkel et al., 2008; Pasztor et al., 2014). Pure stands of Norway spruce are particularly conducive to large-scale eruptions of bark beetles, and even-aged management creates edges that are highly susceptible to strong winds (Hanewinkel et al., 2014; Thom et al., 2013). Our analysis thus suggests that as disturbances increase under climate change (Seidl et al., 2017; Thom et al., 2017a), forests that have been homogenized by past land use are at particular risk.

4.2 The role of legacies on future C uptake

Past studies investigating drivers of the forest carbon balance have largely focused either on historic factors (Keenan et al., 2014; Naudts et al., 2016) or future changes in the environment (Manusch et al., 2014; Reichstein et al., 2013). Only few studies to date have explicitly quantified the effect of legacies from natural disturbance and land use when assessing climate change impacts on the future carbon uptake of forest ecosystems. However, disregarding legacy effects could lead to a misattribution of future forest C changes. Here we harnessed an extensive long-term documentation of vegetation history to study impacts of past natural disturbance and land use as well as future climate on the future NEE of a forest landscape. We found long-lasting legacy effects of both past natural disturbance land use and on the forest carbon cycle (see also Gough et al., 2007; Kashian et al., 2013; Landry et al., 2016; Nunery and Keeton, 2010), supporting our hypothesis regarding the importance of legacies for future C dynamics. While the legacy effect of past land use was strong, the impact of natural disturbances on the future NEE was an order of magnitude lower (Fig. 4). Here it is important to note that our results are strongly contingent on the intense and century-long land use history in Central Europe. A dynamic landscape simulation study for western North America, for instance, emphasized the dominant role of natural disturbances to determine future NEE (Loudermilk et al., 2013). In our study system, however, land use legacies may have a stronger effect on future NEE than past natural disturbances and future changes in climatic conditions (Fig. 4). Disregarding legacy effects may thus cause a substantial bias when studying the future carbon dynamics of forest ecosystems. It has to be noted, however, that our study only considered three relatively moderate climate change scenarios. Hence we might underestimated the effect of climate change on NEE, if future climate change will follow a more severe trajectory (see e.g., Kruhlov et al, 2018). Furthermore, it is likely that over longer future time frames as the one studied here the effects of climate change will become more important relative to past legacy effects (Temperli et al., 2013).

While we here focused on the strength of legacy effects, our results also provide insights into their duration. Land-use related differences in C stocks persisted throughout the simulation period, with trajectories converging only towards the end of the 21st century. Hence, our data indicate that land use legacies affect the forest C cycle for at least one century in our study system. Despite the considerably lower impacts of natural disturbances, the legacy effect of the second disturbance episode also lasted for several decades (Fig. 4). Future efforts should aim at determining the duration of past legacies more precisely, considering a variety of different forest conditions (e.g., Temperli et al., 2013). Moreover, while we here focus on the effects of wind and bark beetle disturbances – currently the two most important natural disturbance agents in Central Europe (Thom et al., 2013) – as well as their interactions, future climate change may increase the importance of other disturbance agents not investigated here (see e.g., Wingfield et al., 2017).

The specific disturbance history of our study area, characterized by an intensive disturbance and land use history and major socio-ecological transitions throughout the 20th century, is key for interpreting our findings. In particular, the cessation of forest management in 1997 had a very strong impact on the future carbon balance of the landscape (an on average 52.8 and 13.4 times higher effect than the first and second episodes of natural disturbances, respectively – see Fig. 4). In addition to disturbance legacy effects, also climate change significantly affected the future NEE. In contrast to the general notion that temperate forests will serve as a strong carbon sink under climate change (Bonan, 2008), our dynamic simulations suggest that climate change will decrease the ability of the landscape to sequester carbon in the future, mainly by forcing a transition to forest types with a lower carbon storage potential (see also Kruhlov et al., 2018; Thom et al., 2017a). However, considerable uncertainties of climate change impacts on the carbon balance of forest ecosystems remain (e.g., Manusch et al., 2014). These uncertainties may arise from a wide range of potential future climate trajectories, but also from a limited understanding of processes such as the CO_2 fertilization effect on forest C uptake (Kroner and Way, 2016; Reyer et al., 2014). In addition to the direct impacts of climate change (e.g., via temperature and precipitation changes) on forest ecosystems, climate change will also alter future natural disturbance regimes (Seidl et al., 2017). The potential for such large pulses of C release from forests is rendering the role of forests in climate mitigation strategies highly uncertain (Kurz et al., 2008; Seidl et al., 2014a).

5. Conclusions

Past natural disturbance regimes and land use have a long-lasting influence on forest dynamics. In order to project the future of forest ecosystems we thus need to better understand their past. We here showed how a combination of historical sources and simulation modeling – applied by an interdisciplinary team of scientists – can be used to improve our understanding of the long-term trajectories of forest ecosystems (Bürgi et al., 2017; Collins et al., 2017; Deng and Li, 2016). Two conclusions can be drawn from the strong historical determination of future forest dynamics: First, as temperate forests have been managed intensively in many parts of the world (Deng and Li, 2016; Foster et al., 1998; Naudts et al., 2016), their contribution to climate change mitigation over the coming decades is likely determined already to a large degree by their past (see also Schwaab et al., 2015). This means that for the time frame within which a transformation of human society needs to be achieved in order to retain the earth system within its planetary boundaries (Steffen et al., 2011), the potential for influencing the role of forests might be lower than frequently assumed. Efforts to change forest management now to mitigate climate change through *in situ* C storage have high potential (Canadell and Raupach, 2008), but will likely unfold their effects too late to make a major contribution to climate mitigation in the coming decades. Second, any intentional (by forest management) or unintentional (by natural disturbances) changes in forest structure and composition may have profound consequences for the future development of forest ecosystems. This underlines that a long-term perspective integrating past and future ecosystem dynamics is important when studying forests, and that decadal to centennial foresight is needed in ecosystem management.

Author contribution

RS, DT and WR designed the study, RG collected historical data from archives, DT and WR performed simulations, DT analyzed the outputs, all authors contributed to writing the manuscript.

Competing interests

The authors declare that they have no conflict of interest.

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Tables

Table 1. Development of total ecosystem carbon stocks (tC ha^{-1}) over time and in different scenarios of disturbance and land use history as well as future climate. Values are based on iLand simulations and indicate means and standard deviations (SD) over averaged landscape values of the replicates in the respective scenarios. “Historic climate” assumes the continuation of the climate 1950 – 2010 throughout the 21st century, while “Climate change” summarizes the effect of three alternative climate change scenarios for the 21st century. The first three columns indicate the respective permutation of the simulated disturbance and land use history, with the first line representing the historical reconstruction of landscape development. Y=yes, N=no.

First nat. dist. episode	Land use	Second nat. dist. episode	year 1905	year 1923		year 1997		year 2013		Historic climate year 2099		Climate change year 2099	
			mean	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD
Y	Y	Y	303.5	331.1	<0.1	403.2	0.7	427.8	0.8	487.7	0.7	466.4	23.7
Y	N	Y	303.5	331.2	<0.1	457.5	0.6	466.7	0.7	487.2	1.0	463.3	20.9
Y	Y	N	303.5	331.0	<0.1	403.2	0.7	430.6	0.7	488.2	0.7	467.0	23.3
Y	N	N	303.5	331.2	<0.1	457.5	0.5	470.9	0.7	487.3	0.7	463.4	21.1
N	Y	Y	303.5	332.7	0.1	404.3	0.8	428.8	0.8	487.8	0.8	466.3	23.7
N	N	Y	303.5	333.0	0.1	458.7	0.5	468.0	0.6	487.8	0.8	464.0	21.3
N	Y	N	303.5	332.7	0.1	404.2	0.7	431.3	0.8	488.3	0.9	466.4	23.6
N	N	N	303.5	333.0	0.1	458.6	0.5	471.7	0.6	487.9	0.9	464.1	21.0

Table 2. Growing stock by tree species ($m^3\ ha^{-1}$). Values are based on iLand simulation runs and indicate species means and standard deviation (SD) over averaged landscape values of the replicates in the respective scenarios. "Historic climate" assumes the continuation of the climate 1950 – 2010 throughout the 21st century, while "Climate change" summarizes the effect of three alternative climate change scenarios for the 21st century.

								Historic climate		Climate change	
	year 1905	year 1923		year 1997		year 2013		year 2099		year 2099	
Tree species	mean	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD
Abies alba	4.2	2.1	0.0	9.7	2.2	12.7	2.6	28.7	6.1	33.7	7.6
Fagus sylvatica	68.0	76.8	0.6	165.6	39.8	198.5	34.4	286.8	2.8	309.7	19.7
Larix decidua	21.5	23.9	0.2	41.7	5.2	40.5	9.7	17.4	7.9	16.2	7.1
Picea abies	116.3	138.6	0.5	235.7	43.6	250.8	40.5	276.3	36.6	229.9	33.6
Other tree species	2.3	6.0	0.2	14.7	1.4	16.0	1.6	13.4	0.5	23.8	1.7
Total	212.3	247.4	0.8	467.4	79.0	518.5	66.0	622.6	35.4	613.3	46.5

Figures

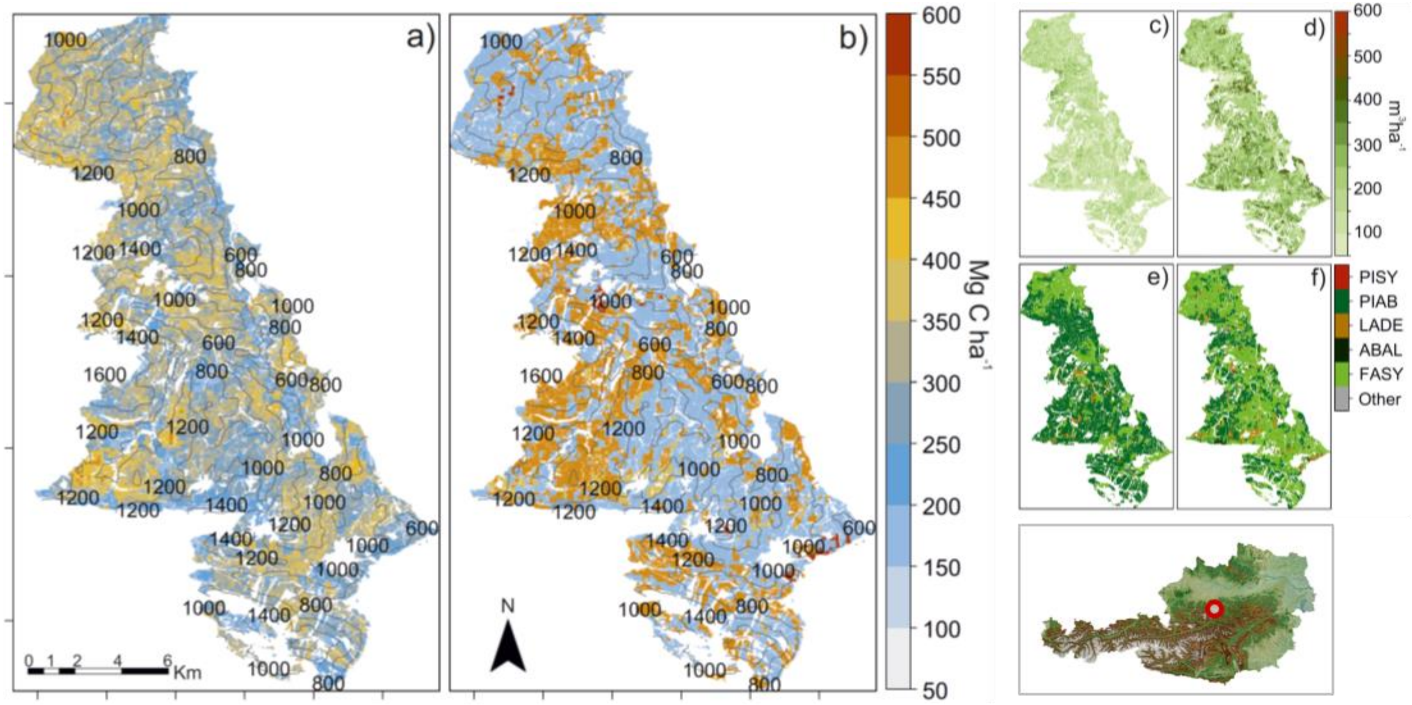

Fig. 1: State of forest ecosystem attributes across the study landscape in 1905 and 2013 as well as location of the landscape in Austria (lower right panel). Panels (a) and (b) show the distribution of total ecosystem carbon, while panels (c) and (d) present growing stock, and panels (e) and (f) indicate the dominant tree species (i.e., the species with the highest growing stock in a 100m pixel) in 1905 and 2013, respectively. PISY = *Pinus sylvestris*, PIAB = *Picea abies*, LADE = *Larix decidua*, ABAL = *Abies alba*, FASY = *Fagus sylvatica*. “Other” refers to either other dominant species

not individually listed here due to their low abundance, or areas where no trees are present. Isolines represent elevational gradients in the landscape (in m asl).

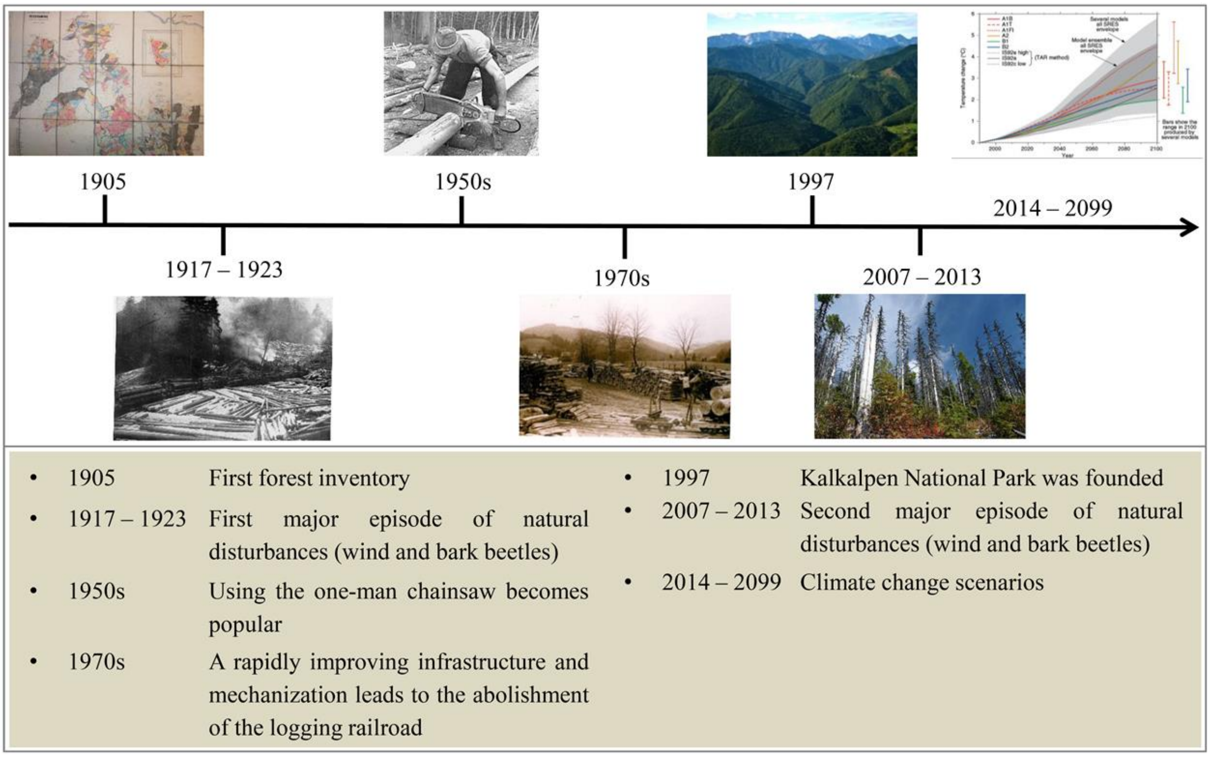

Fig. 2. Timeline of historic events of relevance for the simulation of the study landscape. Image credits: 1905 and 1917 – 1923: archives of the Austrian Federal Forests; 1950s: https://waldwissen.at; 1970s: https://atterwiki.at; 1997: http://kalkalpen.at; 2007 – 2013: photo taken by the authors of this study; 2014 – 2099: http://climate-scenarios.canada.cau.

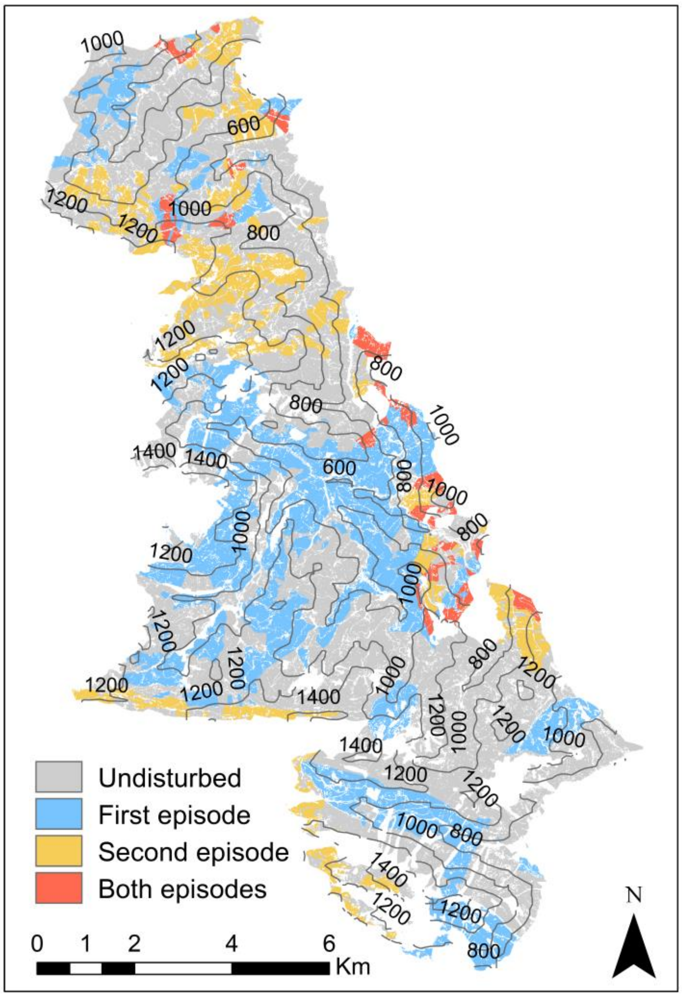

Fig. 3: Disturbance activity in two episodes of natural disturbance, from 1917 – 1923 (first episode) and 2007 – 2013 (second episode). Isolines represent elevational gradients (in m asl).

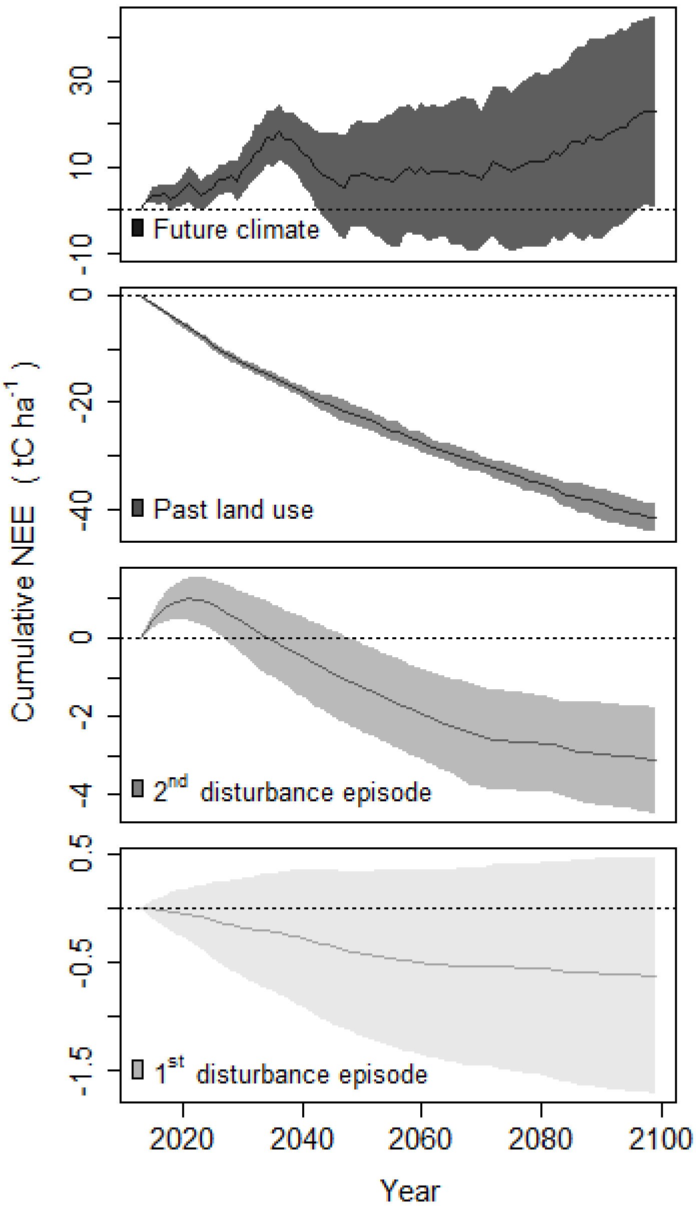

Fig. 4. Mean cumulative change in future net ecosystem exchange (NEE) induced by climate change as well as legacies of past land use and natural disturbance (i.e., the first (1917-1923) and second (2007-2013) disturbance episodes, respectively). Differences in NEE were derived from a factorial simulation experiment, comparing each factor to its baseline (e.g., future climate scenarios to baseline climate) while keeping all other factors constant. Shaded areas denote the standard deviation in NEE for the respective scenarios. NEE is the carbon flux from

the ecosystem to the atmosphere (i.e., NEE = -NEP). Note that y-axis scales differ for each panel.