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From sink to source: changing climate and disturbance regimes could tip the 21st century carbon balance of an unmanaged mountain forest landscape

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Forests are one of the most important components of the global carbon cycle. Consequently, forest protection as a nature-based climate solution has garnered increasing interest. Protected areas instated to safeguard biodiversity provide an opportunity to maximize carbon storage *in situ,* with important co-benefits between conservation and climate change mitigation. However, changing climate and disturbance regimes put this carbon storage function at risk. Here we investigated carbon sequestration and storage in a protected landscape in the German Alps (Berchtesgaden National Park) throughout the 21st century. We simulated the impacts of climate change as well as increasing wind and bark beetle disturbances on cumulative Net Ecosystem Production using a process-based forest landscape model. Considering a wide range of potential changes in wind frequency and speed under a variety of climate change scenarios, we addressed the question under which future conditions the landscape will turn from a carbon sink to a carbon source. While the landscape was a net carbon sink at the end of the simulation in 76 per cent of the simulation runs, increasing disturbances and climate change greatly reduced its carbon sink capacity. Under RCP2.6, the landscape remained a robust carbon sink even under elevated disturbance (probability of turning from sink to source between 0 per cent and 25 per cent). In contrast, carbon release was likely under RCP8.5 even with little change in the disturbance regime (probability: 30 per cent to 95 per cent). Productive areas in lower elevations that currently have the highest carbon density on the landscape were contributing most strongly to a reduction of the carbon sink strength. Our study reveals that the effect of protected areas acting as nature-based climate solutions might be overestimated if the risks from changing climate and disturbance regimes are neglected. We therefore call for a more explicit consideration of future forest dynamics in the discussion of the potential role of forests in climate change mitigation.

Introduction

Forests play an important role in the global climate system and are frequently found at the centre of discussions on climate change mitigation and natural climate solutions (Bonan, 2008; Whitehead, 2011; Kaarakka *et al.*, 2021; Mori *et al.*, 2021). Suggestions on how to leverage the carbon sequestration and storage ability of trees for climate protection range from large-scale afforestation to strict protection of forests to safeguard areas where large amounts of carbon are stored (Canadell and Raupach, 2008; Luyssaert *et al.*, 2008). However, beyond questions of conflicting land uses hampering the implementation of such projects, the ability of forests to sequester and store carbon is challenged by disturbances and climate change itself (Kurz *et al.*, 2008; Elkin *et al.*, 2013; Reyer *et al.*, 2014, 2017). Increasing forest mortality (Senf *et al.*, 2018) puts forests at risk and can strongly reduce their carbon storage and sink strength (Lindroth *et al.*, 2009).

Natural disturbances are a considerable source of uncertainty for the future carbon balance of forest ecosystems. A general increase in forest disturbance has been observed in Europe over the past decades and a further increase is expected

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in the future (Seidl *et al.*, 2014b, 2017). A particularly large element of uncertainty concerns future wind disturbances, both regarding future wind frequency and speed. For Central Europe, a general increase in wind activity is forecast (Mölter *et al.*, 2016) with possibly large increases in both frequency (up to a 33 per cent increase in storm frequency, related to a shift in storm tracks and increased westerly flows, Donat *et al.*, 2010; Zappa *et al.*, 2013) and speed (i.e. wind speed increases of up to 10–15 per cent, Beniston *et al.*, 2007; Fink *et al.*, 2009). These changes are generally attributed to changes in large-scale circulation patterns, such as the North Atlantic Oscillation (NAO) as well as increases in the available potential energy in the atmosphere, resulting from increased atmospheric temperature and moisture (Donat *et al.*, 2010; O'Gorman, 2010). Wind disturbances have already increased strongly in recent years in Europe (Gregow *et al.*, 2017), with higher change rates than many other major disturbance agents such as fire (Sebald *et al.*, 2021; Senf and Seidl, 2021). The increase in wind disturbance, combined with other elements of climate change (e.g. changing temperature and precipitation regimes) and the resultant increase in the activity of other disturbance agents (e.g. bark beetle outbreaks), may impair forest-based climate change mitigation strategies in Europe, as it could tip the forest carbon balance from a sink to a source (Lindroth *et al.*, 2009).

Protected areas, i.e. areas set aside for conservation purposes and developing without human interference, are expected to substantially contribute to climate change mitigation by sequestering carbon and storing it for long timespans (Luyssaert *et al.*, 2008; Erb *et al.*, 2018). In many parts of the world the stronger sink effect of protected areas is also due to a recovery from past management that caused carbon debts and leads to a period of increased carbon uptake after management has ceased (Erb *et al.*, 2018). This means that the sink strength of protected areas could weaken over time as carbon debts are recovered and the carbon sequestration rate decreases. Additionally, protected areas are not exempt from natural disturbances; in fact, recent studies have shown considerable disturbance impacts in protected forest areas of Europe (Senf and Seidl, 2018) and the globe (Seidl *et al.*, 2020). This puts into question whether protected areas will indeed be able to make a disproportionally strong contribution to climate change mitigation throughout the 21st century. Here we studied a strictly protected landscape in the German Alps (Berchtesgaden National Park) to investigate the impacts of intensifying disturbances (wind and bark beetles) under climate change on the forest's carbon balance. The primary goal of our study was to investigate whether future disturbance regimes can shift the landscape from a carbon sink to a carbon source in the 21st century. In particular, we addressed three questions:

1. How are varying wind speeds and frequencies of storm events impacting the carbon balance of a forest landscape under climate change?
2. What are potential thresholds of increasing wind speed and frequency at which the landscape might shift from carbon sink to source?
3. Which parts of the landscape are particularly affected by the changes in climate and disturbance regimes?

Material and methods

Study landscape

Berchtesgaden National Park (BGNP) is a protected area (IUCN category II) located in the Northern Alps in the German state of Bavaria. It was established in 1978 and covers 20 808 ha of forests, alpine meadows, rocks and water bodies. Historically, the Berchtesgaden landscape experienced many centuries of intensive land use, because of a large demand for wood for local salt mining beginning in the 16th century. In the early 20th century reforestation and conservation efforts began, culminating in the foundation of the national park (Zierl, 2009). Today, the majority of the landscape is exempt from management (75 per cent), with management on the remainder of the area focused on restoration activities (Thom and Seidl, 2022). The climate is cool temperate (mean annual temperature 5.3°C) with high precipitation (1665 mm mean annual precipitation sum). Temperature decreases while precipitation increases with elevation (minimum: 603 m a.s.l., maximum: 2713 m a.s.l.). Geologically, the area is dominated by limestone and dolomite with mainly shallow Rendzina soil types. Forests are mainly composed of Norway spruce (*Picea abies* (L.) H. Karst.), European beech (*Fagus sylvatica* L.) and European silver fir (*Abies alba* Mill.). Conifer dominance increases with elevation. In the highest elevations (above 1600 m a.s.l.), the forest is dominated by Swiss stone pine (*Pinus cembra* L.), European Larch (*Larix decidua* [Mill.]) and Dwarf mountain pine (*Pinus mugo* Turra) that form the tree line at approximately 1800 m a.s.l. Due to the steep elevation gradient there is a considerable decrease in productivity from lower to higher elevations, resulting in higher total ecosystem carbon stocks at lower elevations under current conditions (Figure 1).

The iLand model

We used iLand, the individual-based forest landscape and disturbance model to investigate the impact of changing climate and disturbance regimes on the carbon balance of BGNP. iLand is a high-resolution, process-based model simulating forest ecosystem processes on multiple scales, from individual trees to landscapes (Seidl *et al.*, 2012a). Primary production is modelled based on a resource-use efficiency approach (Landsberg and Waring, 1997) and is influenced by daily climate conditions (temperature, precipitation, radiation and vapour pressure deficit), atmospheric CO_2 concentrations (varying annually) and soil conditions (sand, silt and clay fractions, effective soil depth and available nitrogen), which are time invariant. The acquisition of carbohydrates by each tree is based on its competitive status derived from available light. The mortality probability of a tree is influenced by its age and size as well as its carbon balance (stress-related mortality). Another cause of tree mortality is disturbance (see more details below). Regeneration in iLand is simulated spatially explicitly, accounting for seed availability and dispersal, seedling establishment and seedling and sapling growth and survival, influenced by the prevailing environmental conditions (Seidl *et al.*, 2012b). iLand dynamically tracks carbon pools and fluxes, both above and below ground, considering carbon in foliage, branches, stems, snags, downed deadwood, fine and coarse roots, litter and soil

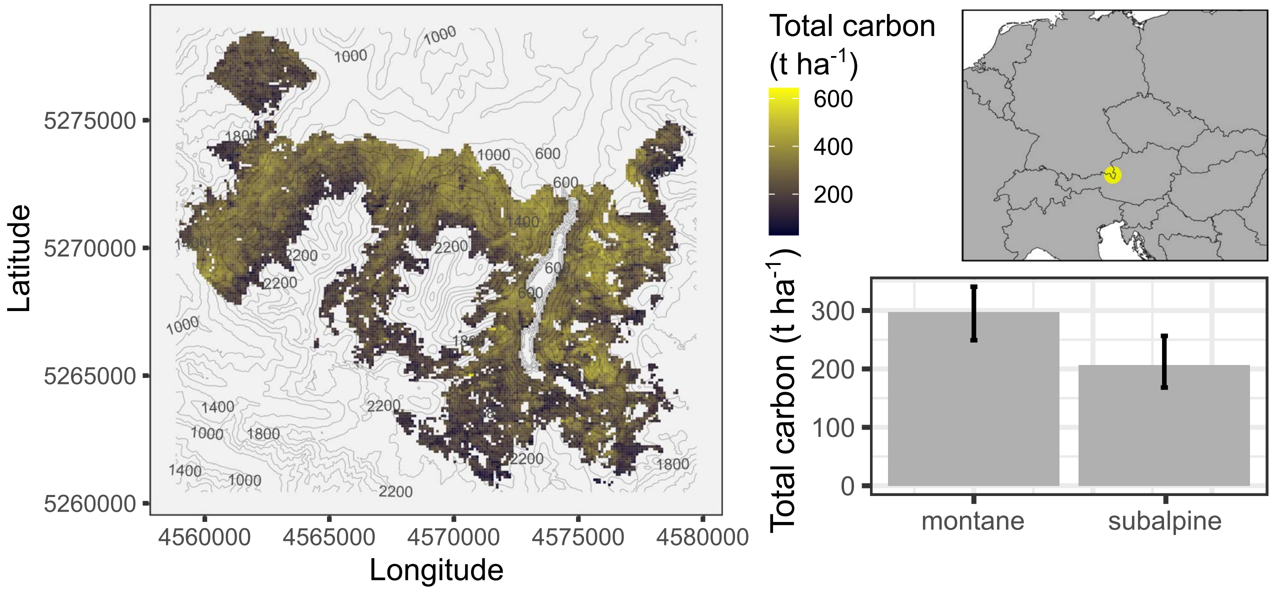

Figure 1 Current total carbon stocks (t ha^{-1}, above and below ground, including live and dead trees as well as litter and soil C) at Berchtesgaden National Park (year: 2020, starting point of the simulation) at the level of one hectare cells (left) and by elevation zones (median and interquartile range, bottom right). The carbon values at the start of the simulation shown here include carbon in downed and standing deadwood and live biomass carbon stocks as well as soil carbon. They are based on a combination of inventory data and a simulation model spinup. Submontane refers to elevation below 800 m a.s.l., montane is the zone between 800 and 1400 m a.s.l., and subalpine above 1400 m a.s.l. The location of the landscape (marked in yellow) within Central Europe is shown at the top right.

compartments separately (see also Supplementary Figure S7, Seidl *et al.*, 2012b).

Disturbances such as wind and bark beetles are simulated spatially explicitly on the landscape. Wind effects are modified by forest structure (stand height, presence of gaps and exposed edges, sheltering effects within the tree population) as well as species identity (species-specific resistance against uprooting and stem breakage). Wind events are simulated dynamically, taking into account edges newly created during a storm event, which are particularly vulnerable (Seidl *et al.*, 2014a). Furthermore, soil freezing is an important factor, influencing whether a tree is uprooted or suffers stem breakage (Seidl *et al.*, 2014a). We here simulated a maximum of one major wind event per year (see details below). For each wind event, the day when it occurs is specified (to account for soil freezing and leaf status of deciduous trees) as well as the predominant wind direction.

Bark beetle dynamics are simulated based on beetle phenology and explicitly take into account bark beetle dispersal, over-wintering success, as well as host tree availability and defence (Seidl and Rammer, 2017). In our study, the iLand bark beetle module is parametrized for the interaction between Norway spruce and the European spruce bark beetle (*Ips typographus* L., Coleoptera: Curculionidae), which is the most important bark beetle species in Central Europe (Seidl *et al.*, 2016; Hlásny *et al.*, 2021). Climate has a direct impact on bark beetles through accelerating beetle phenology and decreasing the level of host tree defence. Disturbance interactions can occur, for example, when low-defence breeding material for bark beetles becomes available after a wind-throw or when beetle attacks create new wind-exposed edges (Raffa *et al.*, 2008; Seidl and Rammer, 2017).

iLand was evaluated thoroughly for the study landscape to ensure its ability to realistically reproduce forest dynamics in Berchtesgaden. Productivity was evaluated across a large spatial gradient (3452 inventory points, spread across the landscape in a systematic grid), with stand age distribution per species ranging from 50 to 892 years. Moreover, the potential natural vegetation (PNV) simulated by iLand was compared against a PNV estimate by local experts (Reger and Ewald, 2012). To test the dynamic disturbance modules for wind and bark beetles, we ran the model for recent historical conditions and compared emerging disturbances to remotely sensed estimates across BGNP during the period 1998–2016 (Senf *et al.*, 2017). The model reproduced observed patterns of productivity, potential natural vegetation and disturbances satisfactorily. A detailed description of the evaluation can be found in the Supplementary Materials of Thom *et al.*, 2022). Furthermore, iLand has been applied and tested extensively in both Europe and North America for a variety of ecosystems and research questions (Thom *et al.*, 2017a, 2017b; Hansen *et al.*, 2018; Honkaniemi *et al.*, 2020; Rammer *et al.*, 2021). A more extensive description of iLand and its disturbance modules can be found in Seidl *et al.* (2012a, 2012b, 2014a), Seidl and Rammer (2017) and Thom *et al.* (2017c). iLand model code, software and documentation are available online at http://iland-model.org/.

Model input and scenario information

To initialize and simulate the BGNP landscape, the model required data for soils, current vegetation, daily climate and disturbance drivers (see Supplementary Table S1 for an overview of the variables needed and data sources used, as well as

Supplementary Figure S1 for the initial stand age distribution of the landscape). A detailed description of landscape initialization for the starting year 2020 and at BGNP is given by Thom *et al.* (2022, including Supplementary Material). The initialization of carbon pools—a particularly important aspect for the present study—was done using a hybrid approach, combining inventory data for live biomass (using allometric functions) and deadwood with a model spinup routine considering historical management for litter and soil carbon pools (see also Supplementary Figure S2 and explanation for details). In the following, we describe the climate and wind disturbance scenarios used, which are instrumental for answering our specific research questions.

We simulated a total of seven climate time series from 2020 onwards (all simulations start from the same initialization), one representing the continuation of historical climate throughout the 21st century and two each for the Representative Concentration Pathways (RCP) 2.6, 4.5 and 8.5. The historical climate was represented by observed climate for the period 1980–2009, from which we randomly sampled 80 individual years with replacement to produce a stable timeseries with conditions similar to recent historical climate as a baseline scenario. For each RCP we chose one scenario with comparably moderate and one scenario with strong increases in simulated disturbance impacts from an ensemble of 22 climate change projections as predicted in Thom et *al.* (2022). Ensemble data were downscaled by the Bavarian Environmental Agency (Zier *et al.*, 2020), and are based on the EURO-CORDEX ensemble (Jacob *et al.*, 2014). For each RCP these were one scenario from the GCM MPI-M-MPI-ESM-LR in combination with the RCM SMHI-RCA4 and one scenario from the GCM ICHEC-EC-EARTH in combination with the RCM KNMI-RACMO22E (see Supplementary Table S2 for scenario details and differences to historical climate).

Because future wind speed and frequency remain highly uncertain, we studied their effects across a wide range of plausible future conditions in a full factorial design of five levels each for wind speed and frequency (i.e. a total of 25 wind scenarios for each climate change scenario). The baseline wind scenario was derived from 14 local weather stations in the Berchtesgaden area and includes the maximum 10-min gust wind speed in each year as well as wind direction and date of the wind event (see Thom et *al.* (2022), Supplementary Materials for details). As cutoff for simulating wind disturbance we used a 10-min gust speed of 9 m s^{-1}, which was identified by Usbeck *et al.*, 2010 as the threshold above which notable forest disturbances occur. Wind frequency scenarios ranged from a baseline scenario (historic number of events, i.e. storms above 9 m s^{-1} in 68 per cent of the years) to a 20 per cent increase in events (storms in 82 per cent of years) in five percent increments. Additional events in scenarios with increasing storm frequency were sampled from historical events and assigned to years that previously did not have a wind event. Wind speed (i.e. 10-min gust speed) scenarios also ranged from historical levels (9.00–16.72 m/s) to 20 per cent higher gust speeds (10.80–20.06 m/s) in 5 per cent increments. Wind speed increases were uniformly applied across the landscape, conserving the difference in local wind speeds caused by topography (see Thom et *al.*, 2022). Our 25 wind scenarios were designed to cover the wide range of expected changes in the wind regime of Central Europe (Mölter *et al.*, 2016). For wind frequency, our most extreme simulated increase of 20 per cent is likely a conservative estimate, as studies have predicted increases of as much as ∼30 per cent for Central Europe (Donat *et al.*, 2010). For wind speed our most extreme scenario (20 per cent increase) was somewhat outside the range reported by Fink *et al.* (2009), i.e. an increase of 5–15 per cent. Yet, it remains within the range of possible future changes, given the high uncertainty in future wind speed predictions (McInnes *et al.*, 2011).

We simulated the 8644 ha forest area of BGNP for 80 years (2021–2100), replicating each combination of climate scenario ($n = 7$, 1 historic, 2 each for RCP 2.6, RCP 4.5 and RCP 8.5) and wind scenario ($n = 25$, 5 wind speeds × 5 wind frequencies) ten times. For each replicate, storm events were randomly assigned to different years to account for the stochasticity in the wind system. In total, this amounts to 1750 simulation runs being analysed.

Analysis

We focused on cumulative Net Ecosystem Production (NEP) at the end of the simulation period as our main response variable, allowing us to assess whether the landscape acted as a carbon sink or source in the 21st century. NEP was calculated by deducting heterotrophic respiration and disturbance loss from Net Primary Production (NPP). Cumulative NEP thus is the net change over all carbon pools in the model throughout the study period, with positive NEP indicating a carbon sink and negative NEP indicating a carbon source. We conducted an analysis of variance to untangle to which extent the design variables of our simulation experiment (climate scenario, wind frequency, wind speed) contributed to cumulative NEP. To analyse the joint effects emerging from climate and wind scenarios in the simulations, such as changes in the simulated bark beetle disturbance regime, we compared the amount of forest disturbed by bark beetles to those disturbed by wind. We investigated under which scenario combination (climate × wind scenario) the landscape changed from a carbon sink to a carbon source. Moreover, we assessed the impact of climate and wind regime changes at the resolution of individual 100 × 100 m grid cells to analyse the spatial variation in changes of the carbon budget. For this analysis we specifically contrasted the historical baseline scenario with the most extreme scenario of change (RCP 8.5, 20 per cent increase in wind speed and frequency). All data preparation and analyses were done in R (version 4.0.4., R Core Team, 2021).

Results

Berchtesgaden National Park was a carbon sink to the atmosphere throughout the 21st century in 76 per cent of the simulated scenarios. However, depending on the simulated climate and wind trajectories, the risk for turning into a carbon source (i.e. negative cumulative Net Ecosystem Production (NEP) at the end of the simulation run in the year 2100) was considerable (up to 95 per cent in the most extreme scenarios). In total, 69.5 per cent of the variance in cumulative NEP was explained by the three covariates: RCP, wind frequency and wind speed scenario. Including interactions between the three covariates improved the model only marginally ($R^2 = 69.8$ per cent). Favouring interpretability over explanatory power we thus omitted

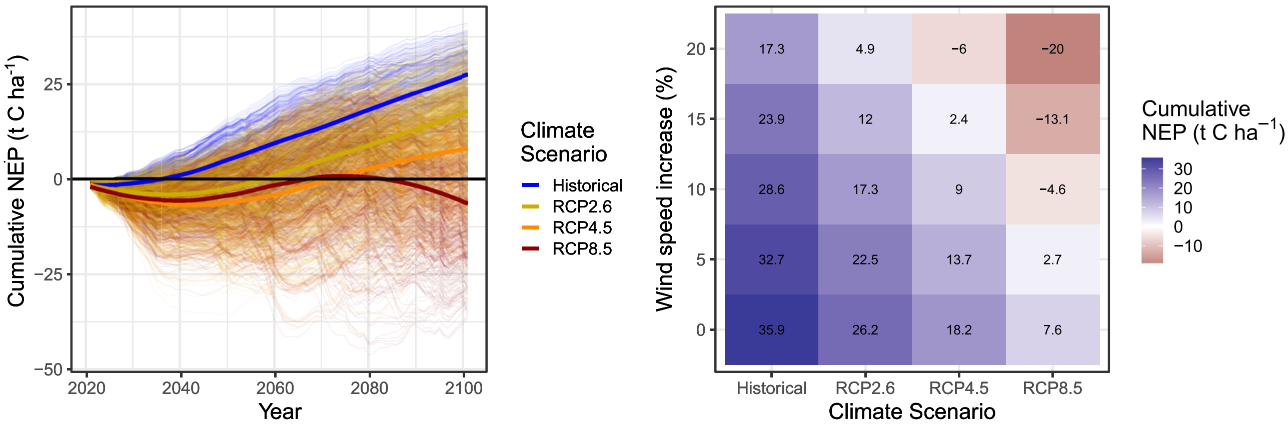

Figure 2 Development of cumulative NEP over time for forests at Berchtesgaden National Park, averaged across 10 replicates of each climate and wind speed scenario (left). Bold lines are smoothed group averages (loess) for each climate scenario. Median cumulative NEP in the year 2100 by climate and wind speed scenario (right). Blue cells indicate the landscape acting as a carbon sink to the atmosphere, red cells indicate a carbon source, with colour saturation indicating sink/source strength.

interactions in our analyses. The single most important factor was RCP, explaining 45.5 per cent of the variance in cumulative NEP, followed by wind speed (23.5 per cent of variance explained). As wind frequency was found to be of subordinate importance (0.5 per cent of variance explained), we focus on the covariates climate scenario and wind speed in the subsequent presentation of the results.

Under historical baseline climate, the landscape always acted as a carbon sink regardless of wind scenario. However, median cumulative NEP in 2100 decreased by 18.6 tons/ha in the most extreme wind scenario (20 per cent faster wind speeds, Figure 2) compared with historical wind regimes. Under moderate climate change (RCP 2.6), the landscape was still a carbon sink in most simulations. Only under the two most extreme wind scenario levels (speed increasing by 15 and 20 per cent), some runs (7 per cent and 25 per cent, respectively) had a negative cumulative NEP in 2100 (Table 1). In all RCP 4.5 runs assuming historical wind regimes the landscape remained a carbon sink. However, with increasing wind speeds, the landscape turned into a carbon source in up to 69 per cent of the simulations (at +20 per cent wind speed) and the median cumulative NEP under the most extreme wind scenario was negative (Figure 2). For the most extreme climate scenario (RCP 8.5), only the historical and 5 per cent increased wind speed scenarios remained a carbon sink to the atmosphere (median trajectory), and all wind speed scenarios had at least a 30 per cent probability of resulting in negative cumulative NEP. Under the most extreme wind speed scenario, 95 per cent of the runs had a negative cumulative NEP in 2100. The difference in median cumulative NEP between the historical baseline and the most extreme wind speed scenario amounted to 27.6 t/ha.

To better understand what drives the NEP patterns emerging from the simulations we explored how climate and wind scenarios influenced important components of carbon uptake (i.e. Net Primary Productivity, NPP) and release (i.e. emissions from dynamically simulated wind and bark beetle disturbances, Table 2). Wind-disturbed volume and area (Supplementary Figures S3–S5) increased strongly with wind speed, but also increased with intensifying climate change. Bark beetle disturbances were primarily driven by climate scenario, but also increased with wind speed, underlining the interaction between wind and bark beetle disturbances (Supplementary Figures S3 and S4). Under historical climate and moderate climate change, most of the disturbed volume resulted from wind. With intensifying climate change, the previous dominance of wind over bark beetle disturbances reverted, however, with bark beetles becoming the most important disturbance agent, especially in lower wind speed scenarios. At higher wind speeds, wind generally remained the dominating disturbance agent, except under RCP8.5 where high warming provided particularly favourable conditions for bark beetle population development. NPP increased with intensifying climate change (due to an increase in atmospheric CO_2 and a reduction of temperature limitations on plant growth at higher elevations) but decreased slightly with increasing wind and bark beetle disturbances. Overall, the interplay between processes influencing carbon uptake and release determined where the landscape changed from a carbon sink to a carbon source. A higher NPP indicated that the landscape could sustain higher levels of disturbance while still remaining a carbon sink (Supplementary Figure S6). On average across all simulated scenarios, we found that when more than 0.73 per cent of the landscape were disturbed annually, BGNP became a carbon source (see Supplementary Figure S6). We also found that the carbon pool responding most strongly to the simulated scenarios was the stem carbon pool (Supplementary Figure S7).

Finally, to understand the spatial variation in carbon sinks and sources on the landscape, we mapped cumulative NEP at the level of 1-hectare cells (Figure 3), focusing the analysis on the end members of our scenario range (i.e. historical climate and wind vs. RCP 8.5 with 20 per cent increase in both wind frequency and speed). Under historical conditions, most of the landscape acted as a carbon sink throughout the 21st century. Especially forests at lower elevations, characterized by high-carbon stocks currently (Figure 1), had high-carbon sequestration rates also in the coming decades (Figure 3). However, the carbon sequestration capacity of low-elevation forests changed drastically when

Table 1 Cumulative NEP (median and 2.5th to 97.5th percentile) at the end of the 80-year simulation for each climate scenario and wind speed scenario.

Climate scenario	Historical			RCP 2.6			RCP 4.5			RCP 8.5		
Wind speed increase [%]	Median NEP (2.5th–97.5th percentile)	Share of negative runs [%]	*n*	Median NEP (2.5th–97.5th percentile)	Share of negative runs [%]	*n*	Median NEP (2.5th–97.5th percentile)	Share of negative runs [%]	*n*	Median NEP (2.5th–97.5th percentile)	Share of negative runs [%]	*n*
0	35.85 (30.11–40.54)	0	50	26.17 (17.28–38.15)	0	100	18.22 (5.34–30.73)	0	100	7.58 (−9.16–22.32)	30	100
5	32.73 (25.01–37.33)	0	50	22.52 (12.80–35.12)	0	100	13.66 (0.05–28.49)	3	100	2.71 (−16.21–18.42)	46	100
10	28.63 (20.04–34.93)	0	50	17.32 (8.03–32.78)	0	100	8.99 (−5.27–24.96)	21	100	−4.62 (−22.68–15.26)	64	100
15	23.93 (10.57–31.96)	0	50	11.98 (−0.92–28.17)	7	100	2.44 (−13.99–21.68)	38	100	−13.14 (−29.85–9.67)	77	100
20	17.34 (1.51–27.96)	0	50	4.89 (−9.14–22.62)	25	100	−6.02 (−21.69–14.93)	69	100	−19.98 (−36.18–3.65)	95	100

Positive values indicate a carbon sink at the end of the 21st century, negative values a carbon source. For each scenario, the percentage of runs that were a carbon source (share of negative runs) and overall number of runs (n) is given. The climate change projections for each RCP for the two climate models are analysed together, and all wind frequency scenarios are analysed together.

considering future climate and disturbance. In the most extreme RCP and wind scenario, a large proportion of the BGNP landscape turned into a carbon source, with a particularly strong signal at lower elevations. Consequently, these low- to mid-elevation areas are particularly pivotal for the future carbon balance of the landscape, as they could turn from strong carbon sinks to the atmosphere to considerable carbon sources.

Discussion

Impacts of disturbances and climate change on the forest carbon balance

Increasing disturbances and climate change can substantially impact the carbon sequestration and storage capacities of forests (Lindroth *et al.*, 2009; Seidl *et al.*, 2014b). Here, we studied the effect of intensifying wind disturbances and their interactions with bark beetle disturbances under climate change on the carbon balance of a strictly protected mountain forest landscape. We found that in most simulations, the landscape was a carbon sink to the atmosphere until the end of the 21st century. However, we also documented substantial reductions of cumulative NEP under changing climate and disturbance regimes, with the landscape increasingly at risk of turning from a carbon sink into a carbon source. While an outright tipping of the carbon balance only occurred in extreme combinations of climate change and wind speed increase, a substantial reduction in sink strength due to increasing disturbances was notable across all scenarios.

We considered future variation in both wind speed and wind frequency, but only wind speed had a considerable impact on cumulative NEP. The limited effect of increased wind frequency is potentially attributable to topographically mediated wind exposure and negative feedbacks within the wind disturbance system. We here assumed that while events become more frequent, primary wind directions and landscape topography (determining local wind exposure, with more exposed ridges and slopes as well as more sheltered areas, Kulakowski and Veblen, 2002) remain the same. This means that with increasing wind frequency, the same stands are more likely to be affected by storms repeatedly. While newly created gaps and edges may be points of attack for subsequent disturbances (positive feedback), stands strongly affected by one wind event have reduced vulnerability to follow-up events because of their low tree height (Gardiner *et al.*, 2016). This negative feedback obscures the effects of higher wind frequency in our simulations. It also explains why the impacts of increased wind disturbance (in combination with subsequent bark beetle outbreaks) are particularly strong in the beginning of the simulation, as there are still many older stands with tall trees that have a high risk of wind disturbance (see also temporal development of NEP in Figure 1). On the other hand, increasing wind speeds can mean that thresholds are exceeded also in stands that were not exposed to critical wind speeds previously, e.g. because of local sheltering effects or a less wind-prone vegetation composition.

While the primary scenario variables we permuted in the simulation were wind and climate, bark beetle disturbances also had a large effect on our results. This is the result of dynamic interactions between climate, wind and bark beetle disturbances. Wind events can act as a trigger for bark beetle outbreaks by creating low-defence breeding material. Climate warming elevates bark beetle activity by providing more suitable conditions for reproduction while also weakening tree defences (Bentz *et al.*, 2010). As a result of these interactions, the absolute amount of bark beetle disturbance as well as the relative share on total disturbed area increased with climate change. In RCP8.5 projections, bark beetles were the most important disturbance agent even under the most intense scenarios of wind speed and frequency. While cumulative NEP was able to recover in the second half of

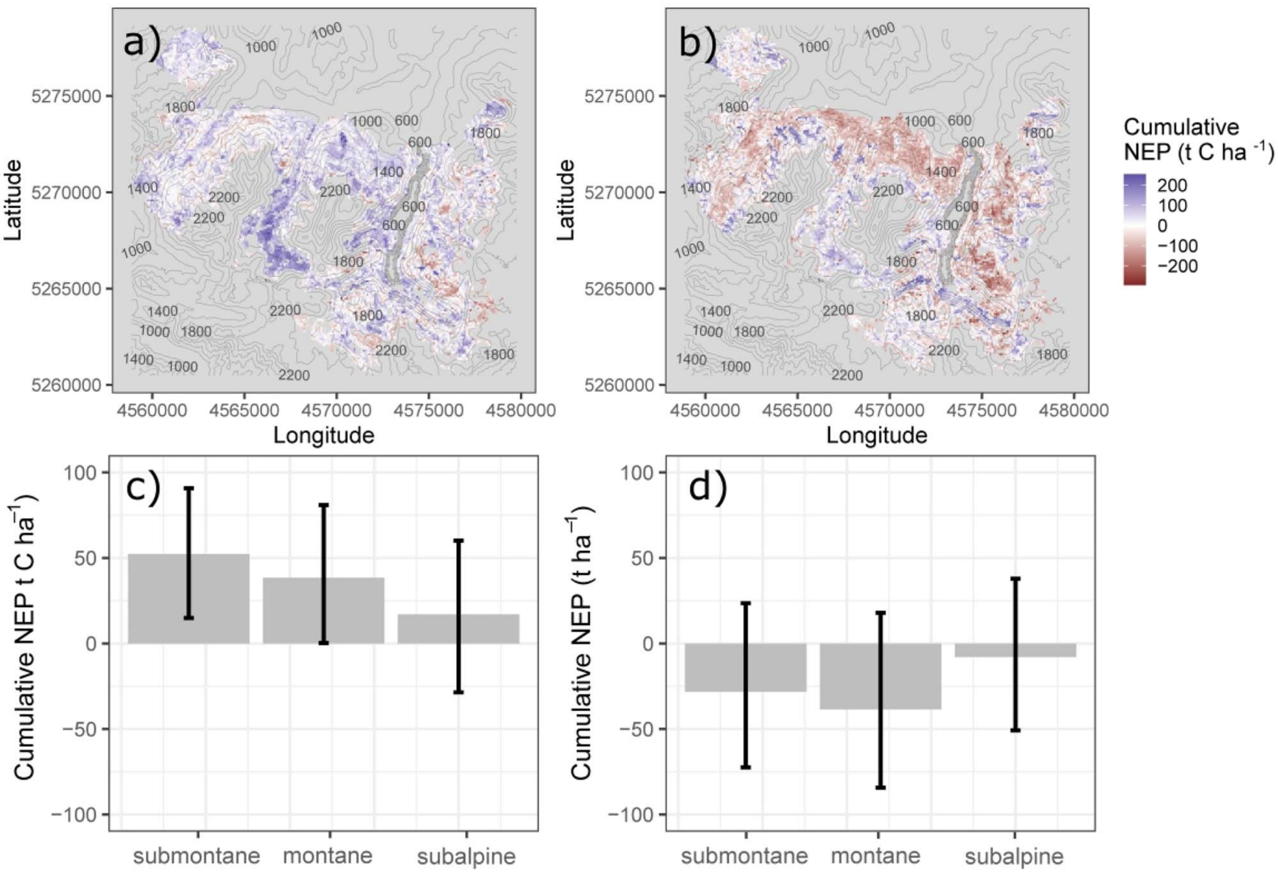

Figure 3 Spatial patterns of cumulative NEP (median and interquartile range) in the year 2100 (averaged over all simulated replicates) for the historical (climate and wind) scenario (a) and the most extreme scenario (RCP 8.5, +20 per cent wind frequency and speed (b). Blue cells indicate 21st century carbon sinks, red cells are carbon sources, with colour saturation indicating sink/source strength. Barplots show cumulative NEP in elevation bands for the historical (c) and most extreme scenario (d). The threshold between submontane and montane elevation zones was set at 800 m a.s.l and at 1400 m a.s.l between montane and subalpine.

the simulation period under mild climate change (after strong initial carbon losses through disturbance), increasing bark beetle impacts slowed or even prohibited this recovery, particularly under RCP 8.5 (see also Figure 2). This highlights the importance of disturbance interaction under climate change (Lucash *et al.*, 2018). It also suggests that the further development of the landscape beyond the end of the 21st century will strongly depend on the interactions of climate, disturbances and forest vegetation (e.g. bark beetle activity remains high under climate change as long as Norway spruce is a significant part of the forest vegetation). As the autonomous adaptation of forest composition takes centuries (Thom *et al.*, 2017b), the impact of some disturbance agents may decrease over time (Sommerfeld *et al.*, 2021), while new disturbance agents such as introduced pests and diseases may become more important.

Cumulative NEP decreased more in some parts of the landscape through increasing disturbances and climate change than in others. This can partially be attributed to local site characteristics such as sheltering effects (Kulakowski and Veblen, 2002) and variation in soils but also to stand characteristics such as current tree species shares (with species such as Norway spruce being more vulnerable to disturbance (Schütz *et al.*, 2006; Thom *et al.*, 2017c). Productive sites, for instance, can initially sequester more carbon but if high productivity is associated with taller trees these sites also have a higher susceptibility to wind disturbance. The lower-elevation areas of BGNP are an example for such feedbacks between productivity and disturbance. These areas suffered a clear loss in sink strength and transitioned from a substantial carbon sink under historic conditions to a carbon source under severe climate change (Figure 3). Hence, the lower-elevation parts of the landscape contributed most strongly to the decline of the carbon sink strength of the landscape, indicating that increased disturbance activity can offset productivity gains under climate change (Reyer *et al.*, 2017).

Uncertainties and limitations

A number of uncertainties exist regarding the future wind regime and its impact on the forest carbon sink. Variation in future storm tracks and the expected speed and frequency of wind events remains high (Shaw *et al.*, 2016). Wind scenarios for Europe range from considerable increases in wind activity to no change and even reductions, but a majority of projections for Central Europe suggest an increase in both wind frequency and speed

Table 2 Volume disturbed annually (median and 2.5th to 97.5th percentile) by wind and bark beetle as well as Net Primary Production for each scenario of change in climate and wind speed.

Climate scenario	Wind disturbed volume [m^3 ha^{-1} $year^{-1}$]				Bark beetle disturbed volume [m^3 ha^{-1} $year^{-1}$]				NPP [t ha^{-1} $year^{-1}$]			
Wind speed increase [%]	Historical	RCP 2.6	RCP 4.5	RCP 8.5	Historical	RCP2.6	RCP 4.5	RCP 8.5	Historical	RCP 2.6	RCP 4.5	RCP 8.5
0	0.48	0.58	0.61	0.68	0.46	0.57	0.87	1.45	8.09	8.20	8.36	8.65
	(0.28–0.79)	(0.39–0.97)	(0.40–1.07)	(0.45–1.20)	(0.37–0.55)	(0.43–0.72)	(0.67–1.09)	(1.01–2.11)	(8.02–8.14)	(8.11–8.34)	(8.20–8.53)	(8.54–8.77)
5	0.66	0.76	0.79	0.88	0.51	0.64	0.97	1.64	8.05	8.18	8.33	8.62
	(0.41–1.05)	(0.54–1.27)	(0.54–1.37)	(0.60–1.48)	(0.42–0.63)	(0.48–0.79)	(0.73–1.24)	(1.10–2.21)	(7.96–8.10)	(8.06–8.29)	(8.16–8.53)	(8.48–8.75)
10	0.85	0.97	1.00	1.13	0.57	0.72	1.08	1.80	8.01	8.13	8.27	8.59
	(0.56–1.39)	(0.70–1.64)	(0.69–1.75)	(0.77–1.89	(0.49–0.68)	(0.55–0.90)	(0.86–1.34)	(1.21–2.38)	(7.91–8.07)	(8.03–8.30)	(8.12–8.51)	(8.43–8.73)
15	1.07	1.23	1.28	1.45	0.66	0.81	1.20	1.92	7.94	8.09	8.24	8.52
	(0.74–1.81)	(0.90–2.07)	(0.89–2.16)	(1.00–2.32)	(0.54–0.82)	(0.60–1.05)	(0.90–1.49)	(1.40–2.44)	(7.80–8.03)	(7.93–8.25)	(8.04–8.46)	(8.37–8.70)
20	1.38	1.57	1.63	1.78	0.75	0.92	1.32	1.94	7.88	8.00	8.16	8.45
	(0.95–2.27)	(1.12–2.57)	(1.14–2.53)	(1.28–2.71)	(0.60–0.93)	(0.72–1.13)	(1.04–1.57)	(1.53–2.39)	(7.71–7.97)	(7.82–8.20)	(7.94–8.41)	(8.26–8.64)

The climate change projections for each RCP for the two climate models are analysed together, and all wind frequency scenarios are analysed together.

(Mölter *et al.*, 2016). The increases in wind speed and frequency simulated here were chosen to cover a wide range of potential future wind regimes for our study landscape. In the case of wind speed, the strongest wind speed change simulated here exceeds commonly expected increases, meaning that these extreme changes have a lower likelihood based on current projections.

In addition to the uncertainty about wind scenarios, there are also uncertainties and limitations related to simulating the forest responses to wind. While wind frequency and speed were altered in our scenarios, other important parts of the wind regime remained constant, in particular the major wind direction and the spatial variation in wind on the landscape (due to topographic effects). Whether this assumption is reasonable remains uncertain, however, as wind directions could change if events such as thunderstorms were to gain importance under climate change (Rädler *et al.*, 2019). Given the overwhelming historic importance of cyclonal storms at BGNP we, however, deem our assumptions a meaningful first approximation of future wind regimes. Nonetheless, future climate modelling efforts should focus on improved projections of extreme events such as peak gust wind speeds. A further limitation of our simulation is the limited interaction between soil conditions and wind disturbance in iLand. While the effect of soil freezing on the likelihood of stem breakage versus uprooting is considered explicitly in the model, other important soil characteristics such as local differences in soil depth and water holding capacity (Everham and Brokaw, 1996) are not considered in the calculation of wind risk. Similarly, changes in soil water saturation under changing precipitation regimes may change disturbance risk in the future, with a potential interaction between drought and wind disturbance (Csilléry *et al.*, 2017). Beyond the two historically most important disturbance agents considered here, new disturbances and interactions between them may arise on the landscape (e.g. novel pests and diseases). Further research into future disturbance regimes is thus needed, e.g. to estimate the role and impact of other disturbance agents on the climate regulating function of forest ecosystems.

Considerations for forest management and climate policy

Here we showed that changes in climate and disturbance regimes can have a considerable impact on a landscape's ability to sequester and store carbon. In light of the hopes put into forests and their role in climate change mitigation and adaptation (Bastin *et al.*, 2019, Kaarakka *et al.*, 2021, Chausson et al., 2020), this a concerning finding. While forests can contribute strongly to climate change mitigation, they are not exempt from climate change impacts that can considerably reduce their ability to act as carbon sinks (Anderegg *et al.*, 2020). Even without changes in the wind regime, climate change impacts considerably reduced the sink strength of our landscape. And when interactions between changing climate and disturbance regimes were considered, the landscape even turned into a carbon source in the most extreme wind speed and climate change scenario combinations. In this context it must be noted that land-use history has a strong influence on the future development of the carbon sink capacity of a particular landscape. In case of BGNP carbon stocks are still recovering from active forest management that ceased about 40 years ago. Consequently, the landscape remains a carbon sink also under moderate climate change and disturbance (Figure 2). Protected areas with carbon stocks closer to a dynamic equilibrium could, however, turn to a carbon source already under moderate climate change forcing (see also Nabuurs *et al.*, 2013).

Our study landscape is a strictly protected area, and the focus of our analysis was on studying natural forest dynamics in the absence of forest management. Nonetheless, the insights gained from our analysis also have important implications for managed forests and their contribution to carbon sequestration and storage. We here showed that the carbon sink strength of forests can be put in jeopardy by climate change and increasing disturbances. While our landscape developed in the absence of management, i.e. only natural disturbances initiated regeneration and a change in species composition, forest managers can actively influence forest development pathways to help safeguard forest carbon sinks. Our results show that disturbances will have a considerable impact and that it may not be possible to maintain current sink strength in some cases. Through adaptive management, foresters should aim to increase the resilience of forests to climate change, by—for example—fostering diversity of species and structural complexity (Fares *et al.*, 2015; Silva Pedro *et al.*, 2015). Forests can play an important role in mitigating climate change, not only globally through sequestering and storing carbon, but also locally through their evaporative cooling and other factors altering the microclimate (Bonan, 2008; Frey *et al.*, 2016; Thom *et al.*, 2017c). Further, they provide raw materials that can replace non-renewable, fossil fuel-based materials (Gustavsson *et al.*, 2006; Yousefpour *et al.*, 2018). However, there may be trade-offs between different climate regulating ecosystem services, e.g. aiming to increase the carbon sink in forests may diminish their albedo (Luyssaert *et al.*, 2018) and increasing *in situ* carbon storage can conflict with the provisioning of raw materials. For all these climate regulating services it is important to recognize that they are not free from risk. Forest-based climate solutions, including both managed and unmanaged forests, have received a lot of attention in relation to climate mitigation policy, and considerable hopes are placed on forests in this regard (Grassi *et al.*, 2017). Our results show that these solutions are not without risks, and further research should be directed towards quantifying realistic contributions of forests to climate change mitigation.

Conclusion

Increasing forest disturbances present a challenge to the role of forests as carbon sinks. Using a forest landscape simulation model to explore combinations of increasing wind disturbance and climate change we found a considerably weakened forest carbon sink strength for a strictly protected mountain forest landscape in Central Europe. Changes in carbon sink strength were particularly driven by increased wind speed. Especially the lower, more productive areas of the landscape suffered losses in sink strength. While a lot of uncertainty remains regarding future wind disturbances, our results show that forest disturbances can greatly reduce the ability of forests to sequester carbon, which needs to be taken into consideration when forests are included in climate change mitigation plans.

Supplementary data

Supplementary data are available at *Forestry* online.

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Data availability

Data and analyses supporting the findings of this study are available at doi.org/10.6084/m9.figshare.20071814. Technical model documentation of iLand as well as the executable and model source code are available online at iland-model.org.

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