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Key Points:

- Future carbon balance diverges across landscapes; current dynamics are not a strong predictor of future trends
- Future resilience in forest composition and structure does not guarantee unchanged ecosystem functioning
- Reorganizing forests sequester more carbon than resilient forests, helping sustain ecosystem functioning under climate change

Supporting Information:

Supporting Information may be found in the online version of this article.

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Forest Reorganization Sustains Carbon Sequestration Under Climate Change

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Abstract Forests currently mitigate anthropogenic climate change by sequestering substantial amounts of carbon, but future carbon dynamics are expected to vary across the temperate forest biome. Previously cold-limited ecosystems with low disturbance activity could increase their carbon uptake, while water-limited ecosystems with high disturbance activity could become a carbon source to the atmosphere. However, forests dynamically adapt to changing climate and disturbance regimes by reorganizing their composition and structure, with unclear consequences for future carbon dynamics. We asked how the carbon dynamics of reorganizing forests differ from those of resilient forests, that is, forests that conserve their composition and structure under climate change, and how shifts in composition and structure drive future forest carbon. We simulated long-term forest and carbon dynamics under current and future climate conditions for three contrasting temperate forest national parks, spanning a gradient from low disturbance activity in Shiretoko, Japan, to intermediate disturbance activity in Berchtesgaden, Germany, and high disturbance activity in Grand Teton, Japan. Under climate change, carbon stores increased in Shiretoko, remained close to current levels in Berchtesgaden, and decreased in Grand Teton. Forests that reorganized, that is, exhibited compositional and/or structural changes, generally took up more carbon than resilient forests. Changes in forest carbon cycling were consistently associated with changes in forest structure across systems, whereas the effects of tree species composition change were less consistent. We conclude that resilience in composition and structure does not guarantee continuity in ecosystem functioning, suggesting that reorganization is necessary to maintain forest carbon stocks in a changing climate.

1. Introduction

Forests globally are changing rapidly in response to climate change (McDowell et al., 2020). Interacting drivers, including warming temperatures, increasing atmospheric CO₂ concentrations, altered water availability, and increasing climate-mediated disturbance activity, influence forest composition and structure (Hagmann et al., 2021; Seidl et al., 2017). As a result of these simultaneous pressures, forests are expected to reorganize, that is, change composition and structure beyond their recent range of variability (Dollinger et al., 2024). We distinguish four response pathways to climate and disturbance (Seidl & Turner, 2022): resilience—no novelty in composition or structure; reassembly—composition-only novelty; restructuring—structure-only novelty; and replacement—novelty in both dimensions. Importantly, these pathways can manifest in different ways, for example, forests can restructure by becoming denser or sparser (Braziunas et al., 2023). We note that in our framework, loss of resilience is not inherently synonymous with regime shift (i.e., forest loss), but rather indicates a shift in forest composition and/or structure in response to climate change (Seidl et al., 2024). Uncovering ongoing reorganization (Perret et al., 2025; Seidl et al., 2024), developing early warning indicators (Knowlton et al., 2025), and identifying drivers and future patterns of reorganization (Dollinger et al., 2024; Iglesias et al., 2018) are vital elements in furthering our understanding of forest change.

It is unclear whether reorganizing forests will maintain similar ecosystem functions as their resilient counterparts, for example, in terms of biogeochemical cycling such as carbon uptake and storage or nitrogen cycling (Turner et al., 2019, 2025). Forests play an important role in the global carbon cycle as they store vast amounts of carbon and are substantial carbon sinks (Harris et al., 2021; Pan et al., 2024). Changes to forests' carbon balance may create amplifying climate feedbacks, with higher rates of carbon released to the atmosphere further intensifying the greenhouse effect (Gatti et al., 2021). Besides their important influence on atmospheric processes, sustained

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forest carbon stocks are positively correlated with aspects of biodiversity (Lecina-Diaz et al., 2018), soil health (Lorenz et al., 2019), and the supply of other ecosystem services (Canedoli et al., 2020; Felipe-Lucia et al., 2018).

Ongoing climate change is already disrupting historic forest carbon balances, with live carbon stocks declining in many regions across the globe (Hall et al., 2024; Nabuurs et al., 2013). Declines are driven by reduced tree growth due to less favorable climatic conditions (Klesse et al., 2020), greater tree mortality due to increasing disturbance frequency and severity (Reilly & Spies, 2016), and altered post-disturbance recovery due to delayed or failed tree regeneration (Stevens-Rumann et al., 2018). At the same time, climate change can increase forest productivity in cold-limited systems benefiting from warmer temperatures and longer growing seasons (Martin-Benito et al., 2018), and elevated CO₂ can improve photosynthetic water-use efficiency (Mathias & Thomas, 2021). However, these gains may be offset by greater water limitation, higher disturbance rates, nutrient constraints, and increases in autotrophic and heterotrophic respiration (and, in fire-prone regions, combustion losses). Consequently, the effect of climate change on net ecosystem production (NEP) and forest carbon stocks is uncertain and strongly context-dependent. This is particularly the case as forests reorganize in composition and structure in response to a changing climate, and carbon cycle effects depend on the direction and magnitude of structural and compositional changes.

It is challenging to assess the consequences of reorganization for forest carbon dynamics. The time scales on which disturbance and recovery cycles unfold make direct observations difficult (Anderegg, Trugman, et al., 2025), space-for-time substitutions offer limited potential to anticipate outcomes in a rapidly changing climate (Anderegg, Blanchard, et al., 2025), and shifts in species composition could cancel out the effects of structural change on the forest carbon balance (Mack et al., 2021). Studies need to address appropriate temporal and spatial scales while also considering a variety of future climate scenarios, representing a range of simultaneously changing climate variables to account for their interactive effects. Water availability, for instance, has strong and contrasting implications for processes driving forest carbon balance depending on the thermal regime: hotter and drier conditions lead to an increase in disturbances such as fire (Westerling et al., 2006) and higher levels of drought-related mortality (Thom et al., 2023), while hotter and wetter conditions could promote regeneration and forest growth (Emmett et al., 2019). Additionally, determining whether forest change has general implications for carbon dynamics across systems or whether particular reorganization pathways manifest in system-specific ways requires comparative analyses across different forest landscapes.

Simulation models can overcome these challenges (Buotte et al., 2020; Wu et al., 2019), enabling us to consistently compare functional responses to climate and disturbance change across forest landscapes and climate scenarios. Here, we simulated future carbon balance across three temperate forest landscapes using the individual-based forest landscape and disturbance model iLand (Rammer et al., 2024; Seidl et al., 2012). We tracked reorganization via shifts in composition and structure and quantified the effects of reorganization on forest carbon dynamics. The three temperate forest landscapes chosen for this study—Shiretoko National Park (JP), Berchtesgaden National Park (DE), and Grand Teton National Park (US)—are similar in their current carbon balance (i.e., they are a moderate carbon sink to the atmosphere) but differ substantially in their disturbance activity, ranging from low (Shiretoko) to high (Grand Teton). We specifically asked, (a) *how does the carbon balance of reorganizing forests differ from that of resilient forests across ecosystems?* We hypothesized that pathways of emerging novel structure (i.e., restructuring and replacement) would have stronger effects on carbon dynamics than shifts in composition (i.e., reassembly) because the former are more directly associated with increases in biomass. Alternatively, carbon dynamics may change even if forests remain resilient in their composition and structure due to physiological responses of trees to environmental changes (e.g., increased photosynthetic efficiency, Crous et al., 2022). Furthermore, we asked, (b) *which indicators of composition and structure are most strongly correlated with future carbon dynamics?* We expected to see contrasting shifts in forest structure across the three study landscapes under climate change: general decreases in basal area and leaf area in Grand Teton due to increased fire activity and climatically limited regeneration versus increases in basal area and leaf area in Shiretoko due to the relaxation of cold limitations on forest productivity. However, we also hypothesized that the relationships between forest reorganization and responses of forest carbon would be similar across landscapes: strong, positive correlations between forest carbon and structural indicators and weaker, less consistent correlations for compositional indicators.

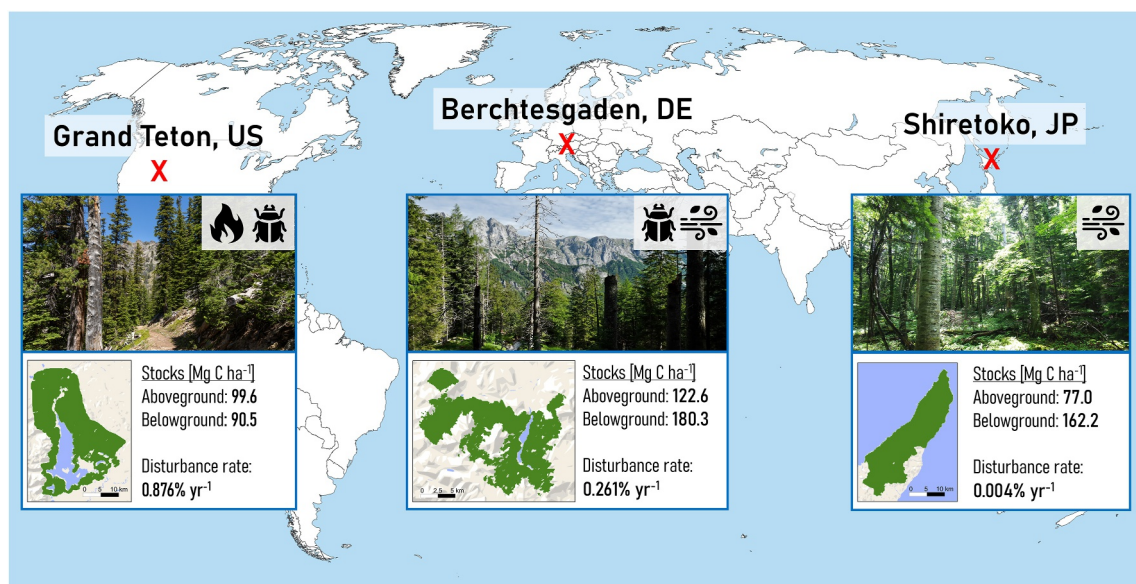


Figure 1. Map showing the location of the three study landscapes as well as example forest conditions, landscape extent (green map insert), and main disturbance agents (icons). Carbon stocks and disturbance rates are based on simulations under reference climate conditions. Image credit: Grand Teton—Timon T. Keller; Berchtesgaden—Rupert Seidl; Shiretoko—Kureha F. Suzuki. Adapted from Dollinger et al. (2024).

2. Methods

2.1. Study Landscapes

We selected three study landscapes based on a global remote sensing analysis of temperate protected areas (Sommerfeld et al., 2018), representing three clusters of distinct disturbance activity. Shiretoko National Park (44°10′33.6″N, 145°11′43″E, from here on referred to as Shiretoko) represents temperate forests with low disturbance activity. The landscape is located on a peninsula in Northeastern Hokkaido, Japan (Figure 1). The climate is oceanic with cold, wet winters and cool summers. Most of the landscape is forested (35,676 ha), with forests covering an elevational gradient from 0 m asl at the coast of the Sea of Okhotsk and the Pacific Ocean to 1,540 m at the tree line. Tree species diversity is high but a few species, both broadleaved (*Betula ermanii*, *Acer mono*) and coniferous (*Abies sachalinensis*, *Pinus pumila*), dominate depending on elevation. Wind disturbances cause a fine-grained pattern of mostly single-tree mortality, and the proportion of the landscape disturbed per year is very low (estimated to 0.004% yr⁻¹, Dollinger et al., 2024).

Berchtesgaden National Park (47°32′56.4″N, 12°55′4.8″E, referred to as Berchtesgaden) represents a temperate forest landscape with intermediate disturbance activity. It is located in southeastern Germany, bordering Austria, and is part of the northern limestone Alps. The climate is sub-oceanic to sub-continental, with cold, wet winters and warm, wet summers. Forests in Berchtesgaden (8,645 ha) cover an elevational gradient from 603 m at the shore of Lake Königssee to 1,750 m asl at the tree line. Native Norway spruce (*Picea abies*) dominates the landscape as it was planted for timber production up until the 1970s. Other common species include European beech (*Fagus sylvatica*), silver fir (*Abies alba*), and European larch (*Larix decidua*). Wind and European spruce bark beetles (*Ips typographus*) cause relatively frequent but small disturbances, disturbing an average of 0.261% of the landscape per year (Dollinger et al., 2024).

Grand Teton National Park (43°48′50.4″N, 110°38′27.6″W, from here on referred to as Grand Teton) represents a temperate forest landscape with high disturbance activity. It is located in the Northern US Rocky Mountains in Wyoming, USA. The climate is continental, with cold, wet winters and hot, dry summers. Most of the landscape is forested (53,665 ha), with forests covering an elevational gradient from 2,000 to 3,100 m asl. Forests at the lower tree line are dominated by lodgepole pine (*Pinus contorta* var. *latifolia*), Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), and quaking aspen (*Populus tremuloides*). Other conifer species, including subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*), gain prominence with increasing elevation. The disturbance regime is characterized by infrequent (100–300 years, Loope & Gruell, 1973) but extensive wildfire disturbances

and periodic outbreaks of mountain pine beetle (*Dendroctonus ponderosae*), disturbing an average of 0.876% of the landscape per year (Dollinger et al., 2024).

The past drivers of the forest carbon balance differ between the three landscapes: in Shiretoko, carbon fluxes are climate-driven, that is, carbon stocks vary little over time as carbon uptake depends mainly on growing season length and temperature limitations (Hirata et al., 2014; Piao et al., 2007), while in Grand Teton carbon fluxes are strongly disturbance-driven, that is, carbon stocks vary distinctly over time, declining in disturbance events and recovering within ~100 years after stand-replacing fire (Kashian et al., 2013). In Berchtesgaden, carbon fluxes are less constant over time than in Shiretoko, but less dynamic than in Grand Teton as both climate and disturbances drive the forest carbon balance (Albrich et al., 2023).

2.2. Simulating Reorganization Patterns and Carbon Cycle Implications

2.2.1. Simulation Model iLand

We used iLand (version 2.1, Rammer et al., 2024; Seidl et al., 2012) to simulate the effect of changing climate and disturbances on reorganization patterns and the future carbon balance under different climate change scenarios across the three study landscapes. iLand can represent a wide array of different disturbance regimes, making the model particularly suitable to simulate our contrasting temperate forest landscapes. Individual trees are the main entities of the simulation, and forest landscape dynamics emerge from interactions among trees as well as between trees and their environment. To reflect the hierarchy of environmental constraints, processes are simulated at different spatio-temporal levels. Disturbance and seed dispersal are spatially explicit and modeled at the landscape-scale, whereas resource availability for trees is modeled for 100×100 m cells with homogeneous environmental conditions (from here on referred to as “stands”). Competition for light is modeled at the individual tree level based on ecological field theory (Walker et al., 1989), where light absorption is calculated for each individual tree (based on its position within a continuous field of light availability, derived from an overlay of individual tree shading patterns) and drives tree productivity and growth. Individual tree mortality is a function of tree age, carbon starvation, and disturbance agents (see below for more details). Tree regeneration is modeled as tree cohorts in cells of 2×2 m, with establishment and growth dependent on seed dispersal, species-specific environmental limitations, and resource availability. Sapling cohorts are recruited as individual trees once they reach a height of 4 m. A more detailed description of iLand can be found in Seidl et al. (2012), Rammer et al. (2024) and on the model website (<https://iland-model.org>). The full model source code is available at <https://github.com/edfm-tum/iland-model>.

2.2.2. Simulating Carbon Dynamics

iLand tracks carbon stocks and fluxes to the atmosphere in both living and dead biomass (Seidl et al., 2012). Carbon fixed by trees (net primary production) is allocated to different compartments based on species- and size-specific allometric ratios for each individual tree (height >4 m). Allocation is hierarchical, prioritizing roots and foliage, followed by reserves and stem pools. Fluxes of carbon from live pools to dead organic matter pools are calculated based on leaf turnover rates, tree mortality, and snag dynamics. Dead organic matter is tracked in dedicated pools—representing standing and downed deadwood, litter, and soil organic matter—following the ICBM/2N approach by Kätterer and Andrén (2001). Material from the litter and downed woody debris pools enters the soil organic matter pool via humification. Decomposition of dead organic matter pools is represented by pool- and species-specific optimal decomposition rates, which are modified by temperature and precipitation (Adair et al., 2008). Carbon leaves the system either via heterotrophic respiration of dead organic matter or by combustion from wildfires. Carbon pools are updated on an annual time step in iLand at the spatial resolution of stands (100×100 m). The system maintains or increases its carbon stocks if carbon uptake equals or exceeds release (i.e., $NEP \geq 0$). Initial live and dead organic matter pools and site-specific process parameters were estimated for each landscape. For Shiretoko this was done by Dollinger et al. (2024, but also see Section A1 in Supporting Information S1), for Berchtesgaden by Thom et al. (2022), and for Grand Teton by Hansen et al. (2020).

2.2.3. Simulating Disturbance Dynamics

We simulated the most important current disturbance agents in each landscape using iLand's dynamic disturbance modules. Wind disturbances were simulated as yearly storm events varying in wind speed, timing, and direction

based on weather station data (Thom et al., 2022), with their effects determined by forest structure, topography, and edge effects (Seidl, Rammer, & Blennow, 2014). Wind is an important disturbance agent in Shiretoko and Berchtesgaden, and iLand's wind module has successfully reproduced realistic patterns of wind disturbance in both landscapes regarding patch sizes, locations, and severity (Dollinger et al., 2024; Thom et al., 2022). In Berchtesgaden, we additionally employed the iLand spruce bark beetle module (Seidl & Rammer, 2017) to simulate the effects of the European spruce bark beetle on its host tree, Norway spruce. Similarly, the BITE module (the biotic disturbance engine, Honkaniemi et al., 2021) was used to simulate the effects of mountain pine beetle on its main host, lodgepole pine, in Grand Teton. The disturbance patterns of both bark beetle species are climate-sensitive and driven by beetle dispersal, colonization, and population dynamics as well as host distribution and have been previously evaluated for Berchtesgaden by Thom et al. (2022) and for Grand Teton by Dollinger et al. (2024). Wildfire disturbances in Grand Teton were simulated using fire event sequences as drivers for the dynamic fire module in iLand, which spreads fire spatially in response to fuel availability, topography, and weather at a resolution of 20×20 m (Seidl, Rammer, & Spies, 2014). Fire event sequences were generated using a statistical approach based on the relationship between aridity and historical fire timing, location, and maximum potential size, considering both surface and crown fires (Dollinger et al., 2024; Turner et al., 2022; Westerling et al., 2011). Simulated fire intensity is determined by the amount of fuel (i.e., the dynamically simulated biomass pools in iLand) available for combustion. Forest structure and composition affect fire intensity, fire type (surface, crown), and severity. Fire spread continues until fuels are depleted or the statistically determined maximum fire size is reached. An evaluation of the iLand fire module for Grand Teton can be found in Hansen et al. (2020).

2.3. Scenarios

The starting point for our simulations was the state of the forest in the year 2020 (Dollinger et al., 2024). We then simulated forest development and carbon dynamics for 180 years (2021–2200) under four scenarios of climate change and one reference climate scenario. The four climate change scenarios (derived from two GCM-RCMs combinations for two RCP scenarios for each landscape) bracket future changes in temperature and precipitation: warm-wet, warm-dry, hot-wet, and hot-dry. The climate models used for each landscape are described in detail in the (Section A2 in Supporting Information S1). Mean annual temperature in 2071–2100 increased by 1.2–2.8°C (range across landscapes) in the warm scenarios, and by 3.8–6.8°C in the hot scenarios, relative to 1991–2020. Projected precipitation trends were highly landscape-specific: all climate models available for Shiretoko projected an increase in mean annual precipitation (on average +70 to +150 mm), while those for Grand Teton consistently projected a decrease (−20 to −200 mm) at the end of the 21st century compared to the reference period. In Berchtesgaden, precipitation increased in wet scenarios (+150 mm) and decreased in dry scenarios (−50 mm).

The 180-year simulation period was chosen as a compromise between the long timeframes of forest dynamics (i.e., multiple centuries) and the comparatively limited reach of currently available climate scenario data (i.e., until 2100). Climate beyond 2100 was sampled from the climate projections available for 2071 to 2100, assuming a stabilization of climate in the 22nd century in all climate change scenarios. The reference climate scenario consisted of a 180-year sequence of climate data sampled from the period 1991–2020. Each scenario was replicated 20 times to account for stochasticity in the simulation, with each replicate representing a unique wind event sequence for Shiretoko and Berchtesgaden and a large-fire event sequence for Grand Teton. In total, we ran 300 simulations: 3 landscapes $\times$ 5 climate scenarios $\times$ 20 replicates.

2.4. Analyses

To investigate how forest reorganization affects carbon balance, we tracked simulated shifts in composition and structure and related those shifts to cumulative NEP. For the former, we followed the approach established by Dollinger et al. (2024), identifying shifts in composition and structure via changes in eight indicators. Specifically, we quantified composition via importance value (IV) of the dominant species, Shannon diversity of tree species (based on IV), as well as community-weighted mean shade- and drought tolerance. Forest structure was quantified via stem density [n ha^{-1}], Shannon diversity of height classes, leaf area index [LAI], $\text{m}^2 \text{m}^{-2}$] and basal area [$\text{m}^2 \text{ha}^{-1}$]. The eight indicators were moderately correlated (for correlation matrix see Section A3 in Supporting Information S1) but were all retained in the analysis because they provide complementary information that allows for a nuanced interpretation of forest change. All indicators were calculated as the average over the last three decades of the simulation period for trees >1.3 m in height at the stand level (100×100 m).

For each stand, shifts were classified as novel if the indicator value under climate change fell outside the stand-specific reference range of values. This range was derived as the minimum-to-maximum range across replicates of simulations under a reference climate, that is, representing a “no climate change”-counterfactual. If at least three out of four indicators of structure or composition lay beyond this reference range, the forest was no longer considered resilient. Our assessment of resilience loss thus requires a majority of indicators to diverge from the reference range (but see Section B4 in Supporting Information S1 for results under a less conservative change detection approach). We note that forests that experience shifts in composition and structure under climate change can still be resilient if the shifts did not push it beyond the stand-specific range of values. Cells that dropped below 50 trees ha⁻¹ by the end of the simulation period were classified as non-forest (Hansen et al., 2020).

Carbon dynamics were quantified via cumulative NEP, that is, the integral of carbon uptake (net primary production) and carbon release (heterotrophic respiration and combustion by wildfire) over the 180-year simulation period. Cumulative NEP is sensitive to changes in both input and output fluxes: for example, a decrease in cumulative NEP can be caused by a decrease in carbon uptake or by an increase in carbon release, or a combination of both. We adopted a forest-centered perspective to report carbon (as opposed to an atmosphere-centered perspective), meaning that negative NEP values indicate a carbon source to the atmosphere (i.e., forest carbon stocks decrease) and positive values a carbon sink to the atmosphere (i.e., carbon stocks increase). Carbon stocks and fluxes were reported per potentially forested area, that is, parts of the total forest area where no trees can grow, for example, due to rock outcrops, were excluded. The divergence of future carbon balance from current carbon balance was quantified via changes in cumulative NEP, that is, the absolute difference in a stand's cumulative NEP under climate change relative to its cumulative NEP under a reference climate.

To quantify how the carbon balance of reorganizing forests differed from those of resilient forests (Q1), we subtracted the cumulative NEP of resilient stands (mean over all resilient stands in the specific simulation run) from the cumulative NEP of reorganizing stands in each landscape. To quantify which changes in composition and structure were most strongly correlated with changes in the future carbon balance (Q2), we calculated the percent change in the eight indicators of composition and structure relative to values under reference runs. The association between indicator changes and the changes in the carbon balance was quantified via Spearman's rank correlation coefficient. Data preparation and all analyses were performed using the R project for statistical computing version 4.2.2 (R Core Team, 2024; a list of all packages used can be found in the Section A4 in Supporting Information S1).

3. Results

3.1. Current and Future Forest Carbon Balance

Under the reference climate (blue lines, Figure 2a), all landscapes were carbon sinks (cumulative NEP > 0). However, landscapes diverged strongly in their carbon balance under scenarios of climate change. Over the 180 simulation years, cumulative NEP under climate change diverged strongly from values under reference climate in Shiretoko (+112.5 to +219.1 Mg C ha⁻¹ across all climate change scenarios). In contrast, cumulative NEP decreased in Grand Teton (−29.7 to −83.0 Mg C ha⁻¹), and the landscape became a carbon source under all simulated climate change scenarios. These shifts were especially pronounced in dry climate scenarios (yellow and red lines, Figure 2a). In Berchtesgaden, cumulative NEP under climate change diverged little from reference (+4.1 to +20.5 Mg C ha⁻¹), but annual variability in NEP increased (Figure 2a). The distribution of forest carbon across above- and belowground pools can be found in the (Section B1 in Supporting Information S1).

In Shiretoko and Berchtesgaden, both carbon uptake and release increased under climate change compared with reference conditions, whereas both fluxes decreased in Grand Teton, especially in dry scenarios (Figure 2b). In Shiretoko, the simulated net increase in NEP was mostly driven by a stronger increase in mean annual carbon uptake (+4.7 Mg C forested ha⁻¹ yr⁻¹ under hot-dry climate change compared to reference) than release (+3.4 Mg C ha⁻¹ yr⁻¹). In Berchtesgaden, both input and output fluxes increased similarly (uptake: +1.7 Mg C ha⁻¹ yr⁻¹, release: +1.6 Mg C ha⁻¹ yr⁻¹), so NEP changed little. In Grand Teton, the simulated decrease in NEP was mainly driven by strong declines in mean annual carbon uptake (−3.5 Mg C ha⁻¹ yr⁻¹). Carbon release also decreased overall—even as disturbance losses increased slightly (+0.2 Mg C ha⁻¹ yr⁻¹)—due to strong declines in heterotrophic respiration (−3.2 Mg C ha⁻¹ yr⁻¹). Under the hot-dry climate scenario, all

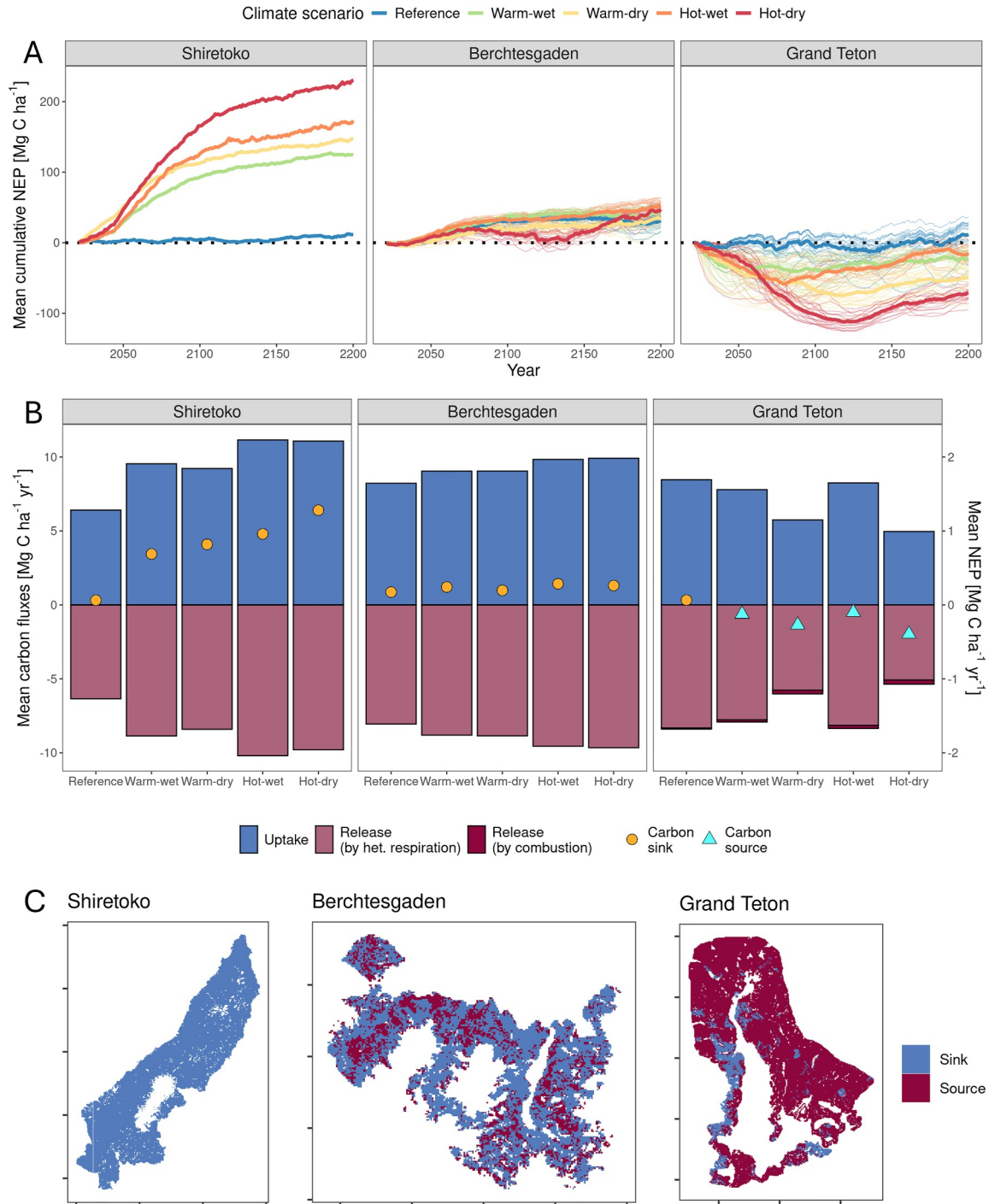


Figure 2. (a) Landscape-mean of cumulative net ecosystem production (NEP) (Mg C ha^{-1}) over the simulation period under reference climate and four climate change scenarios. Bold lines denote the mean over all 20 replicate runs (shown in fine individual lines). Note: in Shiretoko, the lines showing the trajectories of single runs ($n = 20$) aren't distinguishable from the mean due to the small variation among replicates. For changes in cumulative NEP beyond 2200, see Section B2 in Supporting Information S1. (b) Landscape-mean of annual carbon fluxes (Mg C ha^{-1}) by landscape and climate change scenarios. Note: NEP values (orange circles: net positive, i. e., carbon sink to the atmosphere; blue triangles: net negative, i. e., carbon source to the atmosphere) are plotted on a secondary x-axis (right side, values differing by a factor of 5) to better show the differences among scenarios. (c) Maps showing the spatial distribution of forests acting as carbon sinks and sources under the most extreme climate scenario simulated (hot-dry) over the 180-year simulation period. Data are aggregated across 20 replicates by a majority vote.

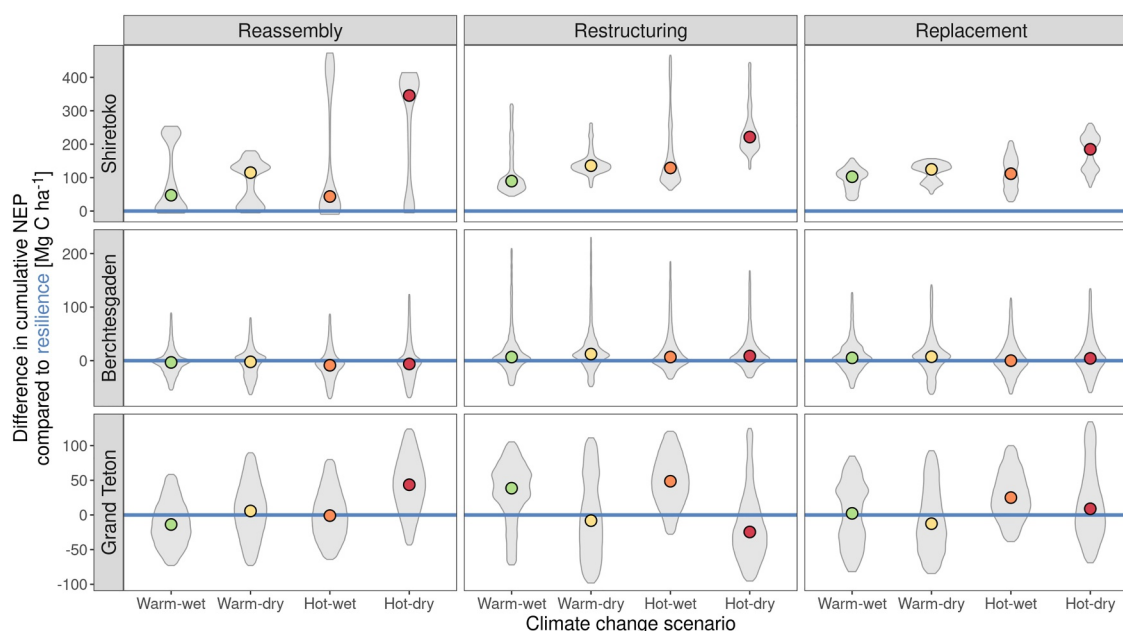


Figure 3. Differences in cumulative net ecosystem production (NEP) of different reorganization pathways compared to resilient forests (blue horizontal line at $y = 0$) under four climate change scenarios. Points show the median and the distribution in the 5th–95th percentile range. Cumulative NEP changes refer to a simulation period of 180 years. Note: y-axis ranges vary by landscape (rows). Results for areas that experienced forest loss are not shown (but see Section B4 in Supporting Information S1 for prevalence of forest loss).

of the forests of Shiretoko remained carbon sinks (Figure 2c), while in Berchtesgaden $33.4 \pm 3.9\%$ (mean $\pm$ standard deviation over 20 replicates) and in Grand Teton $82.7 \pm 5.8\%$ of the forests turned into carbon sources to the atmosphere.

3.2. Carbon Implications of Forest Reorganization

3.2.1. How Does the Carbon Balance of Reorganizing Forests Differ From That of Resilient Forests?

Carbon stocks in resilient forests increased slightly in Shiretoko ($+8.3$ to $+11.9$ Mg C ha^{-1} across all climate change scenarios), changed very little in Berchtesgaden (-5.6 to $+6.0$ Mg C ha^{-1}), and decreased in Grand Teton (-34.7 to -98.8 Mg C ha^{-1}). The effect of forest reorganization on cumulative NEP differed by landscape and climate change scenarios (Figure 3). In Shiretoko, reorganizing forests almost always had higher cumulative NEP than resilient forests. Increases were strongest under the hot-dry climate scenario. In Berchtesgaden, the carbon balance of resilient forests differed little from reorganizing forests. Reassembling forests had slightly lower cumulative NEP than resilient forests (-2.2 to -8.6 Mg C ha^{-1}), but differences among pathways and climate change scenarios were generally small. In Grand Teton, the implications of reorganization differed according to the precipitation scenario. Under future drying, the cumulative NEP of reorganizing forests was generally lower than that of resilient forests. Conversely, under wet climate change scenarios, reorganizing forests had generally higher cumulative NEP than resilient forests, especially under the restructuring ($+38.6$ to $+48.6$ Mg C ha^{-1}) and replacement ($+2.3$ to $+25.1$ Mg C ha^{-1}) pathways. Across landscapes, cumulative NEP increased most strongly in forests experiencing structural novelty (restructuring and replacement) compared with forests that experienced compositional novelty (reassembly). Increases were particularly pronounced where forests experienced structural novelty only (see Section B3 in Supporting Information S1). Overall, there was high variability in carbon cycle responses within the same reorganization pathway: in Berchtesgaden and Grand Teton, the variability in the response of cumulative NEP to forest reorganization (vertical extent of the distributions in Figure 3) included the values for resilience in all scenarios. The functioning under reorganization only differed from resilient forests in Shiretoko (where resilience was rare under climate change, see Section B4 in Supporting Information S1).



Figure 4. (a) Proportion of landscape experiencing increases in compositional (rows 1–4) and structural indicators (rows 5–8) under hot-dry climate change [%]. Cell values show the proportion of the landscape in which an indicator increased under climate change compared to simulations under reference climate (mean across all 20 replicates). Green colors: the indicator increased on more than 50% of the landscape, pink colors: the indicator increased on less than 50% of the landscape; the darker the color, the farther the proportion is from 50%. (b) Spearman rank correlation coefficient between indicator change and changes in cumulative net ecosystem production (NEP). Values for indicator change and changes in cumulative NEP were calculated at the end of the 180-year simulation period at stand-scale. See (Section B6 in Supporting Information S1) for scatter plots of indicator change and changes in cumulative NEP.

3.2.2. Which Indicators of Composition and Structure Are Most Strongly Correlated With Future Carbon Dynamics?

Here we focus on results for the hot-dry climate scenario because simulated responses were strongest under this scenario (cf. Figure 2a), making an analysis of drivers most relevant. Results for the other climate scenarios can be found in the (Section B5 in Supporting Information S1). Across landscapes, compositional indicators generally responded similarly to climate change: currently dominant species decreased, while shade- and drought-tolerant species increased (Figure 4a). However, the response of species diversity and structural indicators diverged across landscapes. Decreases in species diversity and structural indicators (e.g., LAI, basal area) were common in Grand Teton but rare in Shiretoko and Berchtesgaden, where LAI and basal area increased under climate change.

The relationship between changes in compositional and structural indicators and changes in cumulative NEP was similar across landscapes. Cumulative NEP generally increased as shade-tolerant species increased, the share of the previously dominant species decreased, and structural indicators increased (Figure 4b). These relationships were particularly strong for LAI and basal area. However, the relationship between drought tolerance and cumulative NEP varied across landscapes: it was negative in Shiretoko, positive in Grand Teton, and barely present in Berchtesgaden. The opposite pattern emerged for species diversity, but correlations were weak. Relationships were generally less pronounced in Berchtesgaden than in Shiretoko and Grand Teton.

4. Discussion

4.1. Future Carbon Dynamics Diverge Across Landscapes

Changing climate and disturbance regimes strongly affected future forest carbon, with cumulative NEP significantly diverging from reference conditions. All study landscapes were moderate carbon sinks under the current climate, but current carbon dynamics were not a strong predictor of future dynamics. Carbon uptake, that is, net primary production, increased in Shiretoko and Berchtesgaden, which is likely the result of improved growing conditions under climate change (Egusa et al., 2020) in combination with relatively high compositional diversity (Silva Pedro et al., 2017). In Berchtesgaden, however, carbon gains were offset by simultaneous increases in carbon release due to increased disturbances causing higher losses from respiration (Amiro et al., 2010; Mayer et al., 2017). Grand Teton turned into a carbon source as carbon uptake decreased due to the combined effects of increased disturbances (Pan et al., 2024; Pietrzykowski et al., 2024) and less favorable climatic conditions for tree regeneration and growth (Hansen & Turner, 2019; Hoecker et al., 2020). The processes of carbon uptake and release can be disproportionally affected by climate and disturbance change, for example, if increases in carbon release due to combustion by wildfire cannot be buffered by increases in carbon uptake (Hudiburg et al., 2023; Zhao et al., 2021). Grand Teton's lower tree line is already operating at the fundamental limit of tree growth with regard to moisture availability (Rother & Veblen, 2016), and global warming could push parts of the system beyond this limit in the coming decades (Iglesias et al., 2018). The response of the carbon cycle to climate change thus depends on the dominant driver of landscape dynamics: climate change relaxes previous thermal limitations on productivity in Shiretoko, while it increases disturbances and drought stress in Grand Teton. Short-interval fires can tip the balance of disturbance and recovery in Grand Teton, because of proportionally greater live biomass loss and slower recovery with fewer trees (Dollinger et al., 2025; Walker et al., 2025). In Berchtesgaden, the carbon gains and losses from changing climate and disturbance regimes roughly balanced each other out.

4.2. Reorganization Sets the Stage for Future Carbon Dynamics

Reorganizing forests on average sequestered more carbon under climate change than resilient forests. The magnitude of this carbon response to reorganization was strongly dependent on the underlying compositional and structural shifts. We observed stark contrasts in the direction of these shifts among forest landscapes despite assuming the same magnitude of climate change. In Berchtesgaden and especially in Shiretoko, structural indicators increased compared with reference conditions, while they decreased under a drying climate in Grand Teton—indicating that forests undergoing restructuring became sparser in Grand Teton while they became denser in Shiretoko and Berchtesgaden. Conversely, reassembly, that is, a change in the tree species composition, was generally associated with increases in cumulative NEP in Grand Teton and Shiretoko, but with decreases in NEP in Berchtesgaden. As forests reassembled in Berchtesgaden, the dominance of Norway spruce—a species planted in previous decades for the purpose of timber production—declined due to increasing disturbance (Honkaniemi et al., 2020) and its reduced competitiveness under the emerging climatic conditions (Wessely et al., 2024). In Shiretoko and Grand Teton, NEP increased as currently dominant but cold-adapted species were outcompeted by species that are better adapted to the emerging climate conditions. The carbon response was especially pronounced in Shiretoko, where tree species diversity is high (36 simulated tree species across the landscape), meaning it is likely that species are present which can sustain or increase their growth under future climatic conditions (selection effect, Schnabel et al., 2021; Zheng et al., 2024). In Grand Teton, tree species diversity is low (six simulated tree species) and most of the available tree species are increasingly challenged by climatic changes (Blomdahl et al., 2022; Rammer et al., 2021). Among reorganizing forests, we found that restructuring had a stronger positive effect on NEP compared with reassembly. This likely results from currently dominating conifer species being typically more productive than the broadleaved species that gradually replace them under future environmental conditions (Augusto et al., 2015; Wessely et al., 2024), particularly in lower elevations (Dollinger et al., 2024).

4.3. Drivers Beyond Reorganization

Forests that are compositionally and structurally resilient to climate change can still experience shifts in their carbon dynamics. The carbon stocks of resilient forests in Shiretoko and Berchtesgaden increased as climate change generally improved conditions for tree growth. Climate change directly affects tree carbon uptake as a result of physiological effects, which can lead to changes in the carbon balance independent of forest

composition and structure. On the one hand, rising temperatures and CO₂ fertilization can increase carbon uptake via enhanced photosynthesis and microbial activity (Rustad et al., 2001). On the other hand, rising temperatures may also accelerate plant respiration (Davidson & Janssens, 2006) and intensify drought stress (Allen et al., 2010), potentially offsetting these gains. Uncertainty remains whether the carbon uptake potential of trees is primarily modulated by environmental drivers, such as CO₂ fertilization, or by tree-internal metabolic limitations (Gessler & Zweifel, 2024; Trugman & Anderegg, 2025). The persistence of the CO₂ fertilization effect is uncertain (Jiang et al., 2020), particularly under limiting nutrients such as nitrogen and phosphorus (Ainsworth & Rogers, 2007; Norby et al., 2010). In parallel, warming and drought can alter microbial community composition and activity (Allison & Martiny, 2008), shifting soil carbon turnover rates as well as feedback to plant productivity (Schmidt et al., 2011). Increases in forest productivity driven solely by the physiological response of trees will most likely saturate quickly or be offset by simultaneous increases in decomposition. This suggests that for carbon gains to persist in the long term, they must be “hardwired” into forests via shifts in composition and structure.

4.4. Methodological Considerations

Our results need to be interpreted within the limitations of the applied simulation model. iLand performed well in model intercomparison studies (Bugmann et al., 2019; Díaz-Yáñez et al., 2024; Petter et al., 2020) and was extensively evaluated against independent data for all three study landscapes (Dollinger et al., 2024; Hansen et al., 2020; Thom et al., 2022), lending confidence to our findings. However, some locally important processes were not simulated in the current study, such as browsing (Kupferschmid et al., 2015), competition from forest floor vegetation (Thrippleton et al., 2018), and disturbance by biotic agents other than the European spruce bark beetle and mountain pine beetle (Yoshida et al., 2005). Additionally, the model only considered macroclimatic effects on decomposition even though microclimate may be important (Braziunas et al., 2025; Eichenberg et al., 2017; Sanczuk et al., 2023). Further uncertainties arise from projections of soil C dynamics, as iLand uses a simple and parsimonious approach for tracking the fate of soil C (Kätterer & Andrén, 2001), and soil C pools were assumed to be in a dynamic equilibrium at the start of the simulation. Furthermore, we simulated forest development until the end of the 22nd century (and prolonged simulations until the end of the 24th century to test for effects of simulation duration, Section B2 in Supporting Information S1) to capture long-term dynamics of forest composition, structure, and functioning, such as species adaptation to emerging climate conditions, and changes in disturbance-recovery cycles. This choice, however, also introduced uncertainties regarding the progression of climate change beyond the 21st century. We assumed a stabilization of climate change in the 22nd century at levels projected for the end of the 21st century, which is a parsimonious yet highly uncertain assumption. Further uncertainties might arise from the fact that extreme climatic events are currently not fully represented in climate models (Alizadeh, 2022; Dorado-Liñán et al., 2022). To our knowledge, this is the first study to comparatively project future landscape-scale carbon dynamics in temperate forests across three continents. While literature on landscape-level carbon trends in temperate forests exists for the Western US (Henne et al., 2021; Smithwick et al., 2009) and Central Europe (Albrich et al., 2023; Hlásny et al., 2011), the literature is sparse for the natural forests of Hokkaido, constraining our ability to gauge the validity of our findings for these particular systems. We note that the three landscapes were not selected to be representative of temperate forests as such, but rather are archetypes of the distinctly different disturbance regimes that occur across the temperate forest biome (Seidl et al., 2020; Sommerfeld et al., 2018). Notwithstanding these limitations, our results provide a comprehensive analysis of potential future forest and carbon dynamics across contrasting temperate forest landscapes.

5. Conclusions

Future carbon dynamics diverge across landscapes and current NEP is not a strong predictor of future trends in carbon uptake and storage. Instead, responses to changing climate and disturbance regimes—particularly whether forests persist in their current composition and structure (resilience) or exhibit compositional and/or structural novelty (reorganization)—strongly shape carbon outcomes. Future carbon dynamics are particularly sensitive to structural changes. This highlights that forest structure has crucial leverage on the temperate forest carbon balance, and that restructuring forests deserves particular attention in policy and management. Forest structure also exerts an important influence on forest disturbance regimes, which in turn affect future carbon trajectories. We found that forest carbon in systems strongly impacted by climate-driven disturbances was particularly vulnerable, with an increased risk of forests turning into a carbon source in the atmosphere. Compensatory effects of

compositional changes, especially shifts toward more drought- and warm-adapted species assemblages, only partly buffer against such future declines in forest carbon (Germain et al., 2025).

Notably, across our simulations reorganizing forests generally had higher cumulative NEP than resilient forests. This finding indicates that strict persistence can lock forests into functionally undesirable states in some contexts (Smithwick et al., 2023). Some forest changes might be essential in a changing climate—deciding when to accept or even facilitate such change rather than resisting it is a major challenge for ecosystem management in the coming decades.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

The data that support the findings of this study are openly available from the Dryad Digital Repository at <https://doi.org/10.5061/dryad.x3ffbg80w>. The code used to analyze the simulation data and generate the results can be found here: https://github.com/CEDollinger/3rd_analysis. Extensive model documentation on iLand can be found at <https://iland-model.org> and the full model source code at <https://github.com/edfm-tum/iland-model>.

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