Global Ecology and Biogeography

WILEY

Global Ecology and Biogeography | A Journal of Macroecology

RESEARCH ARTICLE OPEN ACCESS

Disentangling Compound Effects of Changing Disturbance and Regeneration Across Temperate Forest Landscapes

Christina Dollinger[1] | Werner Rammer[1] | Akira S. Mori[2] | Monica G. Turner[3] | Rupert Seidl[1,4]

[1]Ecosystem Dynamics and Forest Management Group, School of Life Sciences, Technical University of Munich, Freising, Germany | [2]Research Center for Advanced Science and Technology, The University of Tokyo, Tokyo, Japan | [3]Department of Integrative Biology, University of Wisconsin-Madison, Madison, Wisconsin, USA | [4]Berchtesgaden National Park, Berchtesgaden, Germany

Correspondence: Christina Dollinger (christina.dollinger@tum.de)

Received: 20 March 2025 | **Revised:** 23 September 2025 | **Accepted:** 8 October 2025

Handling Editor: Irena Simova

Funding: C.D., W.R. and R.S. were supported by the European Research Council (ERC) under the European Union's Horizon 2020 Research and Innovation Programme (grant agreement no. 101001905). A.S.M. acknowledges support from the Japan Science and Technology Agency (JST, funding no. JPMJRX21I4 and JPMJRS23I4), and Theme 4 of the Advanced Studies of Climate Change Projection (SENTAN Program, grant no. JPMXD0722678534), and supported by the JSPS KAKENHI (funding no. 22KK0102). M.G.T. acknowledges funding from the University of Wisconsin-Madison Vilas Trust and the US National Park Service Reserve Funds (Task Agreement P22AC00588).

Keywords: climate change impacts | disturbance ecology | protected areas | regeneration | simulation modelling | temperate forests

ABSTRACT

Aim: Global change alters many ecological processes simultaneously. Yet, the interactive and compound effects of these changes remain difficult to quantify. Here, we addressed the question of how changes in disturbance and regeneration processes interactively alter temperate forest landscapes across three continents.

Location: Temperate forests of the Northern Hemisphere.

Time Period: 21st century.

Major Taxa Studied: Trees.

Methods: We conducted a simulation experiment to (i) disentangle the effects of interacting disturbance and regeneration processes on forest structure and composition and (ii) quantify how a changing climate modulates these interaction effects.

Results: Simultaneously changing disturbance and regeneration processes led to a tenfold amplification of forest change compared to changes in either disturbance or regeneration. Interaction effects were context-dependent: At low to intermediate disturbance rates (< 1% of landscape disturbed per year), high rates of regeneration buffered against declines in forest structure. In contrast, the interactions of high disturbance and high regeneration rates amplified changes in forest composition. Climatic changes dampened structural change while amplifying compositional change. At high disturbance rates, however, the modulating effects of climate change were small, and forest change was primarily driven by disturbances.

Main Conclusions: We conclude that the consequences of changing disturbance and regeneration need to be assessed jointly to understand their outcomes. Our findings highlight the importance of interaction effects of simultaneously changing ecological processes in shaping the future of forest ecosystems.

1 | Introduction

Forests are experiencing drastic shifts in their structure and composition due to global change (McDowell et al. 2020). Climate warming as well as changes in precipitation sums and seasonality influence important demographic processes such as tree mortality and regeneration (Nigro et al. 2025)—which in turn fuel forest change. However, attributing observed changes to individual underlying processes remains difficult (Baltzer et al. 2021). For instance, a decrease in stem density can result from increased tree mortality or decreased tree regeneration. Disentangling the root causes of change and understanding how individual processes influence forest ecosystems are prerequisites to addressing change in ecosystem management effectively (Siegel et al. 2023). To illustrate with the above example: Should preventing old trees from dying—to buffer increasing mortality—or planting young trees—to counteract regeneration loss—be the focus when responding to decreasing stem density in management? Managing changes in forest structure and composition is important because they profoundly influence important ecosystem services (Rasche et al. 2013). For example, forest structure is intricately linked to the ability of forest ecosystems to sequester and store carbon from the atmosphere and thus is important for regulating the climate system (Thom and Keeton 2019), whereas forest composition is closely linked to habitat value and strongly determines the species that dwell in forest ecosystems (Barnagaud et al. 2014).

Two key processes of forest demography with strong leverage on forest structure and composition are tree mortality and regeneration. In forest ecosystems, tree mortality often happens in pulses termed disturbances (e.g., caused by wildfire, insect outbreaks or windthrow, Pickett and White 1985). Disturbances influence forest structure and composition in the short term (e.g., affecting certain tree species or structural cohorts disproportionately, Burton et al. 2020) as well as in the long term (e.g., by changing light availability on the forest floor and promoting light-demanding and fast-growing early-seral species, Mazon et al. 2023). Disturbances have increased in frequency and size over past decades in many parts of the world and are expected to continue changing in the coming decades across temperate forest ecosystems (Kasischke and Turetsky 2006; Patacca et al. 2023; Senf and Seidl 2021). Regeneration is the process of germination and establishment of trees, resulting from seed production and dispersal, as well as seed germination, establishment and early growth. It is influenced by climate, light availability on the forest floor and biotic interactions (e.g., with herbivores and forest floor vegetation). Tree regeneration strongly determines forest structure and species composition, for example, via the rate, identity and spatial patterns at which trees establish (Donato et al. 2016). As a result of global change, tree regeneration is changing, with distinct effects of increasing drought and temperatures (Hansen et al. 2018) as well as invasive alien species (Dey et al. 2019); therefore, future changes in regeneration processes are likely (Clark et al. 2021).

Forest disturbance and tree regeneration are intricately linked and can have compound effects on forest structure and composition (Turner and Seidl 2023). Increasing rates of disturbance (i.e., higher percentages of landscape area disturbed per year), for instance, might be buffered in systems with high regeneration rates (Davis et al. 2023). Similarly, reduced rates of regeneration might only have minor impacts in systems where canopy openings from disturbance are small and infrequent. Because of their interactive nature, disturbance and regeneration must be analysed in concert to understand their ecosystem-level consequences. Moreover, simultaneous directional changes in *both* disturbance and regeneration hold the potential for substantial compound effects. For example, if global change results in increased disturbance activity (e.g., more wildfires due to increased temperature and drought, Wang et al. 2025) while simultaneously reducing the capacity of trees to regenerate (e.g., because more frequent and severe post-fire drought reduces the success of tree establishment, Hansen and Turner 2019), tipping points could be crossed, resulting in major ecosystem transitions (Rammer et al. 2021). However, the contexts and conditions that cause such thresholds to be exceeded remain difficult to quantify and a major current challenge of ecological research (Jackson et al. 2009).

Process-based simulation models offer a unique opportunity to disentangle the effects and context dependencies of individual processes and understand their compound impacts. Specifically, conducting experiments in silico allows us to manipulate some processes individually while keeping all others constant to assess the effects of process-level changes across different contexts. Manipulating processes such as disturbance and regeneration at the scale of forest landscapes (i.e., the spatial scale at which their interactions unfold) remains challenging in real-world experiments, not least because of the limits in replicating landscapes (Phillips 2007). Observational approaches, in turn, are challenged by the lack of a true counterfactual, as the effects of global change are pervasive, and unchanged reference conditions are increasingly difficult to find. Simulation models enable us to study the interactive effects of simultaneously changing ecological processes in isolation and in combination with the effects of a changing climate, so as to assess landscape-scale consequences for forest structure and composition relative to the counterfactual of the absence of climate change.

To study the interactive effects of potential changes in disturbance and regeneration as drivers of forest structure and composition, we investigated three temperate forest landscapes—Shiretoko National Park (Japan), Berchtesgaden National Park (Germany) and Grand Teton National Park (USA). These landscapes represent a gradient from low to high disturbance activity, covering a broad range of disturbance regimes found in temperate forest landscapes of the Northern Hemisphere. For these landscapes, we (i) quantified the individual effects of disturbance and regeneration on forest structure and composition, (ii) assessed their interactive effects, and (iii) analysed the modulating effect of climate on these processes and interactions. Our specific research questions were (i) 'How do changes in individual processes of disturbance and regeneration (e.g., increases in disturbance patch size, decrease in seed production) affect forest change?' We hypothesised that effects of changing disturbance and regeneration are contingent on the system-specific baseline, with landscapes with high disturbance rates being most sensitive to increases in disturbance, and landscapes with low regeneration rates being most sensitive to decreasing regeneration. We subsequently asked, (ii) 'How do changes in disturbance and regeneration processes interact to drive forest change?' We

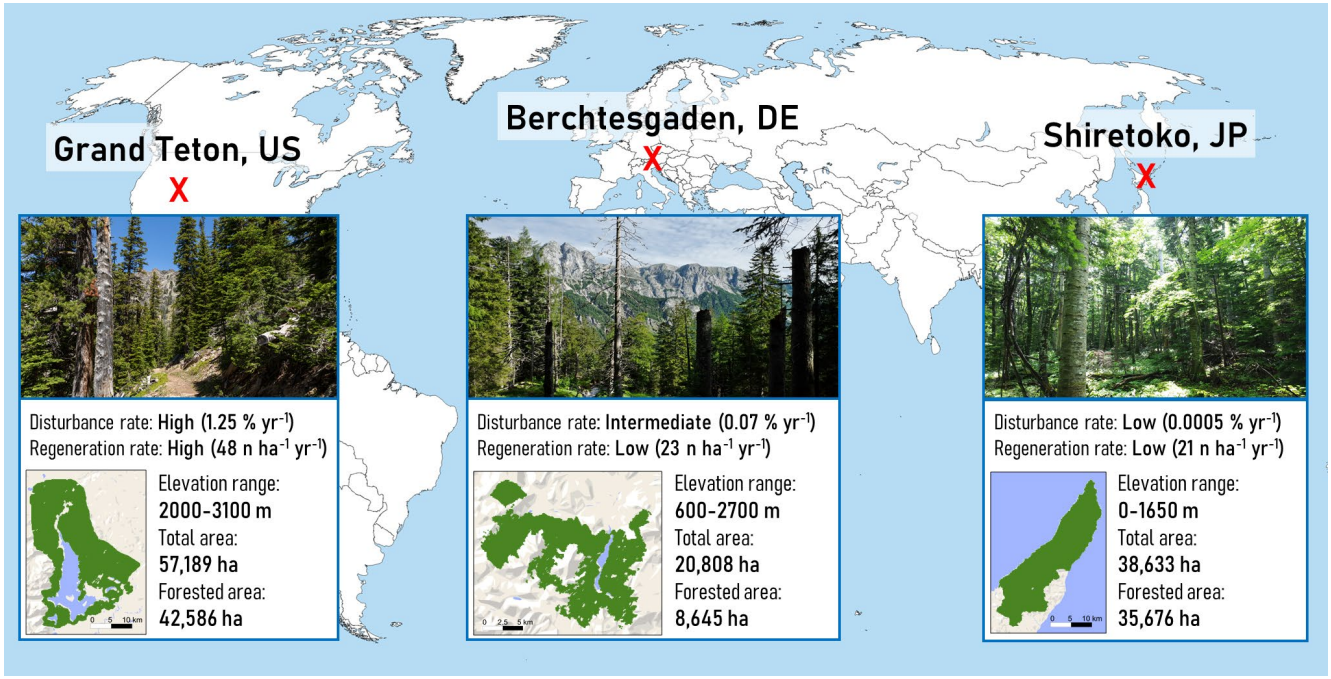

FIGURE 1 | World map showing the location of the three study landscapes and their extent as well as example forest conditions. Disturbance and regeneration rates are based on simulations under reference conditions. Image credit: Grand Teton—Timon T. Keller; Berchtesgaden—Rupert Seidl; Shiretoko—Kureha F. Suzuki. Figure adapted from Dollinger et al. (2024).

expected interactions to result in additive or synergistic change (Ratajczak et al. 2018), indicating compound effects of changing disturbance and regeneration processes on forest structure and composition. Finally, we asked (iii) 'How does climate modulate the interactive effects of changing disturbance and regeneration processes?' We expected climate to have both amplifying (e.g., drier conditions leading to regeneration failure, Hansen et al. 2018) and dampening (e.g., warming temperature leading to increased forest productivity, Emmett et al. 2019) effects on forest change. Additionally, we hypothesised that the effects of climate change would be most pronounced at low disturbance rates and high regeneration rates.

2 | Methods

2.1 | Study Landscapes

We studied three temperate forest landscapes representing distinct levels of disturbance activity, identified via a remote sensing analysis across 50 temperate forest ecosystems on five continents (Sommerfeld et al. 2018). The landscape representing the lowest disturbance activity is Shiretoko National Park (Japan, 44°10′33.6″ N, 145°11′43″ E, from here on referred to as Shiretoko), located on the northeastern tip of Hokkaido (Figure 1). The forests are species-rich, mixed conifer-broadleaf forests dominated by Sakhalin fir (*Abies sachalinensis*) and Erman's birch (*Betula ermanii*). The main disturbance agent is wind, creating frequent but very small patches of tree mortality. Berchtesgaden National Park (Germany, 47°32′56.4″ N, 12°55′4.8″ E, referred to as Berchtesgaden), located at the southeastern tip of Germany, represents landscapes with moderate disturbance activity. The forests are mixed conifer-broadleaf forests dominated by Norway spruce (*Picea abies*) and European beech (*Fagus sylvatica*). The main disturbance agents are wind and bark beetles (European spruce bark beetle, *Ips typographus*, host tree Norway spruce). Grand Teton National Park (United States of America, 43°48′50.4″ N, 110°38′27.6″ W, referred to as Grand Teton) represents landscapes with high disturbance activity, affected by large, infrequent wildfires and fine-grained bark beetle disturbances (mountain pine beetle, *Dendroctonus ponderosae*, host tree mainly lodgepole pine *Pinus contorta var. latifolia*) during fire-free intervals. The forests are conifer-dominated with lodgepole pine and Douglas-fir (*Pseudotsuga menziesii var. glauca*) as dominant species. The three study landscapes also represent distinctly different rates of tree regeneration. Specifically, regeneration rates (here defined as the number of saplings recruited into the tree layer per hectare and year) are low in Shiretoko and Berchtesgaden and high in Grand Teton. All landscapes were designated as IUCN Category II protected areas in the 20th century. For more details on the three study landscapes, see Dollinger et al. (2024).

2.2 | Simulation Model

Forest landscape responses to changing disturbance and regeneration processes were studied using the simulation model iLand ('the individual-based forest landscape and disturbance model', Rammer et al. 2024; Seidl et al. 2012). iLand is based on first principles of ecology, with forest dynamics emerging from the interactions of individual trees among themselves and with their abiotic and biotic environment. Processes are modelled at nested spatial and temporal scales, with processes at broader scales (e.g., resource availability) constraining processes at finer scales (e.g., individual tree growth). Primary productivity is dependent on local light availability (calculated from an individual tree's position within a continuous field of light availability, created by overlaying

the shading influence of neighbouring tree crowns) and limited by climate and soil conditions. Tree mortality can occur due to aging, carbon starvation or disturbance agents, which are modelled spatially explicitly on the landscape. Tree regeneration is modelled by considering spatially explicit seed availability, establishment probabilities influenced by abiotic drivers as well as light availability, and the competition and growth of trees in the sapling stage. Extensive model documentation on iLand can be found at https://iland-model.org and the full model source code is available at https://github.com/edfm-tum/iland-model. Here version 1.9 of iLand was used. Initial forest vegetation conditions, representing the state of the landscapes in the year 2020, were derived from a combination of forest inventory data, remote sensing information and model spin-up (Dollinger et al. 2024). Non-forest habitats were not considered in the simulation. iLand has been parameterised and evaluated against independent data in all three study landscapes, indicating that the model is well able to simulate forest dynamics across systems (Dollinger et al. 2024; Hansen et al. 2020; Thom et al. 2022).

2.3 | Experimental Design

We conducted a manipulative experiment in silico, studying changes in four processes in a full factorial design. Specifically, we varied two processes of disturbance (disturbance frequency and size) and two processes of tree regeneration (seed production and sapling growth; Table 1). We simulated three levels of change for each process in addition to a reference level representing historical conditions (see below on how reference conditions were set). Changes in each process were unidirectional, consistent with the expected effects of global change on these processes as reported in the literature (i.e., increasing disturbance frequency and size, and decreasing seed production and sapling growth, Clark et al. 2021; Hansen and Turner 2019; Patacca et al. 2023; Senf and Seidl 2021). We modified processes individually and in combination under current climate to answer research questions Q1 and Q2 (Table 2). In addition, we ran simulations under projections of climate change (see below for details) to investigate how climate change modulates effects of

TABLE 1 | Experimentally modified processes: rationale, direction and change levels.

Driver	Process modified	Rationale and references	Direction	Change levels
Disturbance change	Disturbance frequency	Increasing disturbance frequency (Baltzer et al. 2021; Patacca et al. 2023)	Increase	Reference, 2, 5, 10
	Disturbance size	Increasing disturbance size (Kasischke and Turetsky 2006; Senf and Seidl 2021)		
Regeneration change	Seed production	Declining capacity to produce seeds (Clark et al. 2021; Gill et al. 2021)	Decrease	Reference, 1/2, 1/5, 1/10
	Sapling growth	High sensitivity of saplings to abiotic stressors (Grubb 1977; Hansen and Turner 2019)		

TABLE 2 | Simulation design employed to answer research questions (Q).

Research question	Simulation design
Q1: Individual effects of changing disturbance and regeneration processes	• Only one process modified at a time (i.e., disturbance frequency and size, seed production and sapling growth) • Other processes kept at reference level (corresponding to current values) • Current climate • $N = 80$ per landscape
Q2: Interactive effects of changing disturbance and regeneration processes	• Full-factorial design: ◦ 4 processes à 4 change levels ◦ All combinations: $4^4 = 256$ scenarios • **Disturbances and regeneration change simultaneously** • Current climate • $N = 1280$ per landscape
Q3: Climate change impacts on the interactive effects of changing disturbance and regeneration processes	• Full-factorial design • Disturbance and regeneration change simultaneously • **Severe climate change** (representing the change expected under RCP 8.5 scenarios) • $N = 1280$ per landscape

Abbreviation: *N*, number of simulations.

changing disturbance and regeneration processes (Q3, Table 2). Overall, we considered four levels for four processes—resulting in 4^4 (i.e., 256) combinations in our experiment, which we simulated under two different climate scenarios (reference climate and a scenario of severe climate change, see section below for more details). To account for stochasticity (e.g., in tree mortality), five replicates were simulated per factor combination, resulting in a total of 2560 simulations per landscape. Simulations were run for 80 years (2021 to 2100), as uncertainties about projected future climate change mount beyond the 21st century.

2.3.1 | Experimental Implementation of Disturbance and Regeneration Change

Reference conditions for disturbance regimes under historical climate were simulated dynamically for each landscape, using the process-based disturbance modules of iLand (Seidl, Rammer, and Blennow 2014; Seidl, Rammer, and Spies 2014; Seidl and Rammer 2017). The approach used to independently manipulate disturbance frequency and size to obtain the levels of change of our experiment (Table 1) while at the same time retaining realistic patch shapes is described in more detail in the Supporting Information (Section A1). We simulated near stand-replacing disturbances, while keeping agent- and landscape-specific disturbance characteristics intact. Within fire patches, only pixels with combustible fuel exceeding 500 kg ha^{-1} burned; on these, all saplings and 90% of mature trees were killed, and 10% of stem biomass and 50% of branch biomass combusted (Fahnestock and Agee 1983). On bark beetle patches, 90% of basal area of the host species (Norway spruce in Berchtesgaden and lodgepole pine in Grand Teton) with a diameter at breast height (DBH) ≥ 15 cm were targeted, while saplings remained unaffected. On wind patches, 90% of the basal area of trees with a DBH ≥ 15 cm were killed regardless of species, while saplings remained unaffected. As only susceptible trees were considered for disturbance mortality, the actually disturbed basal area and spatial patterns of tree mortality within a patch were constrained by the forest conditions present on the patch. To assess the implications of this choice in simulated severity, we conducted an additional set of simulations with a broader severity gradient (50%, 75% and 99% targeted basal area; see Section A3 in Supporting Information). Similarly to our experimental implementation of disturbance change, we also generated an experimental gradient in regeneration change, using dynamic simulations with the default iLand parameterisation—evaluated successfully for the three study landscapes (Dollinger et al. 2024; Hansen et al. 2020; Thom et al. 2022)—as reference. More details on how iLand simulates regeneration and the experimental implementation of regeneration change can be found in the Supporting Information (Section A1).

2.3.2 | Climate Change

Reference climate was defined as the climate for the period 1991–2020, resampled with replacement to obtain an 80-year time series for simulation. For each landscape, reference climate was obtained from downscaled climate model data matching well with observations from the recent past (Dollinger et al. 2024). Research questions Q1 and Q2 were addressed under reference climate conditions (Table 2). To assess how the effect of climate change modulates the effects of experimentally changed disturbance and regeneration processes (Q3, Table 2), we also simulated all runs of the experiment under severe climate change (RCP 8.5), using locally downscaled climate scenario data. A scenario of severe climate change was chosen to capture the maximum effect of climatic changes on forest change but results under less severe climate change scenarios can be found in the Supporting Information (Section A4). While iLand is designed to simulate the effect of climate change on disturbance and regeneration change dynamically, we here decoupled disturbance and regeneration from changes in climate. In other words, disturbance and regeneration processes were modified by the same amounts regardless of climate scenario in the experiment. The altered climate regime simulated for research question Q3 considered changes in climate and atmospheric CO_2 concentrations, and affected simulated tree growth, establishment success and inter-species competition to interactively influence forest change. More details on the climate models used and their projected climatic changes can be found in the Supporting Information (Section A1).

2.4 | Analyses

Forest change was analysed for forest structure and composition, quantifying their deviation from reference conditions (i.e., simulations at default process rates under reference climate) in the last year of the 80-year simulation period. As we were mainly interested in the landscape-level consequences of different levels of disturbance and regeneration, we calculated forest change as a binary response at cell level (100 × 100 m), subsequently aggregating these binary values to the landscape level by calculating the percentage of cells that experienced change. A value of 100% thus means that the complete landscape area undergoes change, while a value of 0% indicates a landscape that did not deviate from reference conditions. A basal area reduction of more than 50% from reference levels indicated structural change. A sensitivity analysis on different threshold values can be found in the Supporting Information (Section A2). As we investigated unidirectional changes in process parameters, we solely focused on a reduction in basal area in our analyses (i.e., corresponding to a one-sided statistical test). We chose basal area as an indicator of structural change because it is sensitive to changes in stem numbers as well as tree diameter distributions. Compositional change was assumed when the most dominant species differed from that under reference conditions. Species dominance was derived as the species with the highest species importance value, calculated as the mean over relative species proportions based on both basal area and stem density.

Forest change was analyzed in response to the individual processes investigated in our experiment (i.e., increased disturbance frequency and size, reduced seed production and sapling growth), and aggregated for disturbance change and regeneration change. Disturbance change was calculated as the percent of landscape area disturbed by year (disturbance rate, % year^{-1}), which integrates across disturbance frequency and size, and regeneration rate as the mean number of saplings recruited into the tree layer (height > 4 m) per hectare and year (regeneration rate, n ha^{-1} year^{-1}), which integrates across seed production and sapling growth. The area base for all calculations was the stocked forest area which, in Grand Teton, was subject to change over

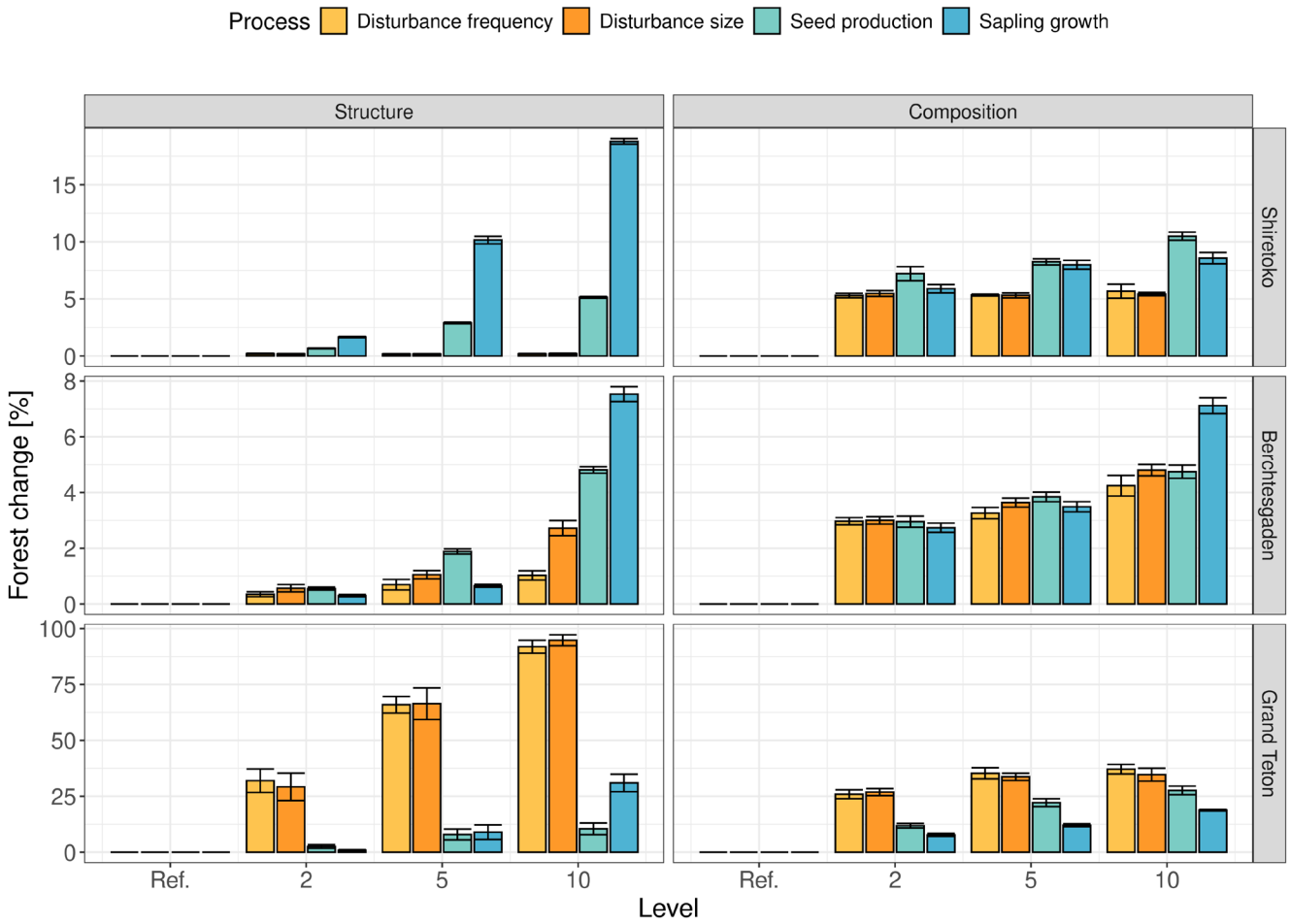

FIGURE 2 | Individual process impacts on structural change (left) and compositional change (right) per landscape under reference climate with all other processes kept at their reference level. Bars show the mean and error bars show the standard deviation in change values in simulation year 80 over all 5 replicates. The *x*-axis is linear but change levels increase non-linearly; the *y*-axis range differs by landscape.

the simulation period due to forest loss. Results for forest loss and forest change along elevational gradients can be found in the Supporting Information (Sections B1 and B2). 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 A5 in Supporting Information).

3 | Results

3.1 | How Do Changes in Disturbance and Regeneration Processes Affect Forest Change Individually?

In Grand Teton, the landscape with the highest reference disturbance level, changes in disturbance processes were more impactful than changes in regeneration (Figure 2). In contrast, Shiretoko, the landscape with the lowest regeneration rate under reference conditions, was most sensitive to changes in regeneration processes. In Berchtesgaden, the landscape with intermediate disturbance and regeneration rates, disturbance and regeneration change had similar effects on forest structure and composition.

Overall, forest structure responded more strongly to process change than forest composition in all three landscapes. However, the absolute values of forest change differed among landscapes and were small for Berchtesgaden, moderate for Shiretoko and high for Grand Teton (Figure 2). In Shiretoko and Berchtesgaden, forest structure was buffered against low levels of disturbance change. Conversely, composition already responded strongly to low levels of disturbance and regeneration change but stabilised at higher rates of change. Increases in the two disturbance processes investigated (i.e., disturbance frequency and size) had largely similar effects on forest structure and composition. The effects of decreases in the two regeneration processes (i.e., seed production and sapling growth) differed. Particularly for higher levels of regeneration change, reduced sapling growth had a stronger effect on forest structure than reduced seed production across all landscapes.

3.2 | How Do Changes in Disturbance and Regeneration Processes Interact to Drive Forest Change?

Simultaneous changes in disturbance and regeneration processes led to substantial compound effects: Forest change was amplified tenfold when disturbance and regeneration changed simultaneously compared to individual changes in the same variables (Figure 3, for a colorblind safe option see Supporting Information,

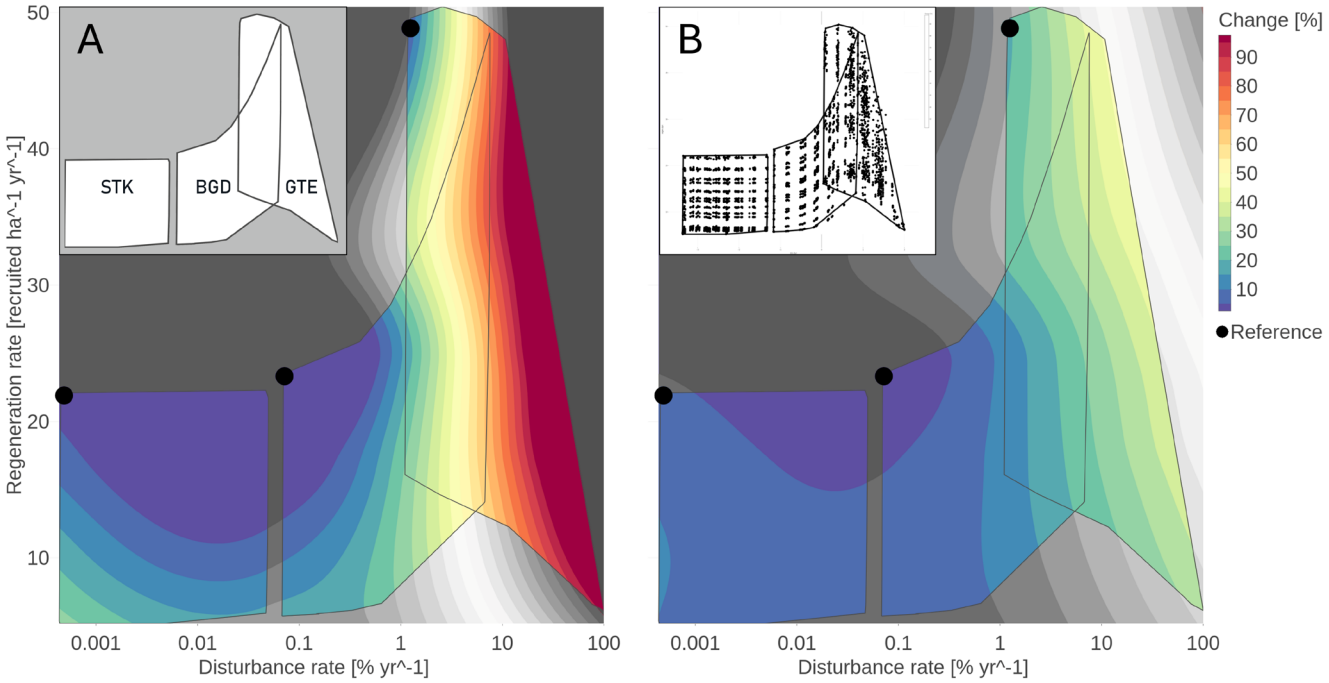

FIGURE 3 | Impact of disturbance and regeneration rate on structural change (left) and compositional change (right) under reference climate in simulation year 80. Colours indicate the percentage of the landscape area affected by forest change. Inset A shows the region of the data space covered by each study landscape (STK = Shiretoko, BGD = Berchtesgaden, GTE = Grand Teton). The values were predicted by LOESS based on results of 3840 simulation runs (see Inset B for data space). Regions of the plot surface beyond the data space are greyed out. *x*-axes have logarithmic scales.

Section B5). For example, in Berchtesgaden, 88.1% instead of 8.0% of the landscape saw declines in forest structure under interacting instead of individual process changes. Interactions between disturbance and regeneration change led to distinct non-linear effects, and both facilitated and dampened forest change depending on the level of disturbance change. For instance, at very low disturbance rates (< 0.1% year^{-1}), increasing disturbance-created canopy openings counterbalanced the effect of decreasing regeneration on forest structure (negative slope of contour lines in Figure 3). Inversely, at intermediate levels of disturbance (i.e., between disturbance rates of 0.1% and 1.0% year^{-1}), high levels of regeneration substantially dampened the effect of increasing disturbances on forest structure (positive slope of contour lines). At high levels of disturbance, interactive effects were weak and responses were mainly driven by disturbance change, with little effect of regeneration rate (vertical contour lines).

Composition showed similar patterns to those described above for structure, but was, overall, less sensitive to increasing disturbance rates and decreasing regeneration rates. However, a notable deviation from the congruence of structural and compositional responses was observed at high disturbance rates (> 3% year^{-1}), where high regeneration rates tended to facilitate compositional change.

3.3 | How Does Climate Change Modulate the Interactive Effect of Changes in Disturbance and Regeneration?

Simulating the impacts of changing disturbance and regeneration under a changed climate affected the responses of forest structure and composition in distinctly different ways (Figure 4; for a colorblind safe option see Supporting Information Section B5). Climate change mostly dampened the effect of changes in disturbance and regeneration on forest structure (mean decrease in structural response of −5.7% across all landscapes and process change levels), especially at low regeneration rates (below ~20 trees recruited ha^{-1} year^{-1}). Conversely, compositional change was generally amplified by climate change (mean increase of 4.1%), especially when disturbance rates were low and regeneration rates were high. The modulating effects of climate change were strongest in Shiretoko, which was the landscape responding most strongly to regeneration change. In contrast, in Grand Teton, disturbance change was the process dominating forest change, and the modulating effects of climate were weak.

4 | Discussion

4.1 | The Response to Changes in Individual Processes

Studying three temperate landscapes spanning a wide range of disturbance and regeneration dynamics (Dollinger et al. 2024; Sommerfeld et al. 2018), we found that systems were particularly susceptible to changes in the process that is already currently limiting. In landscapes with high current disturbance activity, increasing disturbance frequency and size—at fixed severity—had a greater impact on forest structure and composition than declines in seed production and sapling growth. Conversely, landscapes with low current disturbance activity were not particularly sensitive to changes in disturbance. We found similar patterns for regeneration, where highest sensitivities to declining seed production and sapling growth were

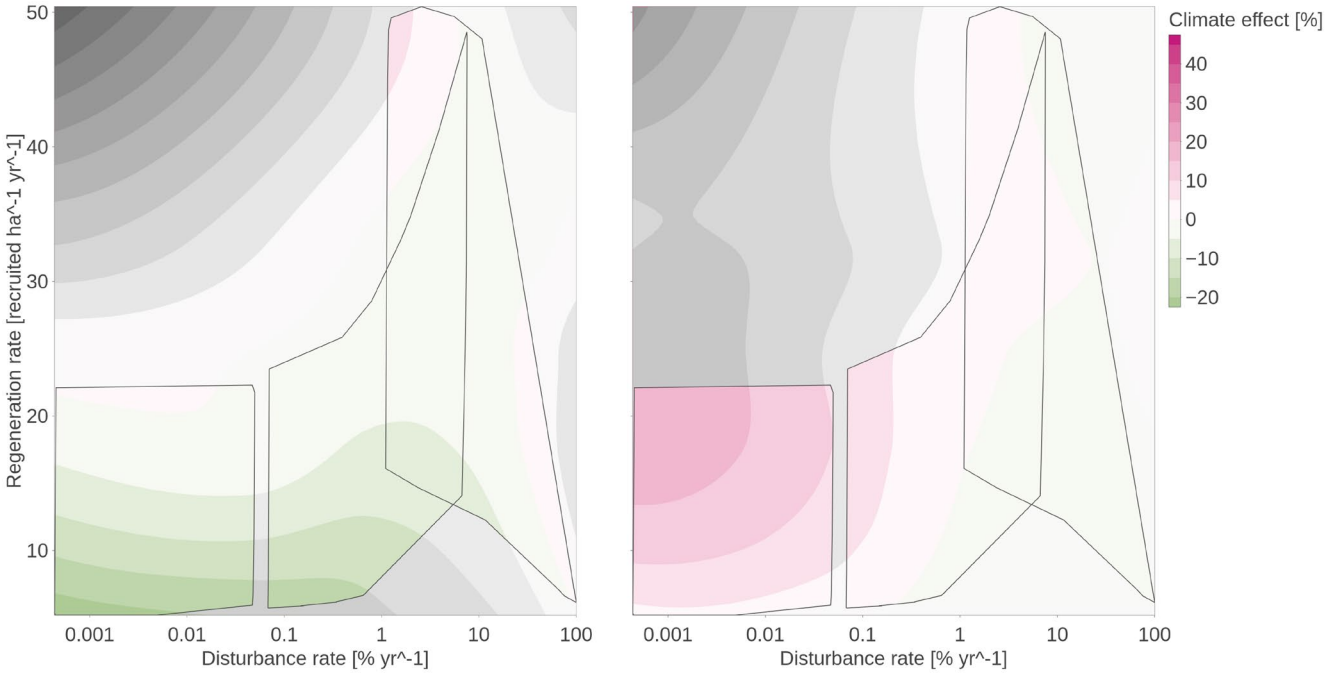

FIGURE 4 | Climate effect on structural change (left) and compositional change (right). Effect values were calculated as the percentage of landscape changed under climate change minus the percentage of landscape changed under reference climate in simulation year 80, and predicted by LOESS with plot surface beyond the data space greyed out. *x*-axes have logarithmic scales.

observed in landscapes with currently low regeneration rates. These findings underscore that similar levels of change in individual processes can have distinctly different impacts on ecosystems, depending on their local context. In Shiretoko, declines in regeneration processes emerged as highly potent drivers of change, while increased disturbances were the main drivers of change in Grand Teton. In Berchtesgaden, both aspects were similarly important but led to the lowest levels of forest change overall.

Notably, the effects of disturbance frequency and size were similar (Figure 2); that is, similar levels of change in these processes led to similar levels of forest change. This implies that even though frequency and size affect forest dynamics via different mechanisms—more frequent disturbances increase immaturity risk, while bigger patches increase the distance to live seed sources (Gill et al. 2021)—the landscape-scale outcomes are similar for the response indicators investigated here. However, the ecological outcomes of changes in disturbance frequency and size could also be modulated by disturbance severity. We note that while we here simulated near stand-replacing disturbances, the simulations were able to capture realistic ecological patterns, such as the dampening feedback between disturbance frequency and severity. When disturbance intervals become shorter than recovery intervals, disturbance severities tend to decrease due to declines in tree vegetation (Parks et al. 2016; Turner et al. 1993). Reduced sapling growth generally had a stronger effect on forest change than reduced seed production in the context of regeneration change. This might be because trees remain in the sapling stage for many years (up to decades in slow-growing mountain forest systems, Mori and Hasegawa 2007), with the effect of reduced sapling growth accumulating over time, while germination from seeds is a process that needs to happen only once for trees to establish. This underscores the impact that ungulate herbivory can have on forest change (Dobor et al. 2024; Nishizawa et al. 2016), as ungulates can effectively reduce sapling growth over multiple years if population densities are high. While we found that all landscapes were buffered against moderate increases (up to a factor of two) in single processes of disturbance, similar levels of reduction in regeneration processes resulted in considerable changes across all systems investigated. This could be the result of an adaptation of forest ecosystems to generally high variability in disturbance, while regeneration rates are generally more stable over time. As such, systems might react more strongly to variation in regeneration rates than disturbance rates.

4.2 | Compound Effects of Simultaneous Changes in Disturbance and Regeneration

We demonstrated that simultaneous changes in disturbance and regeneration processes can have strong compound effects on forest structure and composition, going considerably beyond the impact of changes in individual processes. Structure responded more strongly to compound changes than composition, supporting observations that composition is less sensitive to change (Winter et al. 2015). We note, however, that we focused on only 80 years of forest dynamics, and compositional effects might unfold over considerably longer time scales (Thom et al. 2022). Notwithstanding the strong interaction effects, increasing disturbance rates emerged as the single most influential driver of forest change in our analyses, determining structural change regardless of regeneration rate once disturbance rates exceeded ~1% year^{-1}. This threshold of disturbance rate has been crossed in recent years even in systems that historically had lower levels of disturbance (Senf and Seidl 2021; Washaya et al. 2024), making profound changes in forest structure likely in these systems

(Hagmann et al. 2021). These changes have implications for the functioning of forest ecosystems, as declines in basal area can be linked to lower rates of carbon storage (Thom and Keeton 2019), weakened protection from natural hazards (Moos et al. 2021), and reduced habitat for species requiring closed canopies and large diameter trees (Richter et al. 2024).

Furthermore, our results support the notion that the impacts of change in ecological processes are strongly modulated by their ecological setting (Sommerfeld et al. 2018). A 100-fold increase in disturbance rate did, for instance, not have any major ecological effects at Shiretoko because reference levels of disturbance are very low. Similarly, Grand Teton—a system with high reference regeneration rates—was relatively unaffected by a strong reduction (more than 70%) in regeneration rates.

Interactive effects between disturbance and regeneration change were pronounced, but they varied across the parameter space investigated and the response variable considered. Increasing disturbances compensated for low regeneration rates when disturbance rates were generally low (Figure 3). The underlying mechanism is likely related to a disturbance-driven increase in resource availability (mainly light) for tree regeneration (Käber et al. 2023). Conversely, high regeneration rates compensated for the effects of disturbances at intermediate rates. This is likely because high regeneration rates allow a swift recovery from disturbance, and thus buffer disturbance effects on forest structure (Kleinman et al. 2019). A third interaction was mainly observed for species composition, where the joint occurrence of high disturbance and regeneration rates facilitated species change. This possibly results from the increased opportunity for new species to establish when disturbance rates are high (i.e., establishment is not restricted by low light levels at the forest floor) and seed availability is high (Anoszko et al. 2022). Overall, these findings illustrate that the interactions between disturbance and regeneration can change in direction and effect size depending on local context, with important implications for forest structure and composition. As such, the impacts of disturbance change cannot be understood without considering regeneration, and vice versa.

4.3 | Climate Change Modulates the Effects of Changing Disturbance and Regeneration

Climate change is a main driver of changing disturbance and regeneration dynamics in forests (Davis et al. 2019). However, we experimentally studied the effect of climate change separately from the effect of disturbance and regeneration change to investigate how climate modulates the effect of changes in ecological processes. Climatic changes mostly had a dampening effect on structural change across the disturbance and regeneration space investigated, with less of the landscape experiencing structural decline compared to runs under reference climate, especially when regeneration rates were low. This could be explained by the fact that warming alleviates the thermal limitations on sapling growth in our mountain forest landscapes where cold temperatures constrain tree growth (Tourville et al. 2023). In contrast, compositional change was amplified by climate change, especially at low disturbance rates and high regeneration rates. This highlights that climatic change alters establishment and competition among species, inciting a compositional shift to more warm-adapted species (Brice et al. 2019), particularly where seed availability is high and juvenile growth not prohibited (e.g., by pathogens or browsing). At high disturbance rates, however, the modulating effects of climate change were small, and forest change was primarily driven by disturbances. This underscores that in real-world systems, climate-mediated increases in disturbances are likely among the most severe climate change impacts across temperate forests (Seidl et al. 2017).

4.4 | Methodological Considerations

Several important limitations need to be considered when interpreting our findings. Our study focused on the interactive changes of four processes (disturbance frequency and size, seed production and sapling growth). Other important processes influencing disturbance and regeneration rate, such as disturbance severity, relative frequency of different disturbance agents, within-patch variability or germination rate, were not considered even though they have been shown to be important drivers of forest change (Kroiss and HilleRisLambers 2015). Disturbance severity, in particular, is a critical and increasingly variable dimension of disturbance regimes under global change (Parks and Abatzoglou 2020). While severity is generally expected to increase (Kautz et al. 2017), in some cases, dampening effects such as fuel limitations due to increased disturbance sizes and frequency (Parks et al. 2016) could lead to reductions in severity. We here report forest change under an assumed disturbance severity of 90%, but note that the actually realized severity was still patch- and agent-specific. The amount of killed basal area was restrained by both the amount of basal area present within the patch perimeter and the host specificity of the disturbance agent (e.g., bark beetles limited to trees of specific species and dimensions). Our analysis of reduced severities (Figure S2) revealed that while the overall magnitude of forest change was lower, the interactive patterns between disturbance and regeneration persisted. Patch locations were randomised on the landscape, which could have led to greater disturbance impacts compared to real disturbance regimes. For instance, if a disturbance event was simulated in a forest that previously was not exposed to this type of disturbance due to its specific location and site characteristics (e.g., topography, climate), adaptations might be lacking, increasing simulated impacts. Additionally, processes beyond disturbance and regeneration are influenced by global change, such as tree growth responding to changed water supply and demand (Fu et al. 2020). In Shiretoko, we only considered one disturbance agent (wind) while considering two each in Berchtesgaden and Grand Teton. This is owed to the fact that no other significant disturbance agents have been described for Shiretoko; nonetheless, this might have contributed to the only small effect of disturbance change in this landscape.

Moreover, we studied discrete levels of change for each process and only considered unidirectional changes in our simulation experiment. We did not include combinations such as decreasing disturbance rates paired with increasing regeneration—a limitation that may underrepresent compensatory dynamics. We note that the levels of change analysed here for the four focal processes should not be understood as expected or projected changes; rather, they were selected to broadly investigate the parameter space across temperate forests (cf. Figure 3). This in

silico experiment allows testing for emergent dynamics, including potential thresholds and nonlinearities, which are difficult to assess empirically at landscape scales. Naturally, our findings depend on the ability of the model to realistically represent forest processes under change. While iLand has high process resolution compared to many other forest landscape models (Bugmann and Seidl 2022), important processes determining the effects of disturbance (e.g., with regard to nutrient feedbacks, Maynard et al. 2014) and regeneration (e.g., the role of mycorrhizae in tree establishment, Delavaux et al. 2023) on forest dynamics are not explicitly included in the model version used here. Notwithstanding these limitations, the model has 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 sites (Braziunas et al. 2018; Dollinger et al. 2024; Hansen et al. 2020; Thom et al. 2022), lending confidence to our findings.

5 | Conclusions

Compound perturbations are long recognised for their potential to produce ecological surprises (Paine et al. 1998). Here we show that simultaneous changes in key ecological processes—as brought about by global change—have strong compound effects on distinct forest ecosystems on three continents, highlighting the general nature of compound effects. Efforts to tackle the impacts of increasing disturbances (e.g., by establishing fire exclusion zones, Keller et al. 2025) or decreasing regeneration (e.g., via tree plantings, Roitsch et al. 2023) should be applied deliberately and should consider the interactive effects of these changes and responses. Forests of the future will be determined by the interactive outcomes of simultaneous changes in ecological processes. Focusing on changes in single drivers may mislead or underestimate the magnitude of likely changes, as interactive drivers hold the strong potential for nonlinear behaviour (Stevens-Rumann et al. 2018), thus amplifying the potential threat of climate change. We argue for increased efforts in ecology to understand these interactions in order to anticipate future ecosystem trajectories.

Author Contributions

Christina Dollinger: conceptualization; methodology; software; investigation; formal analysis and visualization; writing – original draft; writing – review and editing. **Werner Rammer:** conceptualization; methodology; software; investigation; formal analysis and visualization; writing – review and editing. **Akira S. Mori:** conceptualization; writing – review and editing. **Monica G. Turner:** conceptualization; writing – review and editing. **Rupert Seidl:** funding acquisition; conceptualization; methodology; software; investigation; formal analysis and visualization; writing – review and editing.

Acknowledgements

C.D., W.R. and R.S. were supported by the European Research Council (ERC) under the European Union's Horizon 2020 Research and Innovation Programme (grant agreement no. 101001905). A.S.M. acknowledges support from the Japan Science and Technology Agency (JST, funding no. JPMJRX21I4 and JPMJRS23I4), and Theme 4 of the Advanced Studies of Climate Change Projection (SENTAN Program, grant no. JPMXD0722678534), and supported by the JSPS KAKENHI (funding no. 22KK0102). M.G.T. acknowledges funding from the University of Wisconsin-Madison Vilas Trust and the US National Park Service Reserve Funds (Task Agreement P22AC00588). We are very grateful to two anonymous reviewers for providing helpful and insightful comments on an earlier version of this work. Open Access funding enabled and organized by Projekt DEAL.

Conflicts of Interest

The authors declare no conflicts of interest.

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.1vhhmgr58. The code used to analyze the simulation data and generate the results can be found here: https://github.com/CEDollinger/2nd_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.

References

Anoszko, E., L. E. Frelich, R. L. Rich, and P. B. Reich. 2022. "Wind and Fire: Rapid Shifts in Tree Community Composition Following Multiple Disturbances in the Southern Boreal Forest." *Ecosphere* 13, no. 3: e3952. https://doi.org/10.1002/ecs2.3952.

Baltzer, J. L., N. J. Day, X. J. Walker, et al. 2021. "Increasing Fire and the Decline of Fire Adapted Black Spruce in the Boreal Forest." *Proceedings of the National Academy of Sciences* 118, no. 45: e2024872118. https://doi.org/10.1073/pnas.2024872118.

Barnagaud, J.-Y., L. Barbaro, J. Papaix, M. Deconchat, and E. G. Brockerhoff. 2014. "Habitat Filtering by Landscape and Local Forest Composition in Native and Exotic New Zealand Birds." *Ecology* 95, no. 1: 78–87. https://doi.org/10.1890/13-0791.1.

Braziunas, K. H., W. D. Hansen, R. Seidl, W. Rammer, and M. G. Turner. 2018. "Looking Beyond the Mean: Drivers of Variability in Postfire Stand Development of Conifers in Greater Yellowstone." *Forest Ecology and Management* 430: 460–471. https://doi.org/10.1016/j.foreco.2018.08.034.

Brice, M., K. Cazelles, P. Legendre, and M. Fortin. 2019. "Disturbances Amplify Tree Community Responses to Climate Change in the Temperate–Boreal Ecotone." *Global Ecology and Biogeography* 28, no. 11: 1668–1681. https://doi.org/10.1111/geb.12971.

Bugmann, H., and R. Seidl. 2022. "The Evolution, Complexity and Diversity of Models of Long-Term Forest Dynamics." *Journal of Ecology* 110, no. 10: 2288–2307. https://doi.org/10.1111/1365-2745.13989.

Bugmann, H., R. Seidl, F. Hartig, et al. 2019. "Tree Mortality Submodels Drive Simulated Long-Term Forest Dynamics: Assessing 15 Models From the Stand to Global Scale." *Ecosphere* 10, no. 2: e02616. https://doi.org/10.1002/ecs2.2616.

Burton, P. J., A. Jentsch, and L. R. Walker. 2020. "The Ecology of Disturbance Interactions." *Bioscience* 70, no. 10: 854–870. https://doi.org/10.1093/biosci/biaa088.

Clark, J. S., R. Andrus, M. Aubry-Kientz, et al. 2021. "Continent-Wide Tree Fecundity Driven by Indirect Climate Effects." *Nature Communications* 12, no. 1: 1242.

Davis, K. T., S. Z. Dobrowski, P. E. Higuera, et al. 2019. "Wildfires and Climate Change Push Low-Elevation Forests Across a Critical Climate Threshold for Tree Regeneration." *Proceedings of the National Academy of Sciences* 116, no. 13: 6193–6198. https://doi.org/10.1073/pnas.1815107116.

Davis, K. T., M. D. Robles, K. B. Kemp, et al. 2023. "Reduced Fire Severity Offers Near-Term Buffer to Climate-Driven Declines in

Conifer Resilience Across the Western United States." *Proceedings of the National Academy of Sciences* 120, no. 11: e2208120120. https://doi.org/10.1073/pnas.2208120120.

Delavaux, C. S., J. A. LaManna, J. A. Myers, et al. 2023. "Mycorrhizal Feedbacks Influence Global Forest Structure and Diversity." *Communications Biology* 6, no. 1: 1066. https://doi.org/10.1038/s42003-023-05410-z.

Dey, D. C., B. O. Knapp, M. A. Battaglia, et al. 2019. "Barriers to Natural Regeneration in Temperate Forests Across the USA." *New Forests* 50: 11–40. https://doi.org/10.1007/s11056-018-09694-6.

Díaz-Yáñez, O., Y. Käber, T. Anders, et al. 2024. "Tree Regeneration in Models of Forest Dynamics: A Key Priority for Further Research." *Ecosphere* 15, no. 3: e4807. https://doi.org/10.1002/ecs2.4807.

Dobor, L., M. Baldo, L. Bílek, et al. 2024. "The Interacting Effect of Climate Change and Herbivory Can Trigger Large-Scale Transformations of European Temperate Forests." *Global Change Biology* 30, no. 2: e17194. https://doi.org/10.1111/gcb.17194.

Dollinger, C., W. Rammer, K. F. Suzuki, et al. 2024. "Beyond Resilience: Responses to Changing Climate and Disturbance Regimes in Temperate Forest Landscapes Across the Northern Hemisphere." *Global Change Biology* 30, no. 8: e17468. https://doi.org/10.1111/gcb.17468.

Donato, D. C., B. J. Harvey, and M. G. Turner. 2016. "Regeneration of Montane Forests 24 Years After the 1988 Yellowstone Fires: A Fire-Catalyzed Shift in Lower Treelines?" *Ecosphere* 7, no. 8: e01410. https://doi.org/10.1002/ecs2.1410.

Emmett, K. D., K. M. Renwick, and B. Poulter. 2019. "Disentangling Climate and Disturbance Effects on Regional Vegetation Greening Trends." *Ecosystems* 22: 873–891. https://doi.org/10.1007/s10021-018-0309-2.

Fahnestock, G. R., and J. K. Agee. 1983. "Biomass Consumption and Smoke Production by Prehistoric and Modern Forest Fires in Western Washington." *Journal of Forestry* 81, no. 10: 653–657. https://doi.org/10.1093/jof/81.10.653.

Fu, Z., P. Ciais, A. Bastos, et al. 2020. "Sensitivity of Gross Primary Productivity to Climatic Drivers During the Summer Drought of 2018 in Europe." *Philosophical Transactions of the Royal Society, B: Biological Sciences* 375, no. 1810: 20190747.

Gill, N. S., T. J. Hoecker, and M. G. Turner. 2021. "The Propagule Doesn't Fall Far From the Tree, Especially After Short-Interval, High-Severity Fire." *Ecology* 102, no. 1: e03194. https://doi.org/10.1002/ecy.3194.

Grubb, P. J. 1977. "The Maintenance of Species-Richness in Plant Communities: The Importance of the Regeneration Niche." *Biological Reviews* 52, no. 1: 107–145. https://doi.org/10.1111/j.1469-185X.1977.tb01347.x.

Hagmann, R., P. Hessburg, S. Prichard, et al. 2021. "Evidence for Widespread Changes in the Structure, Composition, and Fire Regimes of Western North American Forests." *Ecological Applications* 31, no. 8: e02431. https://doi.org/10.1002/eap.2431.

Hansen, W. D., D. Abendroth, W. Rammer, R. Seidl, and M. G. Turner. 2020. "Can Wildland Fire Management Alter 21st-Century Subalpine Fire and Forests in Grand Teton National Park, Wyoming, USA?" *Ecological Applications* 30, no. 2: 1–15. https://doi.org/10.1002/eap.2030.

Hansen, W. D., K. H. Braziunas, W. Rammer, R. Seidl, and M. G. Turner. 2018. "It Takes a Few to Tango: Changing Climate and Fire Regimes Can Cause Regeneration Failure of Two Subalpine Conifers." *Ecology* 99, no. 4: 966–977. https://doi.org/10.1002/ecy.2181.

Hansen, W. D., and M. G. Turner. 2019. "Origins of Abrupt Change? Postfire Subalpine Conifer Regeneration Declines Nonlinearly With Warming and Drying." *Ecological Monographs* 89, no. 1: e01340. https://doi.org/10.1002/ecm.1340.

Jackson, S. T., J. L. Betancourt, R. K. Booth, and S. T. Gray. 2009. "Ecology and the Ratchet of Events: Climate Variability, Niche Dimensions, and Species Distributions." *Proceedings of the National Academy of Sciences* 106: 19685–19692. https://doi.org/10.1073/pnas.0901644106.

Käber, Y., C. Bigler, J.-H. Ris Lambers, et al. 2023. "Sheltered or Suppressed? Tree Regeneration in Unmanaged European Forests." *Journal of Ecology* 111, no. 10: 2281–2295. https://doi.org/10.1111/1365-2745.14181.

Kasischke, E. S., and M. R. Turetsky. 2006. "Recent Changes in the Fire Regime Across the North American Boreal Region—Spatial and Temporal Patterns of Burning Across Canada and Alaska." *Geophysical Research Letters* 33, no. 9. https://doi.org/10.1029/2006GL025677.

Kautz, M., A. J. Meddens, R. J. Hall, and A. Arneth. 2017. "Biotic Disturbances in Northern Hemisphere Forests—A Synthesis of Recent Data, Uncertainties and Implications for Forest Monitoring and Modelling." *Global Ecology and Biogeography* 26, no. 5: 533–552.

Keller, T. T., D. C. Abendroth, K. H. Braziunas, et al. 2025. "Can Fire Exclusion Zones Enhance Postfire Tree Regeneration? A Simulation Study in Subalpine Conifer Forests." *Ecological Applications* 35, no. 7: e70121. https://doi.org/10.1002/eap.70121.

Kleinman, J., J. Goode, A. Fries, and J. Hart. 2019. "Ecological Consequences of Compound Disturbances in Forest Ecosystems: A Systematic Review." *Ecosphere* 10, no. 11: e02962. https://doi.org/10.1002/ecs2.2962.

Kroiss, S. J., and J. HilleRisLambers. 2015. "Recruitment Limitation of Long-Lived Conifers: Implications for Climate Change Responses." *Ecology* 96, no. 5: 1286–1297. https://doi.org/10.1890/14-0595.1.

Maynard, D., D. Paré, E. Thiffault, B. Lafleur, K. Hogg, and B. Kishchuk. 2014. "How Do Natural Disturbances and Human Activities Affect Soils and Tree Nutrition and Growth in the Canadian Boreal Forest?" *Environmental Reviews* 22, no. 2: 161–178. https://doi.org/10.1139/er-2013-0057.

Mazon, M. M., K. Klanderud, and D. Sheil. 2023. "Exploring How Disturbance and Light Availability Shape the Elevation Ranges of Multiple Mountain Tree and Shrub Species in the Tropics." *Landscape Ecology* 38: 1–14. https://doi.org/10.1007/s10980-023-01670-6.

McDowell, N. G., C. D. Allen, K. Anderson-Teixeira, et al. 2020. "Pervasive Shifts in Forest Dynamics in a Changing World." *Science* 368, no. 6494: 964–975. https://doi.org/10.1126/science.aaz9463.

Moos, C., A. Guisan, C. F. Randin, and H. Lischke. 2021. "Climate Change Impacts the Protective Effect of Forests: A Case Study in Switzerland." *Frontiers in Forests and Global Change* 4: 682923.

Mori, A., and S. F. Hasegawa. 2007. "Structural Characteristics of Abies Mariesii Saplings in a Snowy Subalpine Parkland in Central Japan." *Tree Physiology* 27, no. 1: 141–148. https://doi.org/10.1093/treephys/27.1.141.

Nigro, K. M., K. Pelz, M. E. Rocca, and M. D. Redmond. 2025. "Trailing Edge Contractions Common in Interior Western US Trees Under Varying Disturbances." *Nature Climate Change* 15, no. 2: 196–200. https://doi.org/10.1038/s41558-024-02235-4.

Nishizawa, K., S. Tatsumi, R. Kitagawa, and A. S. Mori. 2016. "Deer Herbivory Affects the Functional Diversity of Forest Floor Plants via Changes in Competition-Mediated Assembly Rules." *Ecological Research* 31, no. 4: 569–578. https://doi.org/10.1007/s11284-016-1367-6.

Paine, R. T., M. J. Tegner, and E. A. Johnson. 1998. "Compounded Perturbations Yield Ecological Surprises." *Ecosystems* 1: 535–545.

Parks, S. A., and J. T. Abatzoglou. 2020. "Warmer and Drier Fire Seasons Contribute to Increases in Area Burned at High Severity in Western US Forests From 1985 to 2017." *Geophysical Research Letters* 47, no. 22: e2020GL089858. https://doi.org/10.1029/2020GL089858.

Parks, S. A., C. Miller, J. T. Abatzoglou, L. M. Holsinger, M.-A. Parisien, and S. Z. Dobrowski. 2016. "How Will Climate Change Affect Wildland

Fire Severity in the Western US?" *Environmental Research Letters* 11, no. 3: 035002.

Patacca, M., M. Lindner, M. E. Lucas-Borja, et al. 2023. "Significant Increase in Natural Disturbance Impacts on European Forests Since 1950." *Global Change Biology* 29, no. 5: 1359–1376. https://doi.org/10.1111/gcb.16531.

Petter, G., P. Mairota, K. Albrich, et al. 2020. "How Robust Are Future Projections of Forest Landscape Dynamics? Insights From a Systematic Comparison of Four Forest Landscape Models." *Environmental Modelling & Software* 134: 104844. https://doi.org/10.1016/j.envsoft.2020.104844.

Phillips, J. D. 2007. "The Perfect Landscape." *Geomorphic Instability and Change* 84, no. 3: 159–169. https://doi.org/10.1016/j.geomorph.2006.01.039.

Pickett, S. T. A., and P. S. White. 1985. *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press. https://doi.org/10.1016/C2009-0-02952-3.

R Core Team. 2024. *R: A Language and Environment for Statistical Computing [Manual]*. R Foundation for Statistical Computing. https://www.R-project.org/.

Rammer, W., K. H. Braziunas, W. D. Hansen, et al. 2021. "Widespread Regeneration Failure in Forests of Greater Yellowstone Under Scenarios of Future Climate and Fire." *Global Change Biology* 27, no. 18: 4339–4351. https://doi.org/10.1111/gcb.15726.

Rammer, W., D. Thom, M. Baumann, et al. 2024. "The Individual-Based Forest Landscape and Disturbance Model iLand: Overview, Progress, and Outlook." *Ecological Modelling* 492: 110785. https://doi.org/10.1016/j.ecolmodel.2024.110785.

Rasche, L., L. Fahse, and H. Bugmann. 2013. "Key Factors Affecting the Future Provision of Tree-Based Forest Ecosystem Goods and Services." *Climatic Change* 118, no. 3: 579–593. https://doi.org/10.1007/s10584-012-0664-5.

Ratajczak, Z., S. R. Carpenter, A. R. Ives, et al. 2018. "Abrupt Change in Ecological Systems: Inference and Diagnosis." *Trends in Ecology & Evolution* 33, no. 7: 513–526. https://doi.org/10.1016/j.tree.2018.04.013.

Richter, T., L. Geres, S. König, et al. 2024. "Effects of Climate and Forest Development on Habitat Specialization and Biodiversity in Central European Mountain Forests." *Communications Biology* 7, no. 1: 1518. https://doi.org/10.1038/s42003-024-07239-6.

Roitsch, D., S. Abruscato, M. Lovrić, M. Lindner, C. Orazio, and G. Winkel. 2023. "Close-to-Nature Forestry and Intensive Forestry—Two Response Patterns of Forestry Professionals Towards Climate Change Adaptation." *Forest Policy and Economics* 154: 103035.

Seidl, R., and W. Rammer. 2017. "Climate Change Amplifies the Interactions Between Wind and Bark Beetle Disturbances in Forest Landscapes." *Landscape Ecology* 32, no. 7: 1485–1498. https://doi.org/10.1007/s10980-016-0396-4.

Seidl, R., W. Rammer, and K. Blennow. 2014. "Simulating Wind Disturbance Impacts on Forest Landscapes: Tree-Level Heterogeneity Matters." *Environmental Modelling & Software* 51: 1–11. https://doi.org/10.1016/j.envsoft.2013.09.018.

Seidl, R., W. Rammer, R. M. Scheller, and T. A. Spies. 2012. "An Individual-Based Process Model to Simulate Landscape-Scale Forest Ecosystem Dynamics." *Ecological Modelling* 231: 87–100. https://doi.org/10.1016/j.ecolmodel.2012.02.015.

Seidl, R., W. Rammer, and T. A. Spies. 2014. "Disturbance Legacies Increase the Resilience of Forest Ecosystem Structure, Composition, and Functioning." *Ecological Applications* 24, no. 8: 2063–2077. https://doi.org/10.1890/14-0255.1.

Seidl, R., D. Thom, M. Kautz, et al. 2017. "Forest Disturbances Under Climate Change." *Nature Climate Change* 7, no. 6: 395–402. https://doi.org/10.1038/nclimate3303.

Senf, C., and R. Seidl. 2021. "Mapping the Forest Disturbance Regimes of Europe." *Nature Sustainability* 4, no. 1: 63–70. https://doi.org/10.1038/s41893-020-00609-y.

Siegel, K. J., K. C. Cavanaugh, and L. E. Dee. 2023. "Balancing Multiple Management Objectives as Climate Change Transforms Ecosystems." *Trends in Ecology & Evolution* 39: 381–395. https://doi.org/10.1016/j.tree.2023.11.003.

Sommerfeld, A., C. Senf, B. Buma, et al. 2018. "Patterns and Drivers of Recent Disturbances Across the Temperate Forest Biome." *Nature Communications* 9, no. 1: 1–9. https://doi.org/10.1038/s41467-018-06788-9.

Stevens-Rumann, C. S., K. B. Kemp, P. E. Higuera, et al. 2018. "Evidence for Declining Forest Resilience to Wildfires Under Climate Change." *Ecology Letters* 21, no. 2: 243–252. https://doi.org/10.1111/ele.12889.

Thom, D., and W. S. Keeton. 2019. "Stand Structure Drives Disparities in Carbon Storage in Northern Hardwood-Conifer Forests." *Forest Ecology and Management* 442: 10–20. https://doi.org/10.1016/j.foreco.2019.03.053.

Thom, D., W. Rammer, P. Laux, et al. 2022. "Will Forest Dynamics Continue to Accelerate Throughout the 21st Century in the Northern Alps?" *Global Change Biology* 28, no. 10: 3260–3274. https://doi.org/10.1111/gcb.16133.

Tourville, J., D. Publicover, and M. Dovciak. 2023. "Forests on the Move: Tracking Climate-Related Treeline Changes in Mountains of the Northeastern United States." *Journal of Biogeography* 50: 1993–2007. https://doi.org/10.1111/jbi.14708.

Turner, M. G., W. H. Romme, R. H. Gardner, R. V. O'Neill, and T. K. Kratz. 1993. "A Revised Concept of Landscape Equilibrium: Disturbance and Stability on Scaled Landscapes." *Landscape Ecology* 8, no. 3: 213–227. https://doi.org/10.1007/BF00125352.

Turner, M. G., and R. Seidl. 2023. "Novel disturbance regimes and ecological responses." *Annual Review of Ecology, Evolution, and Systematics* 54: 63–83. https://doi.org/10.1146/annurev-ecolsys-110421-101120.

Wang, W., X. Wang, M. D. Flannigan, et al. 2025. "Canadian Forests Are More Conducive to High-Severity Fires in Recent Decades." *Science* 387, no. 6729: 91–97. https://doi.org/10.1126/science.ado1006.

Washaya, P., R. Modlinger, D. Tyšer, and T. Hlásny. 2024. "Patterns and Impacts of an Unprecedented Outbreak of Bark Beetles in Central Europe: A Glimpse Into the Future?" *Forest Ecosystems* 11: 100243. https://doi.org/10.1016/j.fecs.2024.100243.

Winter, M.-B., R. Baier, and C. Ammer. 2015. "Regeneration Dynamics and Resilience of Unmanaged Mountain Forests in the Northern Limestone Alps Following Bark Beetle-Induced Spruce Dieback." *European Journal of Forest Research* 134, no. 6: 949–968. https://doi.org/10.1007/s10342-015-0901-3.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** GCM-RCM-RCP combinations. **Figure S1:** Results of a sensitivity analysis for the threshold used for defining structural decline. **Figure S2:** Results of runs with four levels of disturbance severity. **Figure S3:** Results of runs under four different climate change scenarios. **Figure S4:** The impact of individual process change on forest loss. **Figure S5:** Impact of disturbance and regeneration rate on forest loss under reference climate. **Figure S6:** Climate effect on forest loss. **Figure S7:** Mean change in structure, composition and forest loss by altitudinal zone. **Figure S8:** Results of LOESS models calculated per landscape. **Figure S9:** Absolute forest change under runs with climate change. **Figure S10:** Colorblind version of Figure 3 in the main text. **Figure S11:** Colorblind version of Figure 4 in the main text.